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[Article]

Comparative Thermal Requirements of Westslope Cutthroat Trout and Rainbow Trout: Implications for Species Interactions and Development of Thermal Protection Standards

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Abstract.—Water temperature appears to play a key role in determining population persistence of westslope cutthroat trout *Oncorhynchus clarkii lewisi*, but specific thermal performance and survival criteria have not been defined. We used the acclimated chronic exposure laboratory method to determine upper thermal tolerances and growth optima of westslope cutthroat trout and rainbow trout *O. mykiss*, a potential nonnative competitor that occupies much of the former range of westslope cutthroat trout. Rainbow trout had a distinct survival advantage over westslope cutthroat trout at water temperatures above 20°C. The ultimate upper incipient lethal temperature of rainbow trout (24.3°C; 95% confidence interval [CI] = 24.0–24.7°C) was 4.7°C higher than that of westslope cutthroat trout (19.6°C; 95% CI = 19.1–19.9°C). In contrast, both species had similar growth rates and optimum growth temperatures (westslope cutthroat trout: 13.6°C; rainbow trout: 13.1°C) over the temperature range of 8–20°C, although rainbow trout grew over a wider range and at higher temperatures than did westslope cutthroat trout. The rainbow trout's higher upper temperature tolerance and greater growth capacity at warmer temperatures may account for the species' displacement of westslope cutthroat trout at lower elevations. Our results indicate that maximum daily temperatures near the optimum growth temperature of 13–15°C would ensure suitable thermal habitat for westslope cutthroat trout populations. The low upper temperature tolerance and optimum growth temperature of westslope cutthroat trout relative to those of other salmonids suggest that this subspecies may be particularly susceptible to stream temperature increases associated with global warming and anthropogenic habitat disturbance.

Westslope cutthroat trout *Oncorhynchus clarkii lewisi* historically occupied a wide range of habitats, from small, headwater streams to large rivers and mountain lakes within drainages in western Montana, Idaho, northwestern Wyoming, eastern Oregon and Washington, and southern Alberta (Liknes and Graham 1988; Behnke 1992; Thurow et al. 1997; Shepard et al. 2005). However, as with many other native salmonids in western North America (Behnke 1992), this subspecies now exhibits a fragmented distribution over large portions of its range (Thurow et al. 1997; Shepard et al. 2005). The subspecies was recently evaluated for listing as a federally threatened species under the Endangered Species Act (USFWS 2003). Although listing was deemed not warranted, leading threats to the persistence of westslope cutthroat trout populations remain, including habitat degradation, hybridization with nonnative rainbow trout *O. mykiss*, and displacement or replacement by nonnative species (Shepard et al. 1997, 2005; Shepard 2004; Rubidge and Taylor 2005). The current distribution of westslope cutthroat trout is restricted primarily to cold, high-elevation, high-gradient streams, whereas mid-to-lower elevation portions of drainages are occupied by nonnative rainbow trout, rainbow trout × westslope cutthroat trout hybrids, brook trout *Salvelinus fontinalis*, and brown trout *Salmo trutta* (Thurow et al. 1997; Paul and Post 2001; Sloat et al. 2001, 2005; Shepard 2004).

The current restricted distribution of native cutthroat trout to headwater reaches in many drainages indicates that water temperature is probably a key factor influencing their persistence (Paul and Post 2001; Sloat et al. 2001; de la Hoz Franco and Budy 2005). High temperature in lower elevations can cause direct mortality of salmonids that are more adapted to cold water, whereas sublethal temperature increases can alter metabolism, growth, and competitive interactions that may favor more warmwater-adapted salmonids (Taniguchi et al. 1998; Taniguchi and Nakano 2000).

Field studies attest to the likelihood that temperature has a major influence on the growth potential and distribution of westslope cutthroat trout (Paul and Post

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2001; Sloat et al. 2001, 2005) and on shifts in dominance from westslope cutthroat trout to nonnative salmonids as a result of warmer temperature from habitat alteration (Sloat et al. 2001, 2005; Shepard 2004). However, specific thermal performance and survival criteria for westslope cutthroat trout have not been defined. Development of species-specific thermal criteria is vital for protecting and restoring populations of native salmonids, particularly in light of climate change, because even small shifts in temperature can have significant effects on species distribution and relative abundance (Fausch et al. 1994; Welch et al. 1998). Thermal protection standards are typically based on a combination of performance (optimum growth temperature) and survival (upper thermal tolerance) criteria derived from laboratory experiments (McCullough et al. 2001) in combination with field distributional data (e.g., Eaton et al. 1995; Schrank et al. 2003). Variation in thermal performance and survival among salmonid species and subspecies (McCullough 1999; Meeuwig et al. 2004; Myrick and Cech 2004) attests to the importance of developing species-specific thermal criteria.

In this study, we compared the performance (growth) and upper lethal temperature of westslope cutthroat trout with those of a main nonnative competitor, rainbow trout. We used comparative thermal optima and survival data to (1) test the hypothesis that westslope cutthroat trout have significantly lower growth optima and upper lethal temperatures than rainbow trout, and (2) develop thermal criteria for conservation and restoration of westslope cutthroat trout.

Methods

Test protocol.—A thermal test facility housed at the U.S. Fish and Wildlife Service Bozeman Fish Technology Center (BFTC) was used to assess fish growth and survival at different temperatures for prolonged periods. Westslope cutthroat trout used in experiments were either eggs or age-0 fish from a wild stock at Rogers Lake, Montana, or age-0 fish from wild stock maintained at the Westslope Trout Company, a private fish hatchery near Ronan, Montana. Both sources are derived from a mixture of pure populations of westslope cutthroat trout from Montana. Rainbow trout used in experiments were obtained as eggs from the Ennis National Fish Hatchery near Ennis, Montana. Rainbow trout were Fish Lake strain, a pure strain derived from a mixture of wild fish parentage (Wagner 1996) without any known cutthroat trout introgression (E. Wagner, Utah Division of Wildlife Resources, personal communication). Eggs and juveniles were reared at the BFTC at approximately 12°C, and juveniles were fed pelleted food to excess daily with an automated belt feeder.

A flow-through thermal testing system provided constant water flow, high concentrations of dissolved oxygen, and metabolite flushing. Water supplied from cold (8°C) and warm (22°C) springs was mixed with water heated by three 40,000-BTU water heaters to achieve treatment temperatures from 8°C to 30°C. Water from the spring sources was aerated with pure oxygen and a diffusing stone, passed through degassing columns, and mixed in 12 separate head tanks. From the head tanks, water was supplied to thirty-six 75-L aluminum test tanks (120 × 35 × 25 cm) at a flow rate of 3 L/min. All connecting pipes and tank surfaces were insulated to reduce heat loss.

We used the acclimated chronic exposure (ACE) thermal test method (Selong et al. 2001) for measurement of long-term (60-d) growth and survival at different temperatures. At the start of an experiment, 50 fish were randomly selected, placed in each of 36 treatment tanks, and acclimated to 14°C for at least 14 d during an initial acclimation period. Fish were distributed so that mean sizes in each tank were similar. After the initial acclimation period, water temperature in each tank was raised or lowered by 1°C per day until the desired test temperature was reached. Temperature adjustments were staggered such that all tanks reached final test temperatures on the same day. After final test temperatures were reached (1–16 d depending on test temperature), fish were held at a constant temperature for the 60-d test period. Fish in each tank were counted and weighed in bulk on days 1, 30, and 60. To minimize handling stress, we did not measure lengths of individual fish in the study.

Fish were fed daily using an automated belt feeder that supplied a constant feed ration over a 12-h period from about 0800 to 2000 hours. Fish were fed amounts in excess of satiation, as indicated by the presence of excess feed in tanks after 24 h. Feed type differed among experiments because of unexpected changes in availability, but the three feeds used (Fin Starter, Silver Cup, and Cutthroat Trout Grower) had similar composition and total energy content (Bear 2005). Tanks were fitted with an overhead cover simulating an undercut bank so as to minimize disturbance to fish and elicit natural behavioral responses.

Tanks were cleaned daily and mortalities removed, weighed (g), and measured (total length [TL] in mm). Temperature, dissolved oxygen, and gas saturation were measured daily in each head tank by use of a YSI 55-M meter (Yellow Springs, Ohio), and the amounts of pure oxygen diffused into the system were adjusted to ensure adequate dissolved oxygen in each tank. Dissolved oxygen concentration varied from 6.1 to

12.2 mg/L during the study (mean = 8.3 mg/L). Total gas saturation varied from 75.3% to 103.0% among all experiments (mean = 84.7%). Dissolved oxygen saturation varied from 84.0% to 122.7% (mean = 100.6%). Oxygen saturation was calculated daily based on dissolved oxygen concentration and temperature (APHA et al. 1992). Oxygen concentration and saturation levels were within optimal levels (>5 mg/L and >80%, respectively; Piper et al. 1982).

Temperature in test tanks was recorded hourly with Onset Optic StowAway Temp loggers (Pocasset, Massachusetts). Daily temperature fluctuations in test tanks averaged 0.3–1.1°C (range = 0–3.7°C); daily fluctuations were typically less than 1°C except for a 1-week period during one experiment, when springwater input was diminished. Natural light was supplemented with overhead halogen lighting adjusted to match the natural photoperiod. Photoperiod over the duration of the experiments averaged 13 h light and 11 h dark.

Survival and growth experiments.—Effects of temperature on survival of westslope cutthroat trout was determined in three experiments at temperatures of 8, 10, 12, 13, 14, 15, 16, 18, 20, 21, 22, 23, 24, 26, 28, and 30°C; a minimum of three replicates was conducted at each test temperature. Growth of westslope cutthroat trout under satiation conditions was assessed at 8, 12, 14, 16, 20, and 24°C. Mean size of westslope cutthroat trout used in experiments varied from 9.4 (102 mm TL) to 19.3 g (126 mm TL).

Two experiments were conducted to determine survival of rainbow trout at temperatures of 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, and 28°C; three replicates were used per test temperature. Growth of rainbow trout under satiation conditions was assessed at 8, 12, 14, 16, 20, and 24°C. One replicate at 12°C was omitted because of high mortality resulting from a water flow malfunction. Mean size of rainbow trout varied from 13.9 (110 mm TL) to 38.3 g (152 mm TL).

Statistical analyses.—Given that both absolute temperature level and exposure time affect thermal tolerance limits (Brett 1952), we used several metrics to compare survival of westslope cutthroat trout and rainbow trout. The ultimate upper incipient lethal temperature (UUILT) for each species was calculated as the LT50 (i.e., the temperature that was lethal to 50% of test fish) at the end of the 60-d experiment. Effects of exposure time on survival were analyzed by plotting mean daily survival rate against temperature to determine temporal patterns in survival and by comparing plots of LT50 for each species over time: days 1, 2, 7, 15, 22, 30, 37, 45, and 52 (Dickerson and Vinyard 1999; Johnstone and Rahel 2003). Survival curves were generated using the nonlinear curve-fitting program in SigmaPlot (2002); the highest r^2 values were used to select the best-fitting models. Differences in survival were also analyzed with two-way analysis of covariance (ANCOVA) that used temperature and species as main effects and average initial body weight as a covariate. Survival data were arcsine transformed, and means were compared with a Tukey's pairwise comparison test at a significance level α of 0.05 or less in the Number Cruncher Statistical System (NCSS 2006).

Relative growth rate (G, expressed as %) was calculated by the formula

$$G = [(Y_2 - Y_1)/(Y_1 \times t)] \times 100,$$

where Y_1 = initial mean weight (g) of individual fish in each tank, Y_2 = final mean weight, and t = time period of the experiment (Ricker 1979). We used relative growth rate to allow comparison of growth among fish of different initial sizes. Regression curves were generated for each species to determine peak growth temperature. Differences in growth by species and temperature were compared by using two-way analysis of variance (ANOVA).

Results

Survival

Survival of juvenile westslope cutthroat trout and rainbow trout, adjusted for differences in initial weight, varied significantly between species (ANCOVA: F = 65.9, df = 1, $P < 0.001$) and among temperatures (ANCOVA: F = 26.1, df = 8, $P < 0.001$); the interaction of species and temperature was also significant (ANCOVA: F = 11.0, $P < 0.001$). Over the test temperature range of 8–18°C, both species had high survival rates of 82–100% (Figure 1) and mean survival rate did not differ. However, at temperatures of 20°C or higher, westslope cutthroat trout had significantly lower survival than did rainbow trout (Tukey's test: $P < 0.05$). Mean survival of westslope cutthroat trout declined significantly ($P < 0.05$) to 35.7% at 20°C, 12.5% at 22°C, and 0% at 24°C (Figure 1). In contrast, rainbow trout survival was similar (98.6–100%) among temperatures of 8–22°C but declined significantly ($P < 0.05$) at higher temperatures: survival was 72.8% at 24°C, 2% at 26°C, and 0% at 28°C. The predicted UUILT for westslope cutthroat trout (19.6°C; 95% confidence interval [CI] = 19.1–19.9°C) was 4.7°C lower than that for rainbow trout (24.3°C; 95% CI = 24.0–24.7°C).

The LT50 of westslope cutthroat trout was significantly lower than that of rainbow trout at all time periods (nonoverlapping 95% CIs), but the difference became more pronounced with longer exposure time (Figure 2). At 20°C, westslope cutthroat trout survival was high (>90%) for 30 d and declined sharply

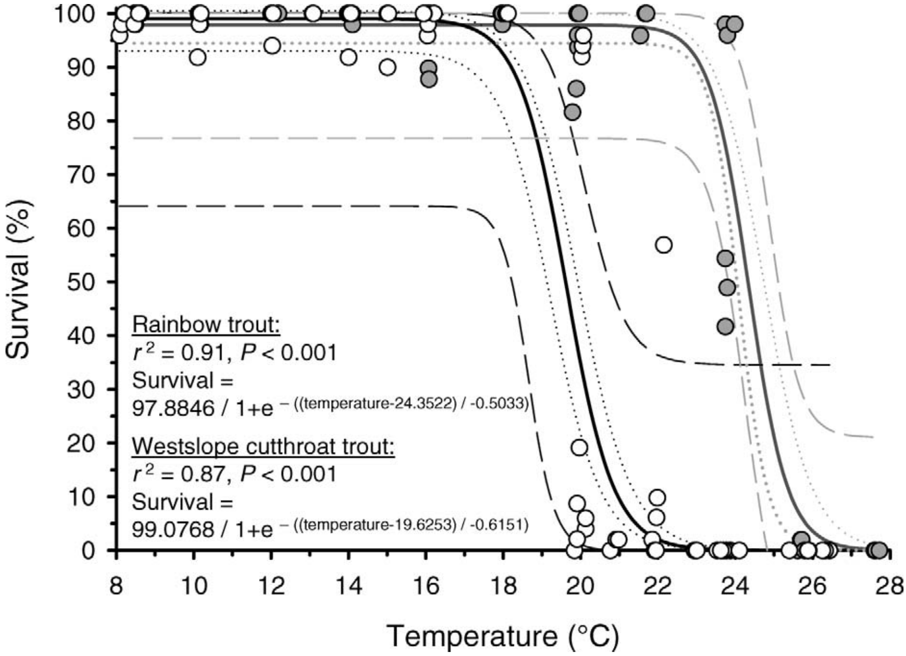

FIGURE 1.—Percent survival of juvenile westslope cutthroat trout (white circles, black line) and rainbow trout (gray circles, gray line) in relation to test temperature during a 60-d experiment. Dotted lines indicate the 95% CI of the regression line; dashed lines indicate the 95% CI of the data. Upper CIs were constrained to 100% survival.

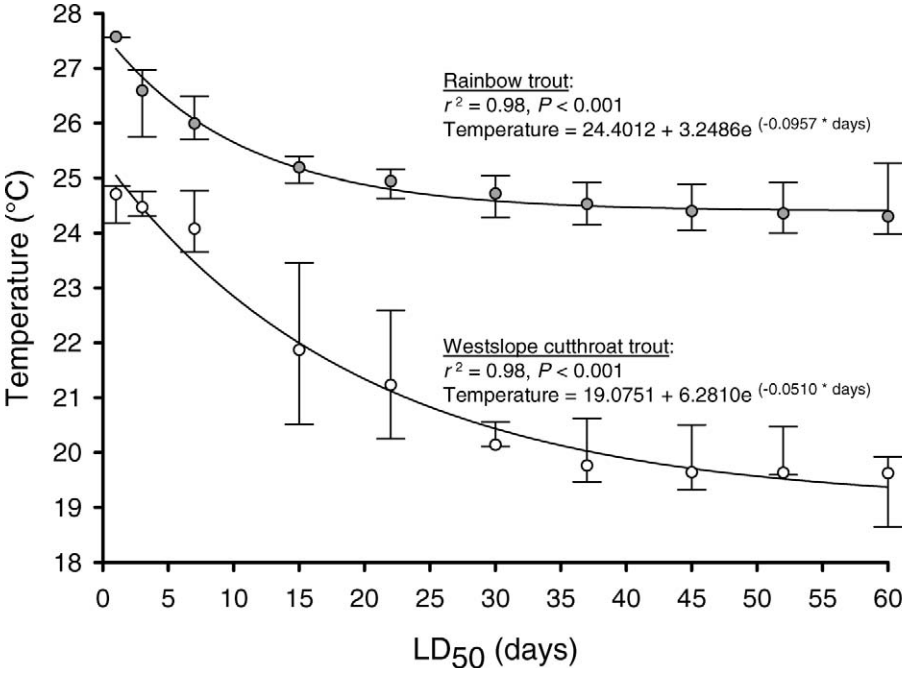

FIGURE 2.—Survival (±95% CI) in relation to temperature for juvenile westslope cutthroat trout (white circles) and rainbow trout (gray circles). Each circle represents the temperature that was lethal to 50% of test fish (LT50) for the given exposure period (d).

thereafter; at 22°C and 24°C, survival declined sharply after 7 d of exposure (Figure 3). At 26°C, mortality was high during ramping and no fish survived past day 3 of the experiment. At 20–24°C, rainbow trout showed much less pronounced declines in survival over 60 d than did westslope cutthroat trout; at 26°C, rainbow trout survival remained high for 7 d before experiencing a sharp decline.

Initial weight had a significant negative effect on survival (ANCOVA: $F = 13.7$, $\mathrm{df} = 1$, $P < 0.001$); the smaller westslope cutthroat trout and rainbow trout exhibited higher survival rates than did larger fish at temperatures near upper tolerance limits. Mean survival in test tanks was 51.9% at 20°C and 24.3% at 22°C for small westslope cutthroat trout (mean initial weight = 8.8–9.5 g). Survival was 3.3% at 20°C and 0.7% at 22°C for larger westslope cutthroat trout (mean initial weight = 19.2–19.5 g). Similarly, mean survival of small rainbow trout (mean initial weight = 12.9–15.8 g) was 98.7% at 20°C and 97.3% at 24°C, and that of larger rainbow trout (mean initial weight = 34.7–37.8 g) was 87.1% at 20°C and 48.3% at 24°C. In contrast, near-zero slopes of survival–weight plots at temperatures of 8–18°C indicated that initial size had no apparent effect on survival at temperatures less than 20°C.

Growth

Westslope cutthroat trout and rainbow trout had similar peak growth temperatures (westslope cutthroat trout: 13.6°C; rainbow trout: 13.1°C) and exhibited no significant differences in growth (ANOVA: $F = 1.46$, $\mathrm{df} = 1$, $P = 0.24$). Temperature had a significant effect on growth (ANOVA: $F = 27.77$, $\mathrm{df} = 4$, $P < 0.001$), but growth did not differ within or between species at test temperatures of 8, 12, and 16°C (Tukey's test: $P > 0.05$). Growth declined significantly ($P < 0.05$) in both species at 20°C, but the difference between species was not significant. Rainbow trout grew at temperatures as high as 24°C (0.11% per day), whereas no westslope cutthroat trout survived long enough at 24°C to assess 60-d growth (Figure 4). For both species, fish became lethargic and ceased feeding as temperatures approached the species' upper lethal limit (20°C for westslope cutthroat trout; 24°C for rainbow trout).

Discussion

Study results supported our initial hypothesis that westslope cutthroat trout have a significantly lower UUILT than rainbow trout. The nearly 5°C higher 60-d UUILT and the substantially greater resistance to prolonged exposure to 20°C or higher temperatures indicate that rainbow trout would gain a significant survival advantage over westslope cutthroat trout at warmer temperatures. In contrast, we found that both species had equally high long-term survival at 8–18°C. As in previous investigations (Benfey et al. 1997; Selong et al. 2001), we found that smaller juveniles of both species exhibited greater thermal tolerance than did larger juveniles.

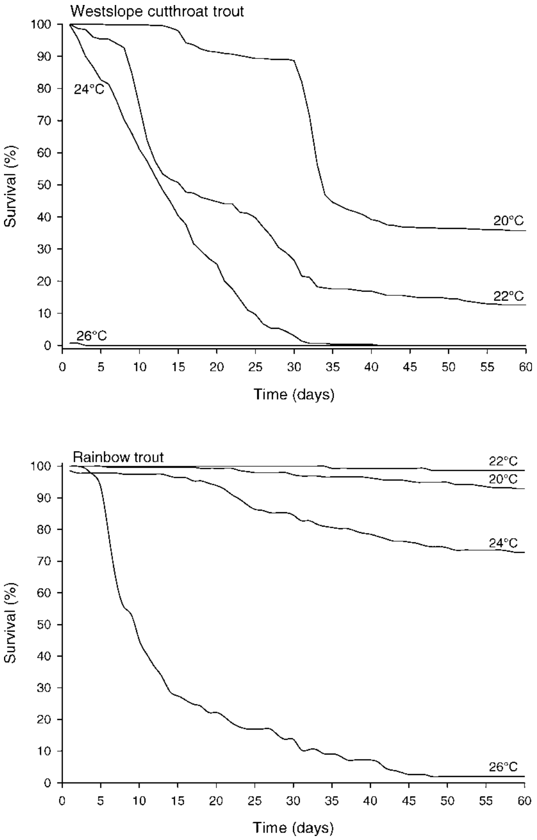

FIGURE 3.—Percent daily mean survival of juvenile westslope cutthroat trout (top) and rainbow trout (bottom) during a 60-d exposure to 20, 22, 24, or 26°C.

The UUILT determinations in fishes have traditionally been based on 7-d test periods (e.g., Brett 1952; Dickerson and Vinyard 1999; Johnstone and Rahel 2003). Based on comparisons of upper lethal limits derived from tests over this time interval, the 7-d UUILT for westslope cutthroat trout in our study (24.1°C) is at the lower bound of the range of upper thermal limits reported for salmonids (McCullough 1999). Other species with 7-d UUILTs near the lower boundary of 24°C include Lahontan cutthroat trout *O. clarkii henshawi* (24–25°C: Dickerson and Vinyard 1999), Bonneville cutthroat trout *O. clarkii utah* (24.2°C: Johnstone and Rahel 2003), and bull trout *Salvelinus confluentus* (23.5°C: Selong et al. 2001).

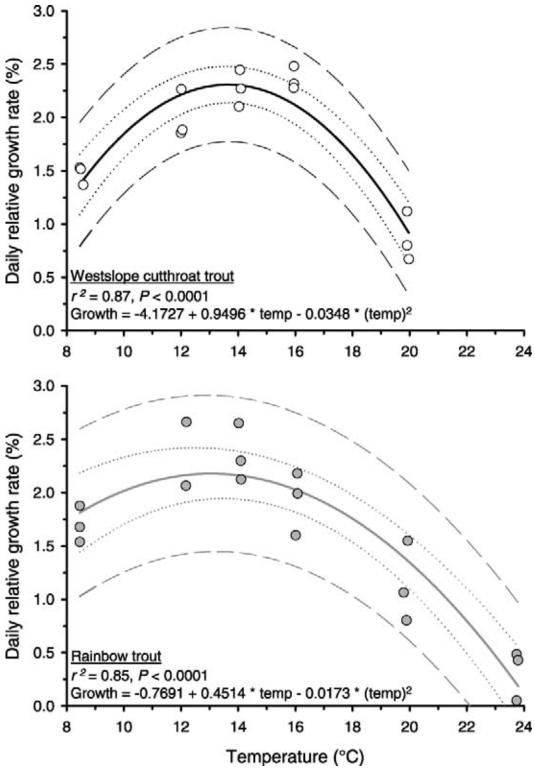

FIGURE 4.—Percent daily relative growth rate of juvenile westslope cutthroat trout (top) and rainbow trout (bottom) in relation to temperature during a 60-d experiment. Dotted lines indicate the 95% CI of the regression line; dashed lines indicate the 95% CI of the data.

Rainbow trout have one of the highest upper temperature tolerances among salmonids (McCullough 1999), and the 7-d UUILT derived from our study (26.0°C) was similar to upper tolerance levels determined in previous investigations (25.6°C: Hokanson et al. 1977; 26.2°C: Kaya 1978). Such differences in upper thermal limits among salmonids are correlated with marked differences in competitive ability (De Staso and Rahel 1994; McMahon et al., in press) and distribution at the stream and landscape scales (Fausch et al. 1994; Sloat et al. 2001).

Short-term tolerance testing may fail to detect delayed effects from chronic exposure to high temperature, based on results from our long-term tolerance testing over 60 d. Sharp declines in survival often occurred well beyond the 7-d time interval. Consequently, the 60-d UUILT was 1.7°C lower for rainbow trout and 4.5°C lower for westslope cutthroat trout than their respective 7-dUUILTs. Because seasonal high temperatures typically last longer than 7 d in nature, temperature testing over longer time intervals is needed to identify the full range of responses to elevated temperature. An advantage of the ACE experimental design used in this study is that temperature tolerance can be assessed over both short (acute) and long (chronic) intervals, facilitating assessment of lethal responses at various exposure and temperature combinations useful for evaluating cumulative effects (Selong et al. 2001). A limitation of our study was a lack of information on fluctuating temperatures. When allowed to recover at lower temperatures during a diel period, fish can survive brief daily exposure to otherwise lethal temperatures identified from constant temperature experiments (Dickerson and Vinyard 1999; Johnstone and Rahel 2003; Schrank et al. 2003; Widmer et al. 2006). Thus, a desired laboratory protocol for assessing temperature tolerance for fish would use tests of acute and chronic exposure at both constant and fluctuating temperatures. Such detailed evaluations are available for few species, yet are vital for fully assessing species' responses to prospective temperature changes from global warming and anthropogenic disturbance.

Counter to our hypothesis and in contrast to their different upper tolerance limits, westslope cutthroat trout and rainbow trout had nearly identical optimum growth temperatures (westslope cutthroat trout: 13.6°C; rainbow trout: 13.1°C) and growth curves over the range of 8–20°C. The optimum growth temperature of both species corresponded to a "coldwater group" of salmonids—those having low optimum growth temperatures—that includes Lahontan cutthroat trout (12–13°C: Meeuwig et al. 2004), bull trout (13.2°C: Selong et al. 2001), and brook trout (14.0°C: McMahon et al., in press). The low optimum growth temperature for rainbow trout in our study was unexpected, occurring at a much lower temperature than the 17.2°C reported by Hokanson et al. (1977). One possible explanation for this difference is the considerably smaller fish (30 mm TL) used by Hokanson et al. (1977), as larger fish tend to have lower optimum growth temperatures than smaller fish (Kwain and McCauley 1978; Meeuwig et al. 2004). Alternatively, growth differences could be attributable to physiological differences among rainbow trout strains, although evidence of distinctive strain or stock differences in thermal tolerance and performance in fishes remains inconclusive (Myrick and Cech 2000, 2004; Imsland et al. 2001; Larsson et al. 2005). Clearly, such a large observed difference in rainbow trout performance between studies indicates the need for further testing.

The fundamental thermal niche, defined by Christie and Regier (1988) as the range from 3°C lower to 1°C higher than the optimum growth temperature, is nearly identical for both species (westslope cutthroat trout:

10.6–14.6°C; rainbow trout: 10.1–14.1°C), as is their thermal preferendum (our unpublished data), thus indicating a high potential for competition. However, in nature the two species segregate along a distinctive elevation–temperature gradient and exhibit little spatial overlap (Paul and Post 2001; Sloat et al. 2001) indicative of temperature-mediated shifts in competitive ability (Taniguchi and Nakano 2000). Our results provide evidence that rainbow trout would gain a distinct survival and growth advantage over westslope cutthroat trout if temperatures exceeded 22°C for even short periods, which possibly explains their replacement of westslope cutthroat trout in lower-elevation stream reaches. In contrast, we found no growth or survival advantage for westslope cutthroat trout over rainbow trout at cooler temperatures. We conducted our study using satiation rations, and differences in growth and survival would probably become more pronounced with the reduced food availability and growth potential (e.g., Brett et al. 1969; Van Ham et al. 2003; Li et al. 2004) characteristic of high-elevation streams during summer (Sloat et al. 2005). In turn, westslope cutthroat trout may have greater tolerance than rainbow trout to the recruitment failures that are common to higher-elevation sites because of their cold summer temperatures and short growing season (Harig and Fausch 2002). Experiments comparing species performance in sympatry (Taniguchi and Nakano 2000), to complement the allopatric comparison performed in our study, are needed to fully assess the degree of temperature-mediated competition between the two species.

Temperature tolerances obtained from laboratory studies are useful for developing thermal habitat protection standards (Armour 1990; McCullough 1999). The upper temperature tolerance limits generally correlate with the maximum temperatures associated with the lower distribution boundaries of salmonids within drainages (Dunham et al. 2003). In turn, the optimum growth temperature can be used as an indicator of the upper range of suitable thermal habitat for the long-term persistence of salmonids (McCullough 1999; Selong et al. 2001; Dunham et al. 2003). For westslope cutthroat trout, our laboratory results corroborate field investigations (Sloat et al. 2001, 2005; Shepard 2004), which indicate that maximum temperatures near an upper limit of 13–15°C would delineate suitable thermal habitat for long-term persistence of westslope cutthroat trout. Such thermal criteria, in combination with other habitat criteria (e.g., Shepard 2004), could be used to predict habitat suitability for identifying and prioritizing reintroduction sites (Scheller et al. 1999; Harig and Fausch 2002). The low upper temperature tolerance and optimum growth temperature of westslope cutthroat trout relative to other salmonids suggest that this subspecies may be particularly susceptible to stream temperature increases associated with global warming and anthropogenic habitat disturbance.

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