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Effect of Temperature on Growth and Survival of Bull Trout, with Application of an Improved Method for Determining Thermal Tolerance in Fishes

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Abstract.—Elevated temperature is considered an important factor in the decline of the threatened bull trout *Salvelinus confluentus*, but the thermal requirements of this species have not been defined. We used the acclimated chronic exposure (ACE) method to assess the upper thermal limits and growth optima of bull trout fed daily to satiation over test temperatures ranging from 8°C to 28°C during 60-d trials. Survival of age-0 bull trout was at least 98% at 8, 10, 12, 14, 16, and 18°C, but 0% at 22, 24, 26, and 28°C after 60 d. The predicted ultimate upper incipient lethal temperature for these trout was 20.9°C. Peak growth, as estimated by regression analysis, occurred at 13.2°C (95% confidence interval, 10.9–15.4°C). Feed consumption declined significantly ($P < 0.001$) at temperatures greater than 16°C, and fish held at temperatures of 22°C and above did not feed. Feed, lipid, and protein efficiencies were similar at 8–18°C but declined significantly ($P < 0.001$) at 20°C. Our results corroborate field investigations suggesting that bull trout have among the lowest upper thermal limits and growth optima of North American salmonids. The slower acclimation times and long-term duration of the ACE method resulted in a more realistic measure of thermal tolerance in natural situations than would have been obtained with traditional methods and afforded sufficient time for sublethal differences in growth rate, feed consumption, and feed efficiency to become apparent.

Temperature has a substantial influence on the distribution of salmonids both within and across watersheds (Bozek and Hubert 1992; Fausch et al. 1994; Rieman et al. 1997) and appears especially important for defining suitable habitat for bull trout *Salvelinus confluentus* (Rieman and McIntyre 1993, 1995). The species has recently been listed as threatened over much of its range in the northwestern United States (USFWS 1998) and ''at risk'' over much of its range in Canada (McCart 1997; Haas 1998). Bull trout are regarded as having one of the lowest thermal tolerances among North American salmonids (e.g., Bonneau and Scarnecchia 1996; Adams and Bjornn 1997; Goetz 1997), and elevated temperature is considered a major factor in their decline (Buchanan and Gregory 1997; Rieman et al. 1997). Field observations indicate that bull trout are typically rare where maximum temperatures exceed 15°C (Fraley and Shepard 1989; Saffel and Scarnecchia 1995; Goetz 1997; Rieman et al. 1997; Rieman and Chandler 1999; Haas 2001). Although such distributional data strongly suggest that bull trout have low upper thermal limits, the effects of temperature on growth and the upper lethal temperature limits have not been defined. Development of thermal protection standards for juvenile salmonids is crucial to protecting and recovering salmonid populations, as this life stage is often the most vulnerable to summer warming from anthropogenic sources (Buchanan and Gregory 1997; McCullough 1999). Our study was designed to aid in the development of such thermal standards for juvenile bull trout.

Temperature criteria have traditionally been established from laboratory studies employing two primary methods, the critical thermal maximum or minimum (CTM) method and the upper or lower incipient lethal temperature (ILT) method. Both

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the CTM and ILT methods were originally developed to investigate thermal effects on physiology (Fry 1947; Brett 1956) and later adopted for the determination of lethal thermal limits for fish in the wild (Brungs and Jones 1977). Fry (1947, 1971), Brett (1956), Kilgour and McCauley (1986), and McCullough (1999) describe the methods in detail and review their relative merits. The CTM method involves heating or cooling test fish at a rapid rate (e.g., 18°C/h) from a series of acclimation temperatures until they lose equilibrium (Becker and Genoway 1979). Rapid heating or cooling rates are chosen to prevent thermal acclimation in the fish, but they are not so fast as to prevent body core temperature from equilibrating with water temperature. The CTM method is advantageous in that measures of acute temperature tolerance can be completed quickly using simple, inexpensive equipment. In addition, CTMs have been determined for many species, often using similar protocols, which facilitates species comparisons (e.g., Lohr et al. 1996; Smith and Fausch 1997). However, their relevance to the actual temperature tolerance of fishes is limited by the unnaturally rapid temperature changes, which preclude the normal acclimation that occurs in nature. A modified CTM method, whereby water temperatures are changed much more slowly (1°C/d) (e.g., Zale and Gregory 1989; Elliott and Elliott 1995), affords fish the ability to acclimate to gradually changing temperatures under environmentally realistic thermal regimens. All CTM methods, however, preclude evaluation of the effect of exposure time on thermal tolerance because temperatures are constantly changing.

The ILT method incorporates the time of exposure or thermal resistance; it entails rapidly transferring fish from an acclimation temperature directly into a constant-temperature test tank where time to death is measured (Brett 1952; Kilgour and McCauley 1986). For each acclimation temperature, several different test temperatures are used. The incipient lethal temperature is then calculated as the temperature at which 50% of the test fish survive indefinitely, analogous to a 50% lethal dose (LD50) or median ''resistance time.'' The process is repeated for other acclimation temperatures to determine the corresponding ILTs, and the results graphed to determine the ultimate incipient lethal temperature. The ultimate incipient lethal temperature is the point on the graph where a plateau in ILTs occurs; it is the most extreme temperature an organism can attain by acclimation (Fry 1971; Elliott 1981). Ultimate incipient lethal temperatures have been calculated for many species, and the ILT method is advantageous because it includes exposure time as a measure of thermal tolerance and therefore has direct relevance to the temperature requirements of fish in nature. However, as with the CTM method, the ILT method may have limitations when it comes to extrapolating test results to natural situations. The abrupt transfer of fish to test temperatures precludes them from acclimating to the gradually changing temperatures experienced under most natural conditions. A recent modification of the ILT method incorporates slower temperature change schedules (1.5°C/h) to better mimic natural temperature changes and reduce thermal shock (Smith and Fausch 1997). However, another potential limitation of the ILT method still remains, as temperature tests are typically run for a short duration ($\leq$7 d; Elliott and Elliott 1995) and the effects of longer exposures are often unknown.

In the search for a more ecologically relevant technique to assess the thermal requirements of fishes, Zale (1984) developed the acclimated chronic exposure (ACE) method. Though originally developed to test the cold temperature tolerance of blue tilapia *Tilapia aurea*, the method is applicable for determining thermal tolerances and optima for aquatic organisms in general. A hybrid of the ILT and modified CTM methods, the ACE method entails gradually adjusting water temperatures at environmentally realistic rates that allow fish to fully acclimate to changing conditions (e.g., 1°C/d). Once a predetermined test temperature is reached, fish are then maintained at a constant temperature for 60 d or until death. A 60-d time frame is used to simulate the duration of exposure to the potentially high or low seasonal temperatures at temperate latitudes (e.g., summer). For each test temperature, median resistance times are recorded and plotted using exponential regression, and the resulting formula is then used to calculate the ultimate incipient lethal temperature (i.e., the temperature at which 50% of the test fish survive for 60 d). Thus, the ACE method is similar to the ILT method in that both allow determination of the ultimate incipient lethal temperature. However, the ACE method better simulates the actual thermal response of fish in the wild because fish are fully acclimated when exposed to test temperatures rather than being abruptly transferred from the acclimation to the test temperature. Because fish are gradually acclimated to the test temperatures, the acclimation and test temperatures are the same, unlike with the ILT method. The ACE method also

avoids the need for multiple test temperatures for each acclimation temperature, thereby allowing determination of the ultimate incipient lethal temperature using fewer trials. Its longer test period also allows chronic thermal effects to be evaluated. Because the development of temperature standards typically includes maximum-growth temperatures as well as thermal tolerance limits (Brungs and Jones 1977; Hokanson et al. 1977; Armour 1990), an additional advantage of the ACE method is that it permits simultaneous assessment of fish growth and health at sublethal temperatures. In this paper, we use the ACE method to define the ultimate upper incipient lethal and maximum-growth temperatures for bull trout and use this method and the CTM method to compare the thermal limits of this species with those of other salmonids.

Methods

Temperature experiments were conducted at the U.S. Fish and Wildlife Service's Fish Technology Center in Bozeman, Montana. Eyed bull trout eggs were obtained in fall 1997 from a wild broodstock maintained at Creston National Fish Hatchery. This first-generation hatchery broodstock was developed from the gametes of 7 females and 14 males captured in 1993 from two streams in the Swan River drainage, Montana, and raised to maturity (Fredenberg 1998). Eggs and juveniles were held in 8°C spring water until testing.

Because elevated metabolite and lowered dissolved oxygen concentrations have been shown to affect both the thermal tolerances (Alabaster and Welcomme 1962; Watenpaugh et al. 1985) and growth rates (Larmoyeux and Piper 1973; Rasmussen and Korsgaard 1996; Buentello et al. 2000) of fishes, we used a flow-through temperature test system to provide continuous high levels of dissolved oxygen, flushing of metabolites, and more natural conditions for stream fish. Water from cold (7–8°C; conductivity, 233 μS) and warm (20–22°C, 431 μS) springs and three 40,000-BTU water heaters was used to provide test temperatures of 8–28°C. Water from each source was passed through a de-gassing column and mixed in separate head tanks to achieve 11 treatment temperatures (8, 10, 12, 14, 16, 18, 20, 22, 24, 26, and 28°C). Water from the head tanks was supplied to 75-L aluminum test tanks measuring 120 × 35 × 25 cm at a rate of 3.8 L/min. Three replicate test tanks were randomly chosen for each treatment temperature. All tanks and connecting pipes were covered with foam insulation to minimize temperature fluctuation. Rigid foam insulation also provided overhead cover over test tanks. Natural light was supplemented with overhead halogen lights maintained on a 9 h:15 h (light:darkness) photoperiod.

TABLE 1.—Ingredient composition of the feed Bull Trout Grower 9802.

Ingredient	Content (g/100g)
Krill meal	27
Herring meal	31
Deboned whitefish meal	12
Liver meal	8
Menhaden oil	9
Wheat gluten	5
Wheat flour	4.4
Vitamin premix 30[a]	1
Lecithin	2
Ascorbic acid	0.5
Trace mineral premix 3[b]	0.1
Total	100
Related information:	
Metabolizable energy (kcal/kg)[c]	2,124.6
Protein (%)	51.5
Lipid (%)	18.5

[a] Contribution to diet (per kg): vitamin A, 10,000 IU; vitamin D_3, 720 IU; vitamin E, 530 IU; vitamin B_{12}, 30 μg; calcium pantothenate, 160 mg; riboflavin, 80 mg; thiamin mononitrate, 50 mg; pyridoxine hydrochloride, 45 mg; folacin, 13 mg; menadione sodium bisulfate, 25 mg; biotin, 1 mg; niacin, 330 mg.
[b] Contribution to diet (mg/kg): zinc, 100; manganese, 70; iron, 3; copper, 2; iodine, 1.
[c] Determined for rainbow trout (NRC 1993).

Fifty age-0 bull trout (7 months posthatch) were randomly selected and weighed (after 36 h fasting), then placed into each test tank at the start of the trial in July 1998. Fish averaged 1.8 g and 45 mm total length, and there was no difference ($P = 0.44$) in mean individual weight among tanks at the start of the study. Fish were held in test tanks for 2 weeks at 8°C prior to temperature adjustment. In accordance with the ACE protocol, temperatures were then raised 1.0°C/d, with the initiation of the increases staggered at 2-d intervals so that all treatments reached the final treatment temperature on the same day. Temperature adjustments took 20 d to complete. After adjustment, fish were held at constant treatment temperatures for 60 d or until death.

Fish were fed a specially formulated diet (Table 1) daily from 0900 to 1700 hours with an automatic belt feeder placed near the head of the test tank. Fish were fed to excess and ration levels adjusted weekly to maintain satiation feed levels. Actual feed consumption was measured once weekly by removing feces and uneaten feed at the end of an 8-h feeding period. This material was dried for 24 h at 100°C and the two constituents separated by sieving with a 710-μm screen (fecal material was

finer after drying than uneaten feed, allowing for the separation). The portion of uneaten feed was weighed, corrected for leaching and moisture loss, and subtracted from the amount of feed offered to determine feed consumption in each tank. Weekly feed consumption estimates were averaged by tank and converted to a mean individual daily consumption for each treatment temperature.

Tanks were cleaned daily and any mortalities removed and weighed. Water temperature was recorded once daily in the head tanks and every 2 h by data loggers in the test tanks. Temperatures in the test tanks were within ± 0.5°C of the final treatment temperature for the duration of the study, and daily fluctuations were less than 0.2°C. Dissolved oxygen and total gas saturation were measured daily with electronic meters. Dissolved oxygen ranged from 7 to 12 mg/L and was always greater than 80% saturation. Total gas saturation ranged from 97% to 103%, which is within the optimal range for trout (Piper et al. 1982).

A second trial was conducted in spring 1999 to further pinpoint upper lethal temperatures. We repeated temperature testing at 20°C and 22°C and added treatment temperatures of 21°C and 23°C, using the protocol described above. Test fish were those from the same cohort used in the first trial but were yearling (14 months posthatch) rather than age-0 fish. Test fish averaged 23.9 g in weight and 135 mm in length.

At the end of the experiment, the absolute growth rate was calculated according to the formula $G = (Y_2 - Y_1)/t$, where Y_2 and Y_1 are the final and initial average weights of the fish per tank and t is the number of days of the experiment (Busacker et al. 1990). Growth was analyzed by fitting the data to a second-order polynomial regression (Eaton et al. 1995; Lyytikainen and Jobling 1998). Feed efficiency (grams of wet weight growth/grams of feed consumed) was determined at each temperature at the completion of the study and compared by analysis of variance (ANOVA; Ott 1993). To estimate thermal resistance, the time to 50% survival (LD50) was plotted against treatment temperature and analyzed using exponential regression (Zale 1984). The resulting regression formula was then used to determine the ultimate upper incipient lethal temperature (UUILT), the temperature survived by 50% of the population for 60 d.

In addition to determining the growth in weight, we assessed the conversion of feed to tissue components (moisture, lipids, protein, and ash) using standard proximate analysis. Body composition was measured at the start of the study from a random sample of 50 fish and at the end of the study with all fish in each tank combined. Fish were frozen for later analysis. The aggregate sample from each tank was mixed with an equivalent weight of distilled water and ground to form a homogenate sample. Tissue moisture was measured by drying a 2-g subsample for 24 h at 100°C and ash content by heating in a muffle furnace for 24 h at 600°C. Protein was measured by thermal oxidation (Leco model CN 2000) and lipids by the diethyl ether extraction method (AOAC 1990). Lipid and protein conversion efficiency (Dockray et al. 1998) was determined by dividing accumulated protein and lipids (final minus initial body composition) by the totals consumed (Table 1). Each body constituent was compared among temperature treatments by means of an ANOVA.

We also conducted a CTM test to compare the acute temperature tolerance of bull trout with that of other salmonids, following the protocol of Becker and Genoway (1979) and using the apparatus described by Lellis and Barrows (1997). In November 1998, 24 age-0 bull trout (5.9–25.0 g) were acclimated for 14 d to each of four acclimation temperatures: 8, 12, 16, and 20°C. Fish were fed daily to satiation but starved for 36 h prior to testing. On two consecutive days, testing was initiated by filling test tanks with 7.5°C spring water and heating it at a rate of 10.2°C/h. Six fish from each acclimation temperature were then placed in two replicate tanks as the test temperature reached their acclimation temperature. The temperature at which each individual lost the ability to maintain upright equilibrium was recorded and the fish was then removed. A mean CTM was calculated for each jar. Results among trial days were pooled because we found no significant differences ($P = 0.30-0.74$) in CTM values between the two days of testing. The relation between CTM and acclimation temperature was described by simple linear regression (Ott 1993).

Results

The survival of age-0 bull trout in the first temperature trial was at least 98% at 8, 10, 12, 14, 16, and 18°C. However, no fish survived test temperatures of 22, 24, 26, and 28°C after 60 d (Figure 1). Time to 100% mortality was inversely related to temperature. All fish died prior to reaching 28°C; the time to 100% mortality was 24 h at 26°C, 10 d at 24°C, and 38 d at 22°C. Bull trout survival over 60 d at 20°C was 79%, intermediate between the 98% survival at 18°C and the 0% survival at

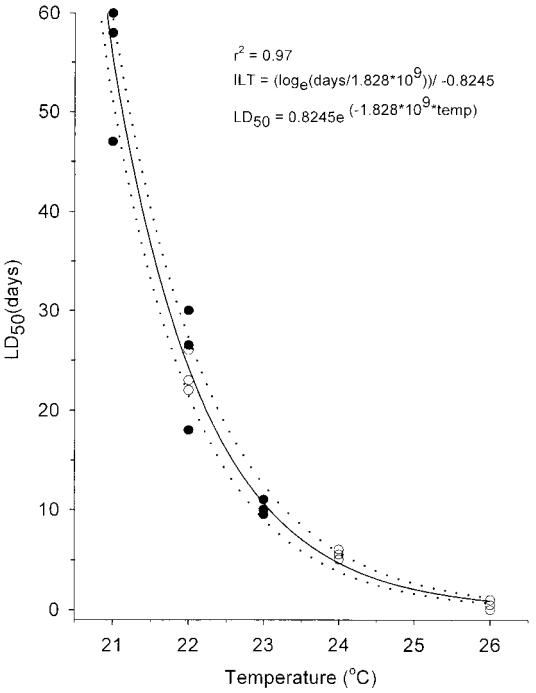

FIGURE 1.—Survival of bull trout in relation to temperature and exposure time during 60-d trials. Only results at temperatures of 21°C or higher are shown, as survival at temperatures of 8, 10, 12, 14, 16, and 18°C was at least 98%. Each circle represents the temperature for the median survival time (LD50) in an individual tank. Open circles indicate trials with age-0 fish, closed circles trials with age-1 fish; ILT is the incipient lethal temperature as a function of exposure time. Dotted lines indicate the 95% confidence interval of the regression line.

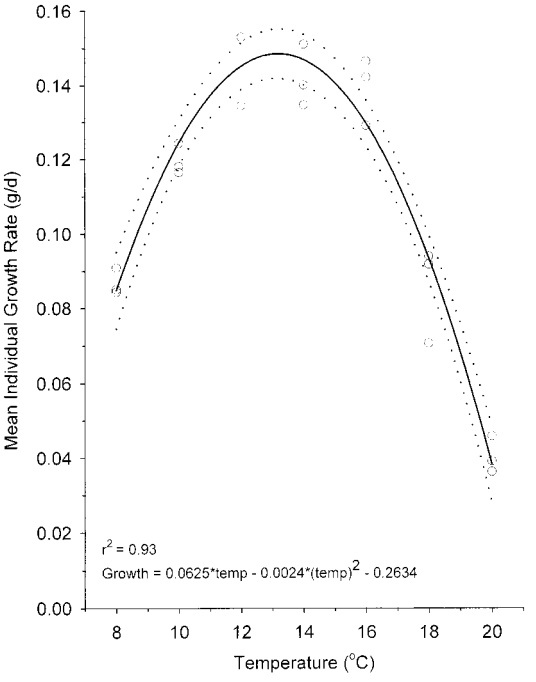

FIGURE 2.—Growth of bull trout in relation to temperature. Each circle represents the mean individual weight gain per tank. Three trials were run at each temperature. Dotted lines indicate the 95% confidence interval of the regression line.

22°C. Mortality at 20°C was first observed at 31 d and continued until the end of the study. Survival in the second trial with age-1 fish at temperatures of 20–23°C showed a similar pattern. Like the age-0 fish, no age-1 fish survived a temperature greater than 22°C for 60 d. Survival at 20°C and 21°C was 53% and 46%, respectively, after 60 d. The time to 100% mortality was 15 d at 23°C and 42 d at 22°C, similar to that for age-0 fish in the first trial. The survival of age-1 fish at 20°C was lower than that of age-0 fish (53% versus 79%), and mortality commenced on day 5, 16 d earlier. The relationship between ILT and the time to LD50 was highly significant ($r^2 = 0.97$, $P < 0.001$; Figure 1). The predicted UUILT (LD50 at 60 d) based on the exponential regression formula (Figure 1) was 20.9 ± 0.1°C (95% confidence interval [CI]).

The growth of age-0 bull trout in 60-d trials varied significantly over temperatures of 8–20°C (Figure 2). Mean individual weight gain ranged from 12.5 g at 12°C to 3.4 g at 20°C (Table 2). The peak growth estimated by regression analysis occurred at 13.2°C. The 95% CI of the peak growth temperature yielded a maximum-growth range of 10.9–15.4°C (Figure 2). The growth rate decreased sharply above and below this range, falling to 60% of the peak growth rate at 8°C and 18°C. The lowest growth was observed at 20°C (19% of peak growth rate), and bull trout behavior was notably different at that temperature. At lower temperatures, fish typically were evenly spaced throughout the tank and in contact with the bottom. At 20°C (and higher temperatures), they swam near the water surface and fed little (see below). The predicted upper and lower thermal limits for growth (intersection of the regression line and *x*-axis) were 20.7°C and 5.2°C, respectively.

Feed consumption followed a pattern similar to that of growth (Table 2). The predicted peak consumption occurred at 13.3°C, decreasing significantly at 10.3°C and 16.3°C (consumption = $0.1491T - 0.0056T^2 - 0.6417$, where T is temperature; $r^2 = 0.89$, $P < 0.001$). Consumption declined markedly at temperatures greater than 16°C.

TABLE 2.—Weight gain, feed consumption, feed efficiency, body composition, and protein and lipid conversion efficiency of bull trout during 60-d temperature trials. Values shown are means (± SE) based on three trials per temperature treatment. The starting temperature was 8°C.

Temperature (°C)	Mean weight (g/fish)		Daily feed consumption (g/fish)	Feed efficiency (g growth/g feed consumed)	Body composition (%)				Protein efficiency (g gained/g consumed)	Lipid efficiency (g gained/g consumed)
	Initial	Final			Moisture	Lipids	Protein	Ash		
Starting	1.8				78.27 (0.37)	3.50 (0.05)	15.12 (0.13)	2.04 (0.10)		
8	1.8	9.1	0.09 (<0.01)	0.50 (0.01)	74.78 (0.05)	5.97 (0.09)	15.46 (0.34)	1.63 (0.02)	0.29 (0.02)	0.37 (0.02)
10	1.8	11.8	0.13 (<0.01)	0.49 (0.01)	74.05 (0.19)	6.28 (0.27)	15.82 (0.16)	1.70 (0.06)	0.29 (0.01)	0.37 (0.04)
12	1.9	14.4	0.17 (0.02)	0.46 (0.02)	73.36 (0.16)	6.84 (0.33)	16.24 (0.13)	1.71 (0.15)	0.28 (0.03)	0.37 (0.01)
14	1.8	13.7	0.16 (<0.01)	0.47 (0.01)	73.58 (0.23)	7.00 (0.17)	16.10 (0.10)	1.78 (0.05)	0.29 (0.02)	0.40 (0.04)
16	1.9	13.6	0.16 (0.01)	0.46 (0.01)	73.37 (0.17)	6.87 (0.24)	16.01 (0.10)	1.83 (0.11)	0.28 (0.01)	0.38 (0.01)
18	1.8	9.0	0.09 (<0.01)	0.45 (0.01)	73.64 (0.25)	6.46 (0.25)	16.48 (0.13)	1.90 (0.05)	0.28 (0.01)	0.36 (0.04)
20	1.8	5.1	0.06 (0.01)	0.26 (0.05)	75.81 (0.36)	5.48 (0.25)	15.36 (0.15)	1.97 (0.06)	0.16 (0.04)	0.22 (0.03)

At 18°C, it was 50% less than peak consumption and at 20°C 66% less. Fish held at temperatures of 22°C or higher did not feed. Feed efficiency (grams of growth/grams of feed consumed) was similar over the range of 8–18°C but declined significantly ($P < 0.001$) at 20°C (Table 2).

In contrast to growth and feed consumption, the body protein, lipid, moisture, and ash composition of juvenile bull trout varied little at temperatures of 8–18°C (Table 2). Fish in all treatments gained protein and lipids and lost moisture and ash. However, at 20°C, the percentage gain of protein and lipids and protein and lipid conversion efficiency declined significantly ($P < 0.001$) from those at lower temperatures.

The mean CTM values for bull trout increased with acclimation temperature, ranging from 26.4°C at 8°C to 28.9°C at 20°C (Table 3). The CTM was linearly related to acclimation temperature (T) by the formula $CTM = 24.62 + 0.2175T$ ($r = 0.99$, $P = 0.008$).

Discussion

Species Comparisons

Our long-term survival experiments over a wide range of temperatures (8–28°C) corroborate field observations suggesting that bull trout have among the lowest upper thermal limits of North American salmonids. The temperature-survival curve (Figure 1) indicates that bull trout can survive temperatures up to 20°C for up to 60 d but that survival decreases rapidly with exposure to even small increases in temperature above this level. As in previous studies comparing age-groups within the same species (e.g., Benfey et al. 1997), we found that age-0 bull trout had slightly greater temperature tolerance than yearlings.

TABLE 3.—Critical thermal maximums (CTMs) of age-0 bull trout at various acclimation temperatures. Means are based on four replicates per acclimation temperature tested.

Acclimation temperature (°C)	Critical thermal maximum (°C)	
	Mean	Range
8	26.4	26.1–26.6
12	27.1	26.3–27.6
16	28.3	28.2–28.5
20	28.9	28.7–29.1

The calculated UUILT for bull trout of 20.9°C at 60 d was about 1–5°C lower than those reported (Table 4) for brook trout, rainbow trout, brown trout, chinook salmon, sockeye salmon, coho salmon, and Arctic grayling. The bull trout UUILT in this study was most similar to that of Arctic char (Baroudy and Elliott 1994). Even relatively small differences in upper lethal temperature can reflect substantial differences in thermal tolerance and performance. For example, a 2°C difference in UUILTs between Dolly Varden and whitespotted char from Japan correlates with marked differences between the two species in growth optima (Takami et al. 1997), in regional distribution as a function of available thermal habitat (Fausch et al. 1994), and in predicted response to potential global warming (Nakano et al. 1996).

The longer test period (60 d) and different acclimation procedure that we used in our study with the ACE method could partially explain the lower UUILT we observed for bull trout compared with the values reported for many other salmonids. However, the predicted UUILT at 7 d from our temperature-survival regression (23.5°C; Figure 1) was still 1–2.5°C lower than the 7-d UUILT determined for most salmonids tested using the ILT method (Table 4). In addition, we believe that the

TABLE 4.—Representative summary of ultimate upper incipient lethal temperatures (UUILTs), critical thermal maximums (CTMs), and maximum-growth temperatures for juvenile salmonids. The UUILT values marked with asterisks were interpolated from temperature–survival graphs or individual UILT values; the others were determined from 7-d test periods unless indicated otherwise.

Species	UUILT (°C)	CTM (°C)	Acclimation temperature (°C)	Maximum-growth temperature (°C)	Reference
		26.4–28.9	8–20		
Bull trout	20.9 (60 d)			13.2	This study
	23.5 (7 d)	24.8–26.2	5–20		
Arctic char	20.8–22.1				Baroudy and Elliott 1994
Salvelinus alpinus				13.8	Lyytikainen and Jobling 1998
				15.1	Larsson and Berglund 1998
Arctic grayling	25*		20		Lohr et al. 1996
Thymallus arcticus		26.4–29.3	8–20		Lohr et al. 1996
Dolly Varden	24.5*				Takami et al. 1997
Salvelinus malma					
Whitespotted char	26.5*				Takami et al. 1997
Salvelinus leucomaenis					
Brook trout	24.5				McCormick et al. 1972
Salvelinus fontinalis		28.3–30.8	8–20		Selong et al., unpublished data
		29	10		DeStaso and Rahel 1994
				14.4–16	Dwyer et al. 1983
Rainbow trout	25.6		16		Hokanson et al. 1977
Oncorhynchus mykiss	26.2		24.5		Kaya 1978
		28.0–29.8	10–20		Currie et al. 1998
				17.2	Hokanson et al. 1977
Cutthroat trout		28	10		DeStaso and Rahel 1994
Oncorhynchus clarki	25*				Dickerson and Vinyard 1999
Brown trout	24.7				Elliott 1981
Salmo trutta		29.9	20		Elliott and Elliott 1995
		28.9–29.8	10–20		Lee and Rinne 1980
				13.9	Elliott and Hurley 1999
Lake trout				10–12	O'Connor et al. 1981
Salvelinus namaycush					Brett 1952
Sockeye salmon	24.5*				Brett et al. 1969
Oncorhynchus nerka				15	Brett 1952
Chinook salmon	25.1*				Brett et al. 1982
Oncorhynchus tshawytscha				18.9–20.5	Brett 1952
Coho salmon	23.7*			15	Edsall et al. 1999
Oncorhynchus kisutch		25.3–28.7	5–15		Becker and Genoway 1979

UUILT for bull trout would have been lower than we observed had we employed the ILT method because of the added thermal stress of shifting fish directly from acclimation temperature to test temperature. Moreover, the delayed mortality of bull trout in our study, which began up to 31 d after initial exposure to test temperatures, suggests that a 7-d UUILT may not accurately reflect the temperature at which 50% of the population can survive indefinitely.

The CTM values for bull trout also indicate less ability to tolerate thermal shock compared with other salmonids. Although the heating rate we used (10.2°C/h) could have allowed some upward acclimation and thus an elevated CTM (Becker and Genoway 1979; Benfey et al. 1997), our CTM for bull trout was consistently lower than that reported for most other salmonids (Table 4). Fish acclimated at 8, 12, 16, and 20°C had values of 26.4, 27.1, 28.3, and 28.9°C, respectively, whereas brook trout CTMs were 2°C higher at the same acclimation temperatures and heating rates (Selong et al., unpublished data; Table 4). Rainbow trout CTMs with acclimation temperatures of 10, 15, and 20°C also were 0.5–1.6°C higher than bull trout CTMs (Table 4; Currie et al. 1998). Salmonid CTM values appear clustered into two groups: a ''coldwater'' group comprising bull trout, Arctic char, and Arctic grayling, and a higher-CTM group comprising brown, rainbow, and brook trout (Table 4). As with upper incipient lethal temperatures, differences in CTM may translate to significant differences in species distribution and behavioral dominance. A 1°C difference in CTM between brook trout and cutthroat trout (Table 4) correlated with greater competitive ability by the more ther-

mally tolerant brook trout at warmer temperatures (DeStaso and Rahel 1994), a possible reason why cutthroat trout, like bull trout, are now confined to cold, high-elevation streams. The even wider gap in CTM values between bull trout and both brook and rainbow trout suggests that such dominance shifts with temperature may be even more pronounced among these species (e.g., Saffel and Scarnecchia 1995; Haas 2001).

The growth rate of bull trout fed to satiation was maximized at 13.2°C. This temperature is in the lower portion of the maximum-growth range of most other salmonids at satiation feeding and is closest to the temperature optimum of Arctic char (Table 4). Bull trout may be disadvantaged in their competition with other salmonids at temperatures that are nearer to the maximum-growth temperatures of those species. For example, rainbow trout are the dominant salmonid in British Columbia streams where maximum temperatures are greater than 14°C, whereas bull trout are dominant where maximum temperatures are less than 13°C (Haas, in press). The predicted upper growth limit for bull trout in our study was 20.7°C, close to that of Arctic char (21.6°C; Thyrel et al. 1999) and lake trout (21.5°C; O'Connor et al. 1981) and about 3°C lower than that reported for sockeye (Brett et al. 1969) and chinook (Brett et al. 1982) salmon and rainbow trout (Hokanson et al. 1977).

Ecological Implications

The upper range of maximum-growth temperatures likely represents the upper limit of suitable habitat for salmonids (McCullough 1999). Christie and Regier (1988) considered the ''fundamental thermal niche'' for fishes as ''−3 and +1°C'' around the optimal growth temperature. For bull trout, the fundamental thermal niche would be 10.2–14.2°C, which corresponds well to the range of maximum-growth temperatures (10.9–15.4°C) that we observed in our study. Field data support the view that temperatures near the growth optimum are near the upper limits for bull trout occurrence. Sharp declines in bull trout abundance in northern Idaho streams were associated with maximum summer temperatures greater than 13.9°C (Saffel and Scarnecchia 1995). An analysis of bull trout occurrence and temperature across 581 sites in the Pacific Northwest revealed that this species is most likely to occur where summer maximum temperatures are less than 13–14°C and summer mean daily temperatures are 8–10°C (Rieman and Chandler 1999). In British Columbia, bull trout abundance was inversely correlated with maximum temperature, with few fish found above 16°C and the density highest where the maximum temperature was less than 13°C (Haas 2001).

Bull trout have been reported in waters above 20°C (Saffel and Scarnecchia 1995; Adams and Bjornn 1997; Rieman and Chandler 1999; Haas 2001) and survived and grew for up to 60 d at temperatures as high as 20°C in our trials. Temperatures above 15–16°C are unlikely to be suitable for long-term survival, however. Reduced growth and feed consumption, the first in a series of sublethal responses indicative of thermal stress (Elliott 1981), were first detected at 15.9°C and 16.3°C, respectively. Because metabolic costs rise exponentially with temperature, even small decreases in feeding and growth can lead to reduced competitive ability and disease tolerance (Wedemeyer and McLeay 1981). At temperatures greater than 18°C, the bull trout in our study had significantly reduced food consumption, growth, and feed conversion efficiency and exhibited outward signs of stress, suggesting that extended exposure to elevated temperatures would rapidly deplete their energy reserves. The survival, growth, and feed efficiency responses to elevated temperatures are likely to be more severe in nature, where food limitation may be a common occurrence in salmonid waters in summer (Ensign and Strange 1990; Welch et al. 1998). A small chronic increase in temperature coupled with reduced food availability causes a marked downward shift in growth rates (Brett et al. 1969; Elliott 1981; Elliott and Hurley 1999). For example, the optimal temperature for growth for sockeye salmon shifts from 15°C to 10°C when food availability is reduced by 50% of the satiation level, and energy conversion is less efficient (Brett et al. 1969). Such effects were masked in our study because test fish were fed a nutrient-rich diet to satiation (Wurtsbaugh and Davis 1977; Dockray et al. 1998). Further study of the relationship between ration level and temperature optima and tolerance is needed because bull trout are found in habitats that vary widely in productivity, ranging from unproductive headwater streams to prey-rich lakes.

Although our study was concerned with the growth and survival of bull trout at summer maximum temperatures, assessment of this species' performance at low temperatures is also needed. Our predicted lower temperature threshold for bull trout growth of 5.2°C is substantially higher than the nearly 0°C threshold observed in Arctic char (Brannas and Wiklund 1992) and brown trout (Koskela et al. 1997), suggesting that our growth curve

is inaccurate below the tested level of 8°C. Because salmonids vary in their performance at temperatures less than 10°C (Brannas and Wiklund 1992), the duration of the lower temperature may be as important in setting the distributional limits and regulating the outcomes of interactions among bull trout and other species as the summer maximum temperature is.

Laboratory Protocols for Thermal Tolerance Studies

Though laboratory studies of thermal tolerance have well-recognized limitations, strictly regulated experiments are advantageous in that the many complex factors affecting growth and survival can be controlled, allowing the effect of temperature to be examined directly (McCullough 1999). Use of a new laboratory procedure could be viewed as problematic because having a standard laboratory approach for establishing thermal criteria is desirable from a regulatory standpoint (e.g., Brungs and Jones 1977). However, we believe that the ACE method offers several distinct improvements over traditional approaches for developing thermal criteria while producing the desired result of establishing the lethal temperature level for a species.

By more closely mimicking the thermal conditions fish experience in nature, we believe the ACE method increases the applicability of laboratory results. Unlike the CTM and ILT methods, which employ rapid or instantaneous temperature shifts, the ACE method allows test organisms to acclimate to environmentally realistic temperature changes. The resulting temperature-survival regression equation (Figure 1) also can be used to predict lethal temperatures at different exposure and temperature combinations, thereby facilitating assessment of cumulative temperature effects (Fry et al. 1946; Zale 1984). Furthermore, our 60-d trials allowed sufficient time for delayed mortality and sublethal differences in growth rate, feed consumption, and feed conversion efficiency to become apparent, differences that are unlikely to manifest themselves with traditional, 7-d trials. Measurement of growth over a wide temperature range also allowed calculation of a temperature−growth curve using polynomial regression, providing an objective, statistically precise estimate of the peak-growth temperature to be used in temperature standard development and species comparisons. Coupled with innovative field investigations of temperature effects at the stream and regional scales (e.g., Fausch et al. 1994; Eaton et al. 1995; Rieman and Chandler 1999; Haas 2001), ACE laboratory studies offer a powerful tool for better defining temperature criteria and assessing fish responses to thermal change.

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