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Effects of constant and cyclical thermal regimes on growth and feeding of juvenile cutthroat trout of variable sizes

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Abstract – The effects of constant (12, 18, and 24 °C) and cyclical (daily variation of 15–21 and 12–24 °C) thermal regimes on the growth and feeding of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) of variable sizes were examined. Higher constant temperatures (i.e., 24 °C) and more variable daily temperatures (i.e., 12–24 °C daily cycle) negatively affected growth rates. As fish mass increased (from 0.24 to 15.52 g) the effects of different thermal regimes on mass growth became more pronounced. Following 14 days exposure to the thermal regimes, feeding rates of individual fish were assessed during acute exposure (40 min) to test temperatures of 12, 18, and 24 °C. Feeding rate was depressed during acute exposure to 24 °C, but was not significantly affected by the preceding thermal regime. Our results indicate that even brief daily exposure to higher temperatures (e.g., 24 °C) can have considerable sublethal effects on cutthroat trout, and that fish size should be considered when examining the effects of temperature.

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Key words: cutthroat trout; temperature; growth; feeding; thermal regime; water quality

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Un resumen en español se incluye detrás del texto principal de este articulo.

Introduction

Temperature is an important factor controlling the quality and quantity of habitat for fishes (Magnuson et al. 1979). In the United States, national water quality criteria for temperature to support fishes are based on lethal temperatures (U.S. Environmental Protection Agency 1998; Poole et al. 2004). Lethal temperatures delineate the boundaries of a species' thermal tolerance zone, but sublethal temperature stress may be important as well (Elliott 1981). Furthermore, thermal stress may result from chronic or acute exposure, depending on the nature of the thermal regime. Tests of thermal response are typically conducted on fish acclimated to constant temperature regimes. Because natural thermal regimes can vary substantially, both seasonally and diurnally (Sinokrot & Stefan 1993), thermal responses measured for fish exposed to constant temperatures may not be good indicators of responses that occur under more realistic (i.e., varying) thermal conditions (Hokanson et al. 1977; Lobón-Cerviá & Rincón 1998; Johnstone & Rahel 2003; Schrank et al. 2003). Therefore, examination of fish response to daily temperature cycles may provide more realistic guidance for water temperature criteria to protect fishes.

Another factor not commonly considered in evaluating the effects of temperature on fishes is the effect of body size. The effects of temperature on physiology, behaviour, and survival may differ for fish of variable size and for different life stages (Magnuson et al. 1979; Johnston et al. 1996). For fishes in general, however, the effects of body size on thermal responses are poorly understood (Elliott 1981). Accordingly, information on the effects of temperature over a range of fish sizes is needed to comprehensively understand the thermal requirements of a species.

In this study, we examined responses of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) exposed to thermal regimes that mimicked natural thermal variation. Increases in water temperatures and daily thermal variation during summer months are believed to have contributed to the decline of Lahontan cutthroat trout (Dunham et al. 2003). This subspecies occupies streams in the Great Basin desert (Gerstung 1988), where the distribution of suitable thermal habitat is constrained by climatic gradients that isolate populations in small enclaves at higher elevations (Dunham et al. 1999). Isolation and fragmentation of suitable habitat has been linked to extinction risk of Lahontan cutthroat trout, with populations most likely to persist in larger habitats (Dunham et al. 1997, 2002). Distributions of populations within streams have been linked to temperature regimes (Dunham et al. 2003), but detailed information on responses of individual fish to natural thermal regimes is lacking.

To better understand the responses of Lahontan cutthroat trout to temperature, we investigated the effects of naturally variable sublethal temperature regimes on individual fish of variable sizes. Past studies in the laboratory have focused on lethal temperatures and largely constant thermal regimes, and the influences of body size have not been considered (Vigg & Koch 1980; Dickerson & Vinyard 1999). We examined the responses of Lahontan cutthroat trout chronically exposed to both constant and cyclical sublethal thermal regimes, and acute responses of individuals with different thermal histories and body sizes. Four groups of fish were exposed to three constant and two cyclical thermal regimes for a period of 14 days. This period essentially represented a test of chronic exposure to different thermal regimes. The response to different thermal regimes was measured as individual growth rates. Following the period of chronic exposure, fish from each thermal regime were subjected to a 40-min exposure to three different acute test temperatures, with responses measured as feeding rates. The combined results of these tests of thermal exposure should have more direct relevance to natural populations of Lahontan cutthroat trout, where both temperatures and body size can vary considerably.

Methods

Laboratory environment

Four groups of 300 Lahontan cutthroat trout were collected from the Lahontan National Fish Hatchery, Gardnerville, Nevada, and transported to the University of Nevada, Reno. The Lahontan National Fish Hatchery is fed from a well with a mean water temperature of 12.2 ± 1.0 °C (J. Branstetter, Lahontan National Fish Hatchery, personal communication). All four groups of fish were progeny of broodstock spawned in the spring of 1998 during normal hatchery operation, but they were collected at different times to sample a broad range of fish sizes (Table 1). The first three groups of fish were representative of the average size available at the time of collection. The fourth group of fish was of smaller size than the average fish available at the time of collection. Fish of group four were sampled in this manner to fill a size gap between group two and three. To test for potential bias associated with nonrandom sampling, all data analyses were performed with and without group four. All four groups were in good condition with fully developed fins and were held under identical conditions after transportation to the laboratory.

Upon arrival to the laboratory, all fish were uniquely marked and 30 individuals were placed into each of 10 independent 120-l tanks. Marks consisted of a combination of two, coloured, Photonic Tags (NEW-WEST Technologies, Santa Rosa, CA, USA) injected into the caudal fin. Tanks were filled with dechlorinated tap water and continuously aerated to maintain high dissolved oxygen. Each tank was supplied with a water filter and temperature controller. Water was filtered with Fluval 103 filters (Rolf C. Hagen Corp., Mansfield, MA, USA) that were cleaned every 5 days. Fish were fed commercial trout pellets at a rate of 2% of the tank's total biomass twice daily for the duration of the experiment. This rate of feeding was assumed to be sufficient because uneaten food was always present in the tanks. Excess food and waste were removed daily from each tank. Every day, 38 l of water were replaced with fresh water of the appropriate temperature. Prescribed tank cleanings were effective in maintaining ammonia levels at or below 0.5 ppm (Stickney & Kohler 1990). Fish were allowed a minimum of 7 days to acclimate to laboratory conditions with a constant water temperature of 12 °C and a photoperiod of 12 h light and 12 h dark.

Following acclimation at 12 °C, each tank was randomly assigned to one of five thermal regimes. Each thermal regime was replicated twice for each of the four fish groups for a total of eight replicates. The five

Table 1. Collection date, mean length (fork length, mm) and standard deviation (SD), and mass (wet mass, g) and standard deviation for four groups of Lahontan cutthroat trout collected from the Lahontan National Fish Hatchery, Gardnerville, NV, USA.

Fish group	Date collected	Mean length (mm ± SD)	Mean mass (g ± SD)
1	6 June 1998	29.46 ± 3.17	0.24 ± 0.07
2	18 September 1998	77.27 ± 6.87	4.21 ± 1.21
3	28 December 1998	120.82 ± 14.33	15.52 ± 5.66
4	2 February 1999	96.00 ± 8.11	7.38 ± 2.00

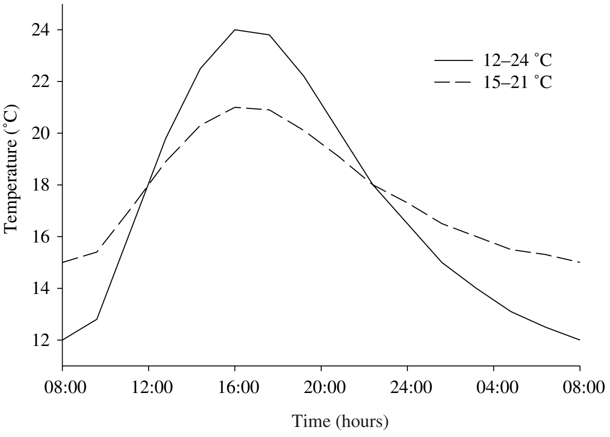

Fig. 1. A 24-h temperature profile for cyclical thermal regimes. A dashed line indicates a cycle of 15–21 °C. A solid line indicates a cycle of 12–24 °C.

thermal regimes were: 12, 18 and 24 °C, and a daily cycle of 15–21 °C with a daily mean of 17.5 °C (Fig. 1), and a daily cycle of 12–24 °C with a daily mean of 17.2 °C (Fig. 1). Tank temperatures were controlled with either a Fisher Scientific (Pittsburgh, PA, USA) Model 210 flow-through heater (constant thermal regimes) or a Kaif Digital Corporation (Scottsdale, AZ, USA) PTC Series programmable temperature controller with submersible heaters (cyclical thermal regimes). Although natural populations of Lahontan cutthroat trout experience a broad range of thermal variation both within and between days, cyclical thermal regimes chosen for this experiment were similar to those commonly observed during summer months throughout the Lahontan Basin (J.B. Dunham, unpublished data). Cyclical thermal regimes used in this experiment had a relatively rapid rate of heating followed by a longer period of cooling (Fig. 1).

For all thermal regimes with temperatures greater than 12 °C, water temperature was raised at a rate of not >4 $°C \cdot day^{-1}$ to reduce potential stress associated with rapid temperature change (Dickerson & Vinyard 1999). Once a tank's target thermal regime was attained, the initial mass (wet mass, g) and length (fork length, mm) of each fish in that tank was measured. Before measurements, fish were fasted for 24 h so they would be postabsorptive. After initial measurements were made, the thermal regime was maintained for 14 day representing chronic exposure. Supplemental to commercial trout pellets, 100 *Daphnia magna* were added to each tank every 2 days to familiarise fish with these prey items. *D. magna* were later used to assess feeding rates.

Growth rate

After exposure to thermal regimes for 14 days, all fish were measured for mass and length to assess growth. Growth rates were quantified as change in mass and length divided by duration of the treatment (14 days). The number of fish measured for each tank was <30 for some tanks because of mortality.

Growth rate data were analysed as a randomised complete block design with five, fixed treatments (thermal regimes) and one blocking factor (fish group). Initial mass was used as a covariate when testing the effect of thermal regime on mass growth rate. Initial length was not included as a covariate for analyses of growth in terms of length because initial length did not have a significant effect on the response ($F_{1,923} = 1.48$, $P = 0.22$). When treatment effects were significant, mean comparisons were performed to test the effects of particular thermal regimes. These included comparisons between 12, 18 and 24 °C (constant thermal regimes), and between 18, 15–21 and 12–24 °C (thermal regimes with similar means and increasing daily variation).

Feeding rate

Following exposure to the five thermal regimes for 14 days, feeding rates were assessed at three test temperatures, 12, 18 and 24 °C. Thus the effect of chronic exposure (thermal regime) and acute exposure (test temperature) on feeding rate could both be examined. Feeding rates were assessed for five fish per tank at each test temperature with each measured fish being tested at one temperature only. Immediately after growth measurements, a single fish was placed in a 55-l tank submerged in a 455-l water bath of the appropriate temperature and allowed to recover and adjust to the experimental conditions for 20 min. A Frigid Units Inc., model BHL-1093 chiller (Blissfield MFG. Co., Blissfield, MI, USA) (acute test temperatures below ambient) or a Kaif Digital Corporation programmable temperature controller (acute test temperatures above ambient) was used to control water bath temperatures. After 20 min, 100 *D. magna* were introduced into the tank and the fish was allowed to feed for 20 min. After each feeding trial, remaining prey were filtered through a 202 μm filter in the bottom of the tank and counted to determine feeding rate ($prey \cdot min^{-1}$).

Feeding rate data were examined as a split-plot, randomised complete block design with five (thermal regimes) by three (test temperatures) treatment combinations and one blocking factor (fish group). Thermal regimes were applied to all of the fish (whole plot) in a tank and five fish per tank (subplot) where exposed to each of the test temperatures. Neither fish mass ($F_{1,331} = 1.58$, $P = 0.21$) nor fish length ($F_{1,331} = 1.03$, $P = 0.31$) was included as covariates in the analysis. A $\log_e$-transformation of feeding rate was used to normalise the data. Because feeding rates for some individuals were zero, a value of 0.1 was added to the number of prey consumed (Kuehl 1994). When transformed data were used, reported mean values were based on the original measurement scale (Kuehl 1994). When treatment effects were significant, mean comparisons were performed to test the effects of particular treatment combinations on feeding rate.

Statistical analyses were performed using the SAS MIXED procedure (SAS Institute Inc. 1992). Analysis of variance with subsamples (Steel & Torrie 1960; Kuehl 1994), computationally identical to nested, or hierarchical, analysis of variance (Zar 1984; Sokal & Rohlf 1995), was used to examine the effects of temperature on growth and feeding of Lahontan cutthroat trout. The four fish groups were treated as random blocks. This type of analysis stratifies experimental units (i.e., tanks) into blocks of homogeneous units (i.e., groups of fish collected at the same time). Blocking can result in reduced experimental error by accounting for systematic variation associated with the time of sampling. Factors that changed systematically among all individuals and may have an effect on the responses examined in this experiment, such as photoperiod, changes in diet, and changes in water quality, may be accounted for by blocking fish into groups based on the time at which they were sampled. Because of unbalanced data, the Satterthwaite approximation was used to estimate degrees of freedom for all tests (Satterthwaite 1946). Significance levels for all analyses were set at $\alpha = 0.05$. When overall models were significant, mean comparisons were performed using a Tukey–Kramer adjustment (Kuehl 1994; Sokal & Rohlf 1995).

Results

Lahontan cutthroat trout were examined in four groups of 300 fish over a period of 9 months. Because of this, fish group was included in all analyses as a blocking factor in order to partition the variation associated with time of sampling (i.e., group) from other factors examined in this experiment (i.e., thermal regime, test temperature, fish size). Fish group significantly affected mass growth rate ($F_{3,40.1} = 11.07$, $P < 0.0001$), length growth rate ($F_{3,32.9} = 12.90$, $P < 0.0001$), and feeding rate ($F_{3,31.1} = 12.48$, $P < 0.0001$). Including fish group as a blocking factor in these analyses was successful in reducing experimental error variance by accounting for variation associated with differences in time of sampling. For all analyses, overall model significance was not affected by inclusion of fish group four, which consisted of fish of smaller size than the average available at the time of collection (Table 1).

Mass growth rate

There was a significant interaction between initial mass and thermal regime ($F_{4,114} = 37.35$, $P < 0.0001$) such that the effect of thermal regime depended on initial mass of the fish. Therefore, mean comparisons were performed at the overall mean of initial fish mass and at the mean initial fish mass of each of the four fish groups (Table 2; Kuehl 1994). Overall, mass growth rate was greatest at 12 °C followed by 18 °C, a cycle of 15–21 °C, a cycle of 12–24 °C, and 24 °C (Fig. 2). The difference between the 12 and the 18 °C thermal regimes was not significant regardless of initial fish mass (Table 2). However, comparisons between other thermal regimes indicated that as initial fish mass increased the effect of temperature became more pronounced (Table 2; Fig. 2).

Length growth rate

Thermal regime significantly affected length growth rate ($F_{4,29.9} = 16.82$, $P < 0.0001$). Mean length growth rate was greatest at 12 °C followed by 18 °C, a cycle of 15–21 °C, a cycle of 12–24 °C, and 24 °C (Fig. 3). This trend was similar to the overall trend observed for mass growth rate; however, unlike mass growth rate, initial fish size did not have an effect on length growth rate. For constant thermal regimes significant depression of length growth rate was observed at 24 °C when compared with either 12 °C ($t = 6.67$, d.f. $= 31$, $P < 0.0001$) or 18 °C ($t = 5.91$, d.f. $= 31.7$, $P < 0.0001$) (Fig. 3). For cyclical thermal regimes significant depression of length growth rate was observed for a cycle of 12–24 °C when compared with either a cycle of 15–21 °C ($t = 2.96$, d.f. $= 29.4$, $P = 0.04$) or the approximate mean temperature of 18 °C ($t = 4.75$, d.f. $= 30.2$, $P = 0.0004$) (Fig. 3).

Table 2. Pairwise comparisons of acclimation regime effects on mass (wet mass) growth rate of Lahontan cutthroat trout at five levels of initial mass (g) with corresponding mean differences (g·day^{-1}).

	Mean difference in mass growth rate (g·day^{-1}) at initial mass (g)				
Treatment comparison	0.24	4.21	6.46	7.38	15.52
12 °C vs. 18 °C	0.01	0.01	0.01	0.01	0.01
12 °C vs. 24 °C	–0.01	0.07*	0.12*	0.14*	0.32*
18 °C vs. 24 °C	–0.03	0.06*	0.11*	0.13*	0.32*
18 °C vs. 15–21 °C	–0.01	0.01	0.03	0.04	0.09*
18 °C vs. 12–24 °C	–0.03	0.03	0.06*	0.07*	0.19*
15–21 °C vs. 12–24 °C	–0.02	0.01	0.03	0.04	0.10*

*Indicates a significant difference at $\alpha = 0.05$ (Tukey–Kramer adjusted *P*-value). For each comparison, except 12 °C versus 18 °C, as fish mass increased the difference in growth rate between the acclimation regimes increased.

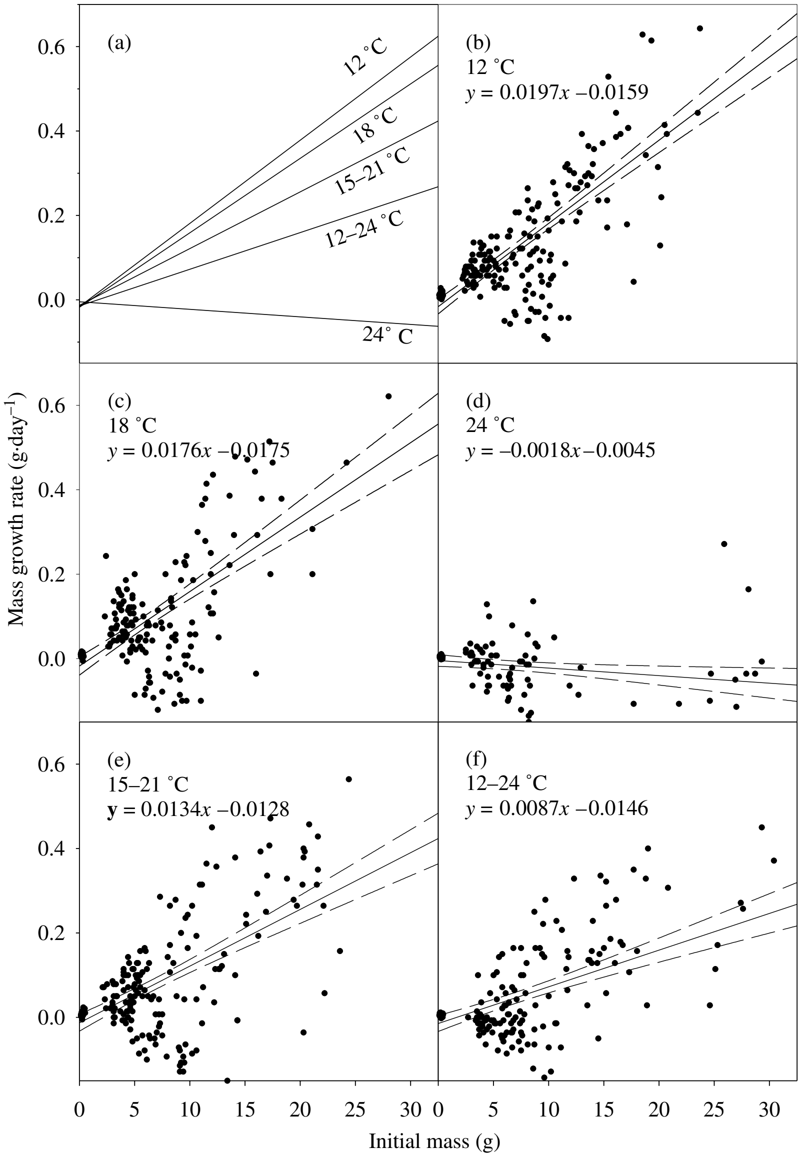

Fig. 2. Mass (wet mass) growth rate (g·day^{-1}) for Lahontan cutthroat trout of different initial masses (g) exposed to five thermal regimes (a) and each thermal regime separately with individual data points and 95% confidence intervals (b–f). Trend lines were computed by regressing mass growth rate on initial mass of individuals using simple linear regression. Unequal slopes indicate the dependence of mass growth rate on initial fish mass, and suggest the thermal regime has a stronger influence on fish with greater mass.

Feeding rate

There was not a significant interaction between thermal regime and test temperature ($F_{8,57.5} = 0.97$, $P = 0.47$). Thermal regime did not significantly affect feeding rate ($F_{4,27.6} = 1.59$, $P = 0.20$), but test temperature did ($F_{2,60.9} = 4.96$, $P = 0.01$). Therefore, feeding rate was not significantly affected by the 14-days thermal regime, but it was affected by acute exposure. Regardless of thermal regime, feeding rate was greatest under acute exposure to 18 °C (0.91 prey·min^{-1}) intermediate at 12 °C (0.82 prey·min^{-1}) and least at 24 °C (0.46 prey·min^{-1}) (Fig. 4). Significant feeding rate depression was observed at 24 °C when compared with 18 °C ($t = 3.04$, d.f. = 60.1, $P = 0.01$). Differences in feeding rate between 12 °C and 24 °C were only marginally insignificant ($t = 2.20$, d.f. = 61.2, $P = 0.08$).

Discussion

Previous work has indicated the importance of temperature in determining survival, growth, and distribution of salmonids in general (e.g., Elliott 1981; Beschta et al. 1987; Holtby 1988; Keleher & Rahel 1996) and Lahontan cutthroat trout in particular (Vigg & Koch 1980; Dickerson & Vinyard 1999; Dunham 1999; Dunham et al. 1999). Although optimal temperatures may differ for various functions, such as growth and feeding (Elliott 1981), temperature had qualitatively similar effects on the performance measures used in this experiment.

Chronic exposure: responses to different thermal regimes

Overall, similar trends were observed when measuring growth as either change in mass or change in length in

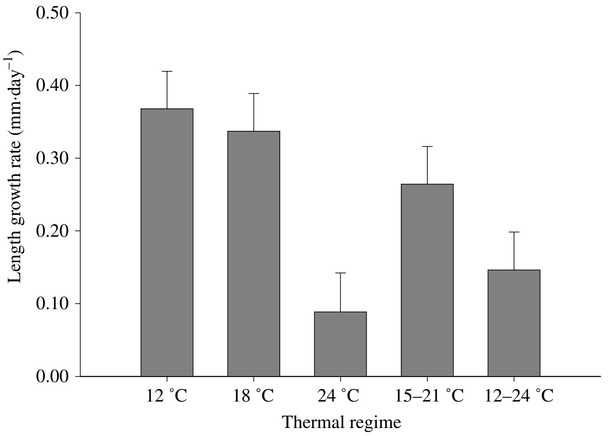

Fig. 3. Length (fork length) growth rate (mm·day^{-1} ± 1 SE) for Lahontan cutthroat trout exposed to five thermal regimes. Compared with either the 12 or the 18 °C thermal regimes, growth rate for fish exposed to 24 °C was significantly depressed. Growth rate was significantly greater at 18 °C and at a cycle of 15–21 °C than at a cycle of 12–24 °C.

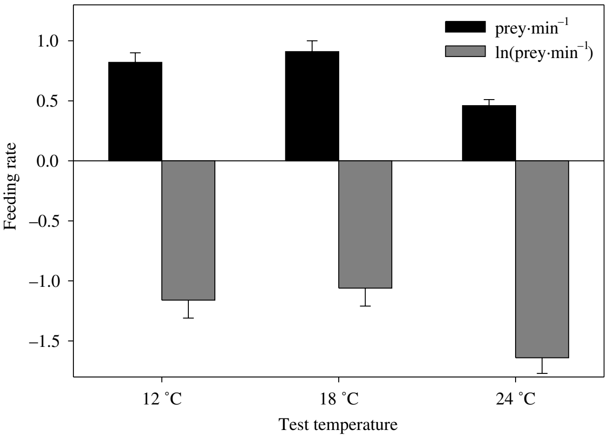

Fig. 4. Feeding rate [prey·min^{-1} ± 1 SE and ln(prey·min^{-1}) ± SE] for Lahontan cutthroat trout exposed to three test temperatures. Significant feeding rate depression was observed at 24 °C when compared with 18 °C, and differences between feeding rate at 12 and 24 °C were only marginally insignificant ($P = 0.08$).

relation to different thermal regimes. For constant thermal regimes, growth was greatest at 12 °C followed by 18 °C and least at 24 °C (Figs 2 and 3). Dickerson & Vinyard (1999) observed similar results and suggested that the upper limit for growth of Lahontan cutthroat trout is between 22 and 23 °C.

Comparisons between 18 °C and the two cyclical thermal regimes (i.e., 15–21 and 12–24 °C) indicated that increasing the magnitude of daily thermal variation around a similar mean had an adverse affect on growth rate (Figs 2 and 3). Likewise, Thomas et al. (1986) observed elevated levels of plasma cortisol and plasma glucose, common indicators of stress, in coho salmon (*O. kisutch*) exposed to daily temperature cycles of 6.5–20 °C as compared with daily temperature cycles of 9–15 °C or a constant temperature of 11 °C. The difference in the magnitude of daily thermal variation is only one possible reason for the observed results in this and other studies. Effects of daily thermal variability may be because of physiological costs associated with cyclical thermal regimes, greater time of exposure to physiologically stressful temperatures, or both. Dunham et al. (2003) observed the presence of Lahontan cutthroat trout at temperatures exceeding 28 °C; however, these high temperatures were experienced for no more than 2 h. Dickerson & Vinyard (1999) observed no mortality of Lahontan cutthroat trout that were exposed to a daily temperature cycle of 20–26 °C for a 7-day period, although chronic exposure to 26 °C resulted in high mortality rates. Similarly, Johnstone & Rahel (2003) observed no mortality during 7-day exposures to moderate (10–20 °C) and extreme (16–26 °C) thermal conditions that included temperatures that would be lethal under conditions of chronic exposure (>24.2 °C) for Bonneville cutthroat trout (*O. clarki utah*). However, a 1 day exposure to 18–28 °C followed by 1 day exposure to 19–29 °C resulted in mortality of all individuals, and it was suggested that time spent at lower temperature (repair/recovery time) was insufficient to compensate for damage resulting from exposure to high temperatures.

In future studies, it may be possible to partition the effects of the magnitude of thermal variation and the time spent at physiologically stressful temperatures by including experimental treatments with similar magnitudes of thermal variation centred on different mean temperatures and treatments with similar mean temperatures that differ in time spent at extreme temperatures. However, in small streams of the Lahontan Basin, increased daily variability in summer stream temperatures is associated with increased mean and maximum temperatures (Dunham 1999). Therefore, the daily variation in temperature modelled in this study, which mimicked patterns of thermal variation observed in the field, is directly relevant to understanding effects of temperature on Lahontan cutthroat trout in the wild.

Effects of body size among different thermal regimes

Although mass and length growth rates had similar overall trends among the different thermal regimes, mass growth rate was highly dependent on fish size, whereas length was not. Mass may be a more sensitive measurement for short-term experiments of this type because it changes at a potentially greater rate (Busacker et al. 1990) allowing for detection of trends otherwise not observable. The interactive effect of thermal regime and initial fish mass on mass growth of Lahontan cutthroat trout indicates that as fish mass increases the effect of temperature on growth changes.

The dependence of mass growth on the interaction between thermal regime and initial mass has important implications for natural populations of Lahontan cutthroat trout. These data indicate that small fish were less sensitive to the effects of different thermal regimes. It is generally accepted that growth will not occur until maintenance requirements are met and that metabolic rate increases with temperature (Brett 1979; Brett & Groves 1979). However, there is evidence that a decoupling of growth rate and metabolism may occur in fish embryos and larvae (Pedersen 1997). This decoupling of growth rate and metabolism may allow smaller fish to meet growth requirements under a wider variety of thermal conditions. An alternative explanation could be that as fish grew larger, they were feeding less efficiently, and therefore growth was reduced. Behavioural interactions may have lead to dominance by a minority of the individuals, and reduced feeding efficiency for many individuals (Keeley 2001).

Further work is needed to determine if the effects of temperature continue to increase or attenuate with increasing mass (i.e., 'do effects increase for fish >15.5 g?'). Lahontan cutthroat trout may adopt migratory life histories and grow to large sizes (>1.00 kg) (Gerstung 1988; Vinyard & Winzeler 2000), and like other migratory salmonids, may encounter a variety of thermal conditions (e.g., Swanberg 1997) with varying effects on survival, growth, and behaviour. It may be the case that natural selection favours greater thermal tolerance in smaller and less mobile juveniles, whereas larger and more mobile individuals are more able to behaviourally thermoregulate by selecting patches of thermally suitable habitat.

Acute exposure: feeding responses to test temperatures

As temperature rises, the amount of food consumed by fishes generally increases to some optimal point (Brett 1979). However, inhibition or reluctance to feed at high temperatures is often symptomatic of physiological stress (Elliott 1981). Feeding rate of Lahontan cutthroat trout under acute exposure to test temperatures was not significantly affected by either the size of fish (mass or length) or recent thermal history (thermal regime). However, feeding rate was greater at 18 and 12 °C than at 24 °C under conditions of acute exposure. Similarly, Selong et al. (2001) observed decreased feed consumption at temperature >16 °C and lack of feeding at temperatures >22 °C for bull trout (*Salvelinus confluentus*). Results of this experiment indicate that 24 °C is potentially stressful for Lahontan cutthroat trout, which is consistent with evidence from studies on stress protein induction in this subspecies. Stress proteins help repair denatured proteins; thereby, protecting organisms from damage because of exposure to a wide variety of stressors, including elevated temperatures (Sanders 1993). Lahontan cutthroat trout begin to synthesise detectable amounts of stress proteins within several hours of exposure to 24 °C, but synthesis is not detectable at 22 °C or less, even after 5 days (L. Weber & M. Hargis, University of Nevada Reno, personal communication).

Although feeding rate was not affected by thermal history (thermal regime) of individuals, it was negatively affected by acute exposure to high temperatures. In a similar study, Johnstone & Rahel (2003) exposed Bonneville cutthroat trout to daily temperature cycles of 10–20 and 16–26 °C, and observed feeding and activity at the low and high temperatures of each thermal regime. While no difference in feeding or activity levels were observed for comparisons between 10 and 16 °C (low points of temperature cycles), feeding and activity levels significantly decreased from 20 to 26 °C (high points of temperature cycles). These data suggest that feeding activity may be inhibited in natural situations during portions of a day when high, sub-lethal temperatures are reached. Lack of feeding during exposure to 24 °C supports the observation that Lahontan cutthroat trout chronically exposed to 24 °C had significantly reduced growth. Also, low growth rates for fish exposed to a daily temperature cycle of 12–24 °C coupled with the feeding rate data suggest that even brief daily exposure to high, sublethal temperatures may result in decreased feeding and growth.

Implications for water quality criteria

Results of this study have important implications for water quality criteria. Water quality criteria for salmonids often incorporate temperature, but there is little agreement on the proper metrics for quantifying temperature (Dunham et al. 2003; Poole et al. 2004). Most temperature criteria are based either on mean daily temperatures or maximum daily temperatures. During summer months, Lahontan cutthroat trout often are found within habitats that reach or exceed 22 °C some time during the day (Dunham et al. 2003). Temperatures of this magnitude are potentially stressful. Reduced growth and depressed feeding rates at high temperatures suggest that even brief exposure to high sub-lethal temperatures has the potential to impact Lahontan cutthroat trout. In addition, the interactive effect of fish mass and temperature on mass growth may be important. Within the range of fish sizes considered in this study, larger fish appear to be more sensitive to the effects of different thermal regimes. Further work is needed to define the nature of thermal responses of

Lahontan cutthroat trout over a more complete range of body sizes, and for other potentially sensitive life history stages.

Resumen

1. Examinamos los efectos de regímenes térmicos constantes (12 °C, 18 °C, y 24 °C) y cíclicos (15–21 °C y 12–24 °C) sobre el crecimiento y la alimentación de *Oncorhyncus clarki henshawi* de varios tamaños.

2. Tanto las temperaturas constantes elevadas (i.e, 24 °C) como las temperaturas diarias mas variables (i.e, 12–24 °C, ciclo diario) afectaron negativamente a las tasas de crecimiento. Al aumentar el peso de los peces (desde 0.24 a 15.52 g), los efectos de distintos regímenes térmicos sobre el crecimiento en peso son más pronunciados. Después de 14 días de exposición a los regímenes térmicos, evaluamos las tasas alimenticias de peces individuales durante una exposición severa (40 minutos) a temperaturas test de 12 °C, 18 °C y 24 °C. La tasa alimenticia se redujo durante la exposición severa a 24 °C pero estas tasas no fueron afectada significativamente por los regímenes térmicos precedentes.

3. Nuestros resultados indican que incluso exposiciones diarias breves a altas temperaturas (e.g., 24 °C) pueden tener efectos sub-letales considerables sobre *O. clarki henshawi*, y que el tamaño de los peces debería ser considerado al examinar los efectos de la temperatura.

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