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COMPARATIVE TOLERANCE OF FOUR STOCKS OF CUTTHROAT TROUT TO EXTREMES IN TEMPERATURE, SALINITY, AND HYPOXIA

Eric J. Wagner^{1,2}, Ronney E. Arndt¹, and Mark Brough¹

ABSTRACT.—Four stocks of cutthroat trout (*Oncorhynchus clarki*) were exposed to high temperature, high salinity, and low dissolved oxygen to determine inherent differences. The fish tested included 2 stocks of Bonneville cutthroat trout (*O. c. utah*), a lacustrine stock derived from Bear Lake and a fluvial-origin stock from southern Utah (Manning Meadow Reservoir). The other 2 stocks tested were from Electric Lake (largely Yellowstone cutthroat trout, *O. c. bowieri*) and Jackson Hole, Wyoming (fine-spotted Snake River cutthroat trout, *O. c.* subsp.). Temperature tests were either critical thermal maximum (CTM) or 96-hour trials using juveniles acclimated between 12.5°C and 18.0°C. Two CTM end points were temperature at first loss of equilibrium (CTM_{eq}) and onset of spasms (CTM_s). There were no significant differences in CTM_{eq} among test fish acclimated to 18.0°C, but CTM_s was significantly higher for Bear Lake Bonneville (30.0°C) than for Snake River (29.6°C) or southern Bonneville (29.7°C) stocks. With fish acclimated at 13.0°C, there were no significant differences among the stocks in CTM_{eq} or CTM_s. Differences among stocks varied significantly among nine 96-hour tests. Overall, it appeared that the southern Bonneville stock had slightly better survival at warmer temperatures than other stocks. In 24-hour survival tests at high salinities, the Snake River stock had the lowest tolerance, with significant mortality occurring at 18‰ (29.5 mS · cm⁻¹ conductivity). The southern Bonneville stock had the highest tolerance, with no mortality until 22‰ (38 mS · cm⁻¹). Bear Lake Bonneville and Electric Lake stocks had 60% and 30% mortality, respectively, at 21‰ (36 mS · cm⁻¹). Hypoxia tolerance measured by resistance time, 24-hour mortality, or probit analysis (LEC₅₀) did not differ among stocks. The 24-hour LEC₅₀ was 2.34 mg O₂ · L⁻¹ for all stocks combined.

Key words: temperature, oxygen, conductivity, critical thermal maximum, Bonneville cutthroat trout, Yellowstone cutthroat trout, Snake River cutthroat trout.

Cutthroat trout (*Oncorhynchus clarki*) have been divided into 4 major and 10 minor subspecies by Behnke (1988), based on phylogenetic divergence. Behnke (1992) has described phenotypic differences among these subspecies as well as their geographic distribution, status, life history, and ecology.

Differences among subspecies are of importance to fisheries managers and anglers. For example, Lahontan cutthroat trout (*O. clarki henshawi*) may reach a maximum size twice that of other subspecies (Behnke 1992). In the rainbow trout (*O. mykiss*) group, redband trout (*O. m.* subsp.) display an ability to adapt to high temperatures, feeding at temperatures lethal to other subspecies (Behnke 1992). Researchers have also noted differences in feeding habits, susceptibility to various methods of angling, return to the creel, and condition among cutthroat trout stocks (Trojnar and Behnke 1974, Nielson and Lentsch 1988, Dwyer 1990, Hepworth et al. 1999).

These genetically based differences among subspecies and stocks are indicators that cut-

throat trout have undergone some degree of natural selection, creating adaptations to particular environments. Genetic differences, e.g., as measured by mitochondrial DNA or enzyme proteins, among subspecies of cutthroat trout have been noted and used to differentiate between them (Loudenslager and Gall 1980, Leary et al. 1987, Shiozawa and Evans 1994).

Several stocks of cutthroat trout are available from certified pathogen-free sources for fisheries management in Utah. These include Bear Lake Bonneville (BL), Bear Lake, Utah-Idaho; southern Bonneville (BV) from Manning Meadow Reservoir, Monroe Mountains, Utah; and Electric Lake (EL), Emery County, Utah, stocks. The EL stock is primarily Yellowstone cutthroat trout (*O. c. bowieri*), with potential introgression by rainbow trout and Bear Lake Bonneville cutthroat trout while in Strawberry Reservoir before transfer to Electric Lake (Martin et al. 1985). The BL and BV are recognized as *O. clarki utah* (Behnke 1992). The history of these broodstocks was reviewed by Wagner (1996) and Hepworth et al. (1997).

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The Snake River stock (*O. c.* subsp.; SN; Behnke 1992), originating from wild stock in Wyoming via Jackson National Fish Hatchery, was also included in this study for comparison.

Water quality is a critical aspect of the fish's environment, but how these subspecies differ in water quality tolerances has not been evaluated. Water quality in Utah is as varied as the landscape, ranging from nearly distilled water in granite watersheds of the Uinta Mountains to over 150,000 mg · L⁻¹ salinity in Great Salt Lake (Gliwicz et al. 1995). Some reservoirs experience low dissolved oxygen during winter ice cover and summer stratification, and others experience high temperature during summer months and irrigation drawdown. Summertime stream temperatures can exceed lethal limits. This study was conducted to determine inherent differences among available cutthroat trout stocks in the ability to withstand water quality extremes, possibly making some stocks more suitable for stocking in harsher environments.

METHODS

We reared 4 cutthroat trout stocks from wild broodstocks from the sources mentioned above from eggs at the Fisheries Experiment Station, Logan, Utah. Stocks were tested for survival differences at extremes of temperature, dissolved oxygen (DO), and salinity. We divided test fish into 2 groups, one acclimated to 13.6 ± 0.6°C and the other to 18.0 ± 0.5°C. Fish acclimated to 13.6°C had been reared at that temperature since hatching. Fish at 18.0°C were transferred to that temperature on 10 September 1996 and remained there for at least 30 (CTM tests) to 90 days (96-hour tests) prior to tests. Additional 96-hour temperature tests were conducted in January 2000 with the 4 stocks acclimated to either 12.5°C or 16.0°C. The temperature difference from previous trials was the result of variation among years in the well water. Hatchery well water had a total hardness as CaCO₃ of 222 mg · L⁻¹, pH of 7.5 to 7.6, and total alkalinity of 222 mg · L⁻¹.

Critical Thermal Maximum

Fish were selected at random and tested individually; 10 fish were sampled from each stock and acclimation temperature. We placed each fish in a 4.0-L Erlenmeyer flask containing 3.0 L of 13°C water. Temperature was

increased at a constant rate of 0.2°C · min⁻¹ on a laboratory hot plate, similar to the rate recommended by Becker and Genoway (1979). Temperature was recorded at 10-minute intervals from a digital probe suspended off the bottom, and change in temperature was calculated for each interval. Time and temperature were recorded at the first loss of equilibrium and at the onset of spasms, whereupon the test was concluded. DO was recorded at the end of the test. We conducted these tests between 25 September and 31 October 1996 using fish of 0.7–2.9 g average weight.

96-hour Temperature Tolerance Tests

Eight 96-hour mortality tests (3 February to 7 April 1997) were used to compare the tolerance of the 4 cutthroat trout stocks to high temperature. All tests were conducted in insulated 800-L indoor circular tanks. Airstones in each tank insured that low DO did not compromise survival.

For each 1997 test, we transferred fish directly from acclimation temperatures (13.6 ± 0.6°C or 18.0 ± 0.5°C) into test tanks. We used 4 cylindrical cages (56-cm diameter) per tank, placing 10 fish of one stock per cage. This insured that all stocks within a tank were exposed to the same water temperature. Test temperatures ranged from 23.0°C to 24.5°C among the 8 tests. Two or 3 tanks per temperature treatment provided the replication for each test.

Three additional 96-hour tests were conducted in January 2000, one with the 4 stocks acclimated to 12.5°C and the other two with fish acclimated to 16.0°C for at least 30 days. The study fish were freeze-branded 1 or 2 weeks prior to testing to identify the stocks. For each test, 20 fish from each stock were put into each of 5 circular tanks, 3 of which had recirculating heaters to control temperature and 2 that served as controls.

Water exchange of half volume was performed once or more (first 2 tests at 18.0°C acclimation temperature), halfway through each test using water of the appropriate temperature. DO was monitored daily with an oxygen meter calibrated with replicate Winkler titrations (APHA et al. 1989) and did not drop below 5.2 mg · L⁻¹. NH₃-N was determined by Nesslerization (APHA et al. 1989) at the end of each test, and levels did not exceed

0.019 mg · L⁻¹. We weighed each fish after it had died or at the end of the test. Mortality was recorded after 96 hours. Mean weights during the temperature tests were as follows: 4.9–23.7 g, BL; 4.0–23.6 g, BV; 2.4–19.8 g, SN; and 4.5–17.6 g, EL.

Salinity Tolerance

Seven salinities were tested in 2 separate 24-hour tests. Salinities of 0.4 (control), 29.6, 32.3, and 33.5 mS · cm⁻¹ (0, 18.0, 19.0, and 20.0‰, respectively) were evaluated in test 1; and salinities of 0, 36.1, 38.2, and 41.6 mS · cm⁻¹ (0, 21.0, 22.0, 23.5‰) were evaluated in test 2. We used 2 replicate 800-L circular tanks per treatment, stocking 10 fish per stock into cylindrical cages in each tank. Salinities were adjusted by adding noniodized rock salt to the water and dissolving it prior to testing. Water between replicate tanks was exchanged prior to adding fish to minimize salinity differences between replicates. Salinity was measured by a specific conductivity probe (Hydro-lab, Austin, TX). Other variables measured concurrently included temperature (14.4 ± 0.4°C) and dissolved oxygen (5.7–7.3 mg · L⁻¹, maintained with airstones bubbling compressed air). Un-ionized ammonia nitrogen at the end of the test did not exceed 0.008 mg · L⁻¹. Mortality was recorded after 24 hours. Total body weights of mortalities were recorded and compared to live weights separately for each stock using a *t* test for paired samples.

Low Dissolved Oxygen Tolerance

Between 15 April and 15 May 1997, we conducted 8 tests using fish acclimated to 13°C. By adding nitrogen gas to the water in a flow-through system similar to that described by Cochran and Babcock (1974), we manipulated dissolved oxygen. Two 800-L circular tanks were used for each test, and each received flows of 11 ± 1 L · min⁻¹. Un-ionized ammonia determined by Nesslerization at the end of 2 tests did not exceed 0.001 mg · L⁻¹. Fish were allowed access to the surface to gulp for air. Loss of equilibrium was the end point (resistance time) for each fish in all tests, and most recovered when returned to normoxic water. Weight of each fish was measured after loss of equilibrium to evaluate possible size

effects on resistance time. The temperature was 14.7 ± 0.8°C for each test.

We performed 2 tests in which dissolved oxygen (DO) was gradually decreased over 6–7 hours; resistance time (time at which equilibrium was lost) and DO at the time of loss of equilibrium were noted. Ten fish from each stock were maintained in plastic-mesh cages for each test, 4 cages per 800-L tank. Mean weights for these tests were BL, 21.9 g; BV, 15.7 g; SN, 10.0 g; and EL, 22.1 g. Test-1 fish were acclimated to the cages for 40 hours and not fed for 96 hours prior to the test. Test-2 fish were fed until test time and given no acclimation time in the cages. Of interest was the comparative response of the 4 stocks to hypoxia under the varied conditions of the 2 tests, avoiding possible biases due to handling stress and oxygen demand for digestion.

Remaining tests were 24-hour challenges at a given DO; average levels ranged from 1.85 to 3.34 mg · L⁻¹ among the 6 tests. The 4 cut-throat trout stocks were freeze-branded one week prior to tests to identify stocks upon removal from a tank. Fish were transferred from outdoor raceways in which DO ranged from 6.6 to 7.8 mg · L⁻¹. For each test we put 10 fish from each stock into each of 2 circular tanks holding 400 L of water. During each test we monitored DO and removed the fish upon loss of equilibrium, weighed them in water, and noted the time. Mean weights during these tests were 25.2–30.7 g, BL; 16.1–21.6 g, BV; 8.8–11.6 g, SN; and 20.2–32.3 g, EL.

Statistical Analysis

LEC₅₀, i.e., the lower limit of dissolved oxygen causing loss of equilibrium within 24 hours, or LT₅₀, the maximum temperature in 96-hour tests that killed half the fish, was calculated for each stock by probit analysis (Newman 1994, SPSS 1994). For DO data we used natural log transformation for probit analysis; we also conducted analysis with stocks pooled. Probit analysis for each acclimation temperature was not possible due to insufficient data, and so data were pooled. Percent mortality was arcsine transformed prior to 1-way analysis of variance (ANOVA) within each test. Normality tests (Kolmogorov-Smirnov) were conducted for each continuous variable, and the data were subsequently analyzed by 1-way ANOVA if the data were normally distributed and, if not, by the Kruskal-Wallis 1-way ANOVA (SPSS

1993). Duncan's test was used for mean comparisons. Using 1-way ANOVA, we analyzed separately transformed mortality data from the salinity trials for each salt concentration. For DO data analysis, median resistance time (average elapsed time of 5th and 6th fish) and average DO at that time were used to compare stocks in 1-way ANOVA. Simple least-squares regression was used to test the strength of the relationship between total body weight and DO resistance time. To assess total body weight effects on mortality in the temperature tests, we compared average live and dead weights by Wilcoxon matched-pairs and signed-ranks tests for each temperature test (stocks pooled), stock (tests pooled), and for combined data. Differences were considered significant at $P \leq 0.05$ for all statistical tests.

RESULTS

Critical Thermal Maximum Tests

Mean CTM_{eq} and CTM_s were significantly higher for fish acclimated at 18.0°C (29.5°C and 29.7°C, respectively) than those acclimated at 13.6°C (28.1°C, 28.6°C). There were no significant differences in CTM_{eq} among stocks acclimated to 18.0°C, but CTM_s was significantly higher ($P = 0.03$) for BL (30.0) than for SN (29.6) or BV (29.7°C; Table 1). For tests with fish acclimated at 13.6°C, there were no significant differences among the 4 stocks in CTM_{eq} or CTM_s .

96-hour Temperature Tolerance Tests

In 96-hour tests, differences among stocks varied among the 11 tests (Table 2). For fish acclimated to 13.6°C and challenged at 24.0°C, mortality for BL and SN was significantly higher (100%) than for EL (73%) and BV (13%). At 23.0°C and 23.5°C, results were much different; BV had significantly higher mortality than the other stocks or did not significantly differ (Table 2). When cold-acclimated fish were challenged at 24.0°C with a larger sample size per tank, BV had the lowest mortality (3.3%) and SN the highest (86.7%; Table 2).

Five 96-hour tests were conducted with fish acclimated to 18.0°C. At 23.2°C, only the EL experienced mortality (3%). At 23.7°C, BV had significantly lower mortality (21%) than SN (95%) or BL (90%). Mortality at 23.9°C

was significantly higher for SN (75%) than the other 3 stocks (10–15%). After raising the test temperature half a degree, mortality reached 100% in SN and BL groups, but was less for EL and BV (75% and 65%, respectively). Probably due to having only 2 replicates, these stock differences were not significant ($P = 0.21$, Kruskal-Wallis test). A repeat of this test resulted in significantly lower mortality for BV (27%) than for SN (87%). Repetition of the tests with another year-class of fish acclimated to 16.0°C provided similar results; BV had significantly lower mortality (1.7%) than EL (30.0%) or SN (68.3%) when challenged at 24.0°C (Table 2). Probit analysis resulted in LT_{50} values of 23.5°C for SN, 23.9°C for BL, 24.0°C for EL, and 24.3°C for BV (Fig. 1). Overall, BV had slightly better survival at high temperatures than the other stocks, but the difference was small.

Mean weight of mortalities was not significantly different from survivor weight for each stock when all tests were pooled for analysis. Analysis of pooled data combining tests and stocks (49 pairs) similarly resulted in no significant difference.

Salinity Tolerance Tests

There were significant differences among stocks in 24-hour survival at high salinities (Table 3). SN had the lowest salinity tolerance, with significant mortality occurring at 29.6 mS · cm⁻¹ conductivity (18‰); BV had the highest tolerance (<5% mortality up to 38 mS · cm⁻¹ [22‰]). BL and EL were intermediate, with 60% or 30% mortality, respectively, at 36 mS · cm⁻¹ (21‰). Size appeared to have little influence on mortality; for only BV, the mean weight of dead fish was smaller than that of survivors (1.8 versus 2.4 g, respectively, $P = 0.032$, t test for paired samples).

Dissolved Oxygen Tolerance Tests

Using the method of gradually decreasing DO over time, resistance times (elapsed time until loss of equilibrium) among the 4 stocks did not significantly differ for either of the 2 trials (Table 4). Similarly, mean DO at the median resistance time did not differ significantly among stocks. A t test for differences in DO between tests (stocks pooled) was not significant, indicating that acclimation to tanks or time off feed had little impact on the lower

TABLE 1. Mean ($n = 10, \pm s$) critical thermal maximum values ($^{\circ}\text{C}$) for 4 cutthroat trout stocks (BL, Bear Lake Bonneville; BV, southern Bonneville from Manning Meadow Reservoir; SN, fine-spotted Snake River; and EL, Electric Lake) acclimated to either 13.6 $^{\circ}\text{C}$ or 18.0 $^{\circ}\text{C}$. Critical thermal maximum was at first loss of equilibrium (CTM_{eq}) and at the onset of spasms (CTM_{s}). Means not significantly different (1-way ANOVA, $P \geq 0.05$) among stocks within a column are followed by a common letter or no letter.

Stock	Acclimation temperature			
	13.6 $^{\circ}\text{C}$		18.0 $^{\circ}\text{C}$	
	CTM_{eq}	CTM_{s}	CTM_{eq}	CTM_{s}
BL	27.9 \pm 0.68	28.6 \pm 0.55	29.7 \pm 0.20	30.0 \pm 0.16 a
BV	28.3 \pm 0.41	28.7 \pm 0.34	29.5 \pm 0.39	29.7 \pm 0.32 b
SN	28.2 \pm 0.31	28.6 \pm 0.32	29.4 \pm 0.41	29.6 \pm 0.39 b
EL	28.1 \pm 0.23	28.5 \pm 0.25	29.6 \pm 0.24	29.8 \pm 0.19 ab
Average	28.1 \pm 0.45	28.6 \pm 0.38	29.5 \pm 0.34	29.7 \pm 0.31

TABLE 2. Summary of mean percent mortality ($n = 2$ or 3 tanks within a test) recorded for 4 cutthroat trout stocks exposed to high temperatures in a series of tests. Stock abbreviations: BL = Bear Lake, BV = Bonneville, SN = Snake River fine-spotted, and EL = Electric Lake. A common subscript letter or no letter among means within a test indicates no significant difference (1-way ANOVA, Kruskal-Wallis, $P \geq 0.05$).

Acclimation temperature	Test temperature ($^{\circ}\text{C}$)	Number of fish per stock per tank	Percent mortality			
			BL	BV	SN	EL
12.5 \pm 0.1 $^{\circ}\text{C}$						
	24.0 \pm 0.5	20	41.7 ab	3.3 a	86.7 b	21.7 a
13.6 \pm 0.6 $^{\circ}\text{C}$						
	23.0 \pm 0.9	10	20.0 a	100.0 b	13.3 a	20.0 a
	23.5 \pm 0.5	10	36.7	33.3	3.3	23.3
	24.0 \pm 0.5	10	100.0 a	13.3 c	100.0 a	73.3 b
16.0 \pm 0.2 $^{\circ}\text{C}$						
	23.5 \pm 0.5	20	0.0	0.0	0.0	6.7
	24.0 \pm 0.3	20	15.0 ab	1.7 a	30.0 b	68.3 c
18.0 \pm 0.4 $^{\circ}\text{C}$						
	23.2 \pm 0.8	10	0.0	0.0	0.0	3.3
	23.7 \pm 1.3	10	90.0 a	21.2 b	95.0 a	51.4 ab
	23.9 \pm 0.7	10	15.0 a	15.0 a	75.0 b	10.0 a
	24.2 \pm 0.5	10	73.3 ab	27.0 b	86.7 a	85.2 b
	24.5 \pm 0.6	10	100.0	65.0	100.0	75.0

lethal limit of DO. Mortality began when DO dropped below 1.9 $\text{mg} \cdot \text{L}^{-1}$ (test 1) or 1.7 $\text{mg} \cdot \text{L}^{-1}$ (test 2). The last fish survived until DO dropped to 1.2 to 1.3 $\text{mg} \cdot \text{L}^{-1}$.

In the 24-hour tests, mortality began when DO dropped below 2.6 $\text{mg} \cdot \text{L}^{-1}$. Least-squares regression for each of these tests indicated no significant relationship or a poor relationship (e.g., $r^2 = 0.254$, DO test 8) between individual total body weight and the resistance time to low DO levels for any of the 4 stocks. There were no significant differences in mortality among stocks except for 1 test in which SN experienced higher mortality (30%) than the other stocks ($\leq 5\%$; Table 5). Resistance time

was not significantly different among stocks in most tests, except 1 trial (DO = 2.18 $\text{mg} \cdot \text{L}^{-1}$) in which BL survived significantly longer than the other stocks (Table 4). Probit analysis of mortality in the 24-hour tests indicated little difference in hypoxia tolerance among stocks (Fig. 1). When stocks were pooled, the LEC_{50} of DO was 2.34 $\text{mg} \cdot \text{L}^{-1}$ (27% of saturation or $\text{PO}_2 = 35.3$ mm Hg).

DISCUSSION

Inherent differences in thermal tolerance among the 4 stocks of cutthroat trout were not evident based upon critical thermal maximum

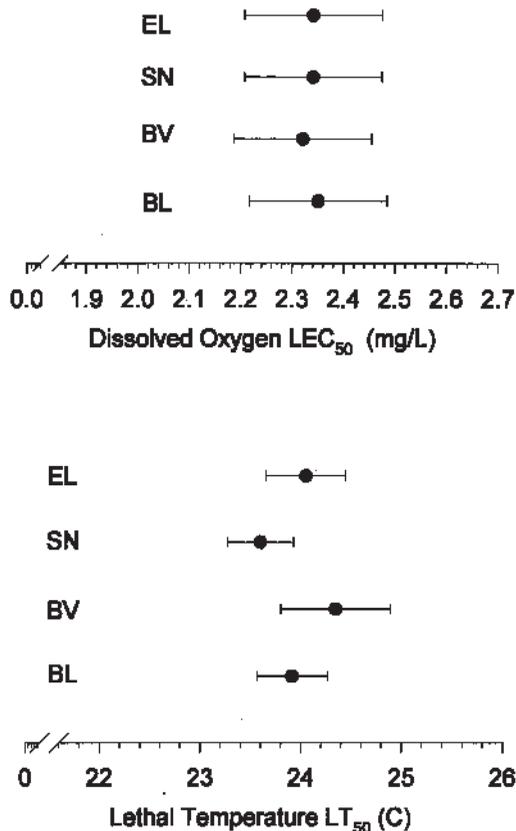


Fig. 1. Lethal temperature ($LT_{50} \pm 95\%$ confidence interval) and dissolved oxygen concentration inducing loss of equilibrium in 50% ($LEC_{50} \pm 95\%$ confidence interval) of each of 4 cutthroat trout stocks (Bear Lake Bonneville, BL; southern Bonneville, BV; Snake River fine-spotted, SN; and Electric Lake, EL).

(CTM) tests. CTM tests conducted by Lee and Rinne (1980) indicated little difference between the native Gila (*Oncorhynchus gilae*) and Apache trout (*O. apache*) and introduced trout species such as rainbow, brown (*Salmo trutta*), and brook trout (*Salvelinus fontinalis*). Similar to results of this study, Lee and Rinne (1980) and Lohr et al. (1996) also noted an increase in CTM at higher acclimation temperatures. CTM values for cutthroat trout in this study (28.1–29.8°C) were similar to those reported for other salmonids at similar acclimation temperatures (Lee and Rinne 1980, Lohr et al. 1996).

Contrary to CTM tests, 96-hour tests generally indicated that BV had a greater thermal tolerance than the other stocks. Given the natural habitats found in the southern Bonneville

TABLE 3. Comparison of percent mortality of 4 cutthroat trout stocks after 24-hour exposure to various salinities (presented as specific conductivity and parts per thousand [in parentheses]). Percent mortality is the average of 2 tanks with 10 fish per stock per tank. Stock abbreviations: BL = Bear Lake, BV = Bonneville, SN = Snake River fine-spotted, and EL = Electric Lake stock. A common subscript letter or no letter among means within a given salinity indicates no significant difference (1-way ANOVA, $P \geq 0.05$).

Salinity mS · cm ⁻¹ (‰)	Percent mortality			
	BL	BV	SN	EL
0.4 (0.0)	0	0	0	0
29.6 (18.0)	0	0	10	0
32.3 (19.0)	0	0	40	5
33.5 (20.0)	0 a	5 a	66 b	0 a
36.1 (21.0)	60 c	0 a	95 d	30 b
38.2 (22.0)	80 ab	45 a	100 b	84 a
41.6 (23.5)	100 a	75 b	100 a	100 a

Basin, this stock would likely have been exposed to selective pressures from high summer temperatures. Duff (1988) reported Bonneville cutthroat trout found in “small head-water streams with degraded habitat and warm summer water temperature (21°C).” Differences in LEC_{50} values were minor, but stock differences may be accentuated if fish are exposed to daily fluctuating high temperatures instead of constant high temperatures, where fish can recover overnight. For example, Otto (1974) observed higher thermal tolerance in western mosquitofish (*Gambusia affinis affinis*) exposed to cyclic high temperatures than in those exposed to constant temperatures. Feminella and Matthews (1984) reported similar findings for the orangethroat darter (*Etheostoma spectabile*). The biological significance of our results still requires field testing, but warm-temperature adaptation might be a useful trait for maintenance of trout populations in shallow reservoirs and streams with high summer temperatures. Intraspecific differences in thermal tolerance have been observed by McCauley (1958) for arctic char (*Salvelinus alpinus*), but not for brook trout. Bidgood and Berst (1969) did not detect any difference in thermal tolerance among rainbow trout from 4 different Great Lakes stocks.

The upper incipient lethal temperature (UILT) is defined as the upper temperature at which 50% mortality is observed at a given acclimation temperature (Amour 1991). In this study cutthroat trout had UILT limits ranging

TABLE 4. Average ($n = 2$ tanks, 10 fish per stock per tank) of the median time to loss of equilibrium (resistance time) for each of 4 cutthroat trout stocks (Bear Lake Bonneville, BL; Manning Meadow Bonneville, BV; Snake River fine-spotted, SN; and Electric Lake, EL), and average dissolved oxygen (DO \pm range) level at the median time for each of 6 tests in which fish were exposed to low dissolved oxygen levels for 24 hours or to gradually decreasing levels. Means within a test that are not significantly different share a common letter or no letters (1-way ANOVA, $P \geq 0.05$).

Dissolved oxygen (mg · L ⁻¹)	Resistance time (minutes)				Test
	BL	BV	SN	EL	
DECREASING DO					
1.34 \pm 0.13	335	273	242	235	2
1.39 \pm 0.07	340	360	275	293	1
CONSTANT DO					
1.85 \pm 0.16	125	63	108	126	4
1.99 \pm 0.18	289	116	295	154	5
2.18 \pm 0.11	634 a	310 b	401 b	371 b	6
2.29 \pm 0.10	518	803	457	314	8

from 23.6°C to 24.3°C. Other researchers have indicated that rainbow trout tolerate slightly higher values at similar acclimation temperatures; Bidgood and Berst (1969) and Charlton et al. (1970) both noted UILT values ranging from 25°C to 26°C. Arctic grayling (*Thymallus arcticus*) in Montana had UILTs of 23.0°C for fish acclimated to 8.4°C or 16.0°C, or 25.0°C for those acclimated to 20.0°C (Lohr et al. 1996).

CTM tests resulted in higher lethal temperature values than 96-hour tests, similar to tests with arctic grayling (Lohr et al. 1996). The 2 methods differ in that CTM is a progressive change in temperature resulting in a “physical disorganization response,” whereas the UILT method is an abrupt change resulting in a lethal response (Becker and Genoway 1979). The CTM method has been useful for comparative studies, such as that of Kowalski et al. (1978) of New York stream fishes. Also, Matthews and Maness (1979) observed significant differences in CTM values among cyprinid species that correspond to fluctuations in fish populations in the South Canadian River in Oklahoma. However, as the 96-hour tests indicated, CTM values should not be regarded as the maximum “safe” temperature for a fish at a given acclimation temperature. Mortality at a given temperature can occur over a much longer period than that allowed in the CTM tests. In this study the 96-hour tests were more sensitive indicators of differences in temperature tolerance, detecting differences where CTM tests did not. Incongruous results were not limited to this study. CTM tests were inconsistent with thermal preference tests for

2 species of darters (Ingersoll and Claussen 1984). The 2 methods measure different responses and thus should both be conducted for future temperature studies.

As in this study, size differences in thermal tolerance were not significant for studies with brook trout and arctic char (McCauley 1958), nor for perch (*Perca flavescens*; Hathaway 1927, Hart 1952). Smale and Rabeni (1995) similarly found no difference in tolerance related to size in tests of 34 species found in Missouri headwater streams.

Salinity tolerance among salmonids seems to vary considerably with species and age (Clarke 1982, Blackburn and Clarke 1987). For example, salinities causing 50% mortality of coho salmon increased from 33‰ in early February to 41‰ in mid-April as the fish progressed through the parr-to-smolt transformation (Blackburn and Clarke 1987). Varnavskiy and Varnavskaya (1984) reported significant mortality in 28‰ seawater for sockeye and coho salmon. Tolerances are also complicated by the fact that salt in the diet can improve salt tolerance (Basulto 1976). Rainbow trout have been reared in water with salinities of 30‰ after 9 days of acclimation (Murai and Andrews 1973). Salt-tolerant strains of rainbow trout have been developed for marine net pen rearing in Finland (Stickney 1991). Tatum (1973) successfully reared rainbow trout in cages in salinities of 20‰ after a 24-hour acclimation period. We found cutthroat trout tolerated salinities approaching 18–22‰.

Salinity tolerance was quite different among the 4 stocks, with highest to lowest tolerance following the order BV > EL > BL > SN; i.e.,

TABLE 5. Mean ($n = 2$ tanks with 10 fish per stock per tank) mortality of 4 cutthroat trout stocks (Bear Lake Bonneville, BL; southern Bonneville, BV; Snake River fine-spotted, SN; and Electric Lake, EL) exposed to low levels of dissolved oxygen (mean \pm range) over a 24-hour period in 6 separate tests. Means within a test not significantly different share a common letter or no letters (1-way ANOVA, $P \geq 0.05$).

Dissolved oxygen ($\text{mg} \cdot \text{L}^{-1}$)	Mortality (%)				Test
	BL	BV	SN	EL	
1.85 \pm 0.16	100	100	100	100	4
1.99 \pm 0.18	95	100	95	100	5
2.18 \pm 0.11	90	95	90	100	6
2.29 \pm 0.10	67	82	75	80	8
2.40 \pm 0.15	5 a	0 a	30 b	5 a	7
3.34 \pm 0.71	0	0	0	0	3

the southern stock was most tolerant and the northern stocks the least. The Great Basin and Intermountain West have experienced several fluctuations of wetter and drier climatic periods over the last 25,000 years (Bright 1963, Smith 1978), which may have altered ancient lake levels and salinity. Lake Bonneville is reported to have undergone 4 periods of low water levels between 8,000 and 22,000 years ago, including one period of complete dessication followed by refilling that occurred 11,000 years ago (Hickman 1978). Such conditions may have exerted selective pressures on the cutthroat trout. Galat et al. (1985) noted that Lahontan cutthroat trout, which evolved in Pleistocene Lake Lahontan that underwent similar water level fluctuations, have adapted to salinities approaching 11.9‰ (15.1 $\text{mS} \cdot \text{cm}^{-1}$).

Cutthroat trout subspecies can be divided into 3 major groups: coastal (*O. c. clarki*) characterized by 68 chromosomes, westslope (*O. c. lewisi*) characterized by 66 chromosomes, and interior cutthroat trout characterized by 64 chromosomes (Loudenslager and Gall 1980, Behnke 1981, 1988). Using starch gel electrophoresis, Loudenslager and Gall (1980) further subdivided the interior cutthroat trout into 2 additional groups: (1) Lahontan cutthroat trout and (2) those cutthroat trout inhabiting the Colorado, Yellowstone, and Upper Snake rivers, and the Bonneville Basin. Further study of this latter group by Martin et al. (1985) using the same techniques indicated that differences were evident between northern (Bear River drainage) and southern (Sevier River drainage) forms of the Bonneville cutthroat trout; they also suggested that fish from the Wasatch Front streams of Utah may form a 3rd group. We

also found differences between the southern and northern forms of the Bonneville cutthroat trout, particularly in temperature and salt-tolerance limits.

DO limits have been reviewed by Barton and Taylor (1996), Davis (1975), and Doudoroff and Shumway (1970), who summarized that mortality for most fish occurs at concentrations between 1 and 3 $\text{mg} \cdot \text{L}^{-1}$. Cutthroat trout in this study had lower DO threshold values (1.9 $\text{mg} \cdot \text{L}^{-1}$ or 22% of saturation or 28.6 mm Hg, PO_2) when DO levels were steadily dropped compared to 24-hour tests (2.3–2.5 $\text{mg} \cdot \text{L}^{-1}$ or 26–29% saturation). Differences in tolerance to hypoxia were not evident among the 4 stocks, indicating little difference in natural selection for that trait. For rainbow trout in 24-hour tests, Alabaster et al. (1957) reported a median tolerance level of 2.6–2.7 $\text{mg} \cdot \text{L}^{-1}$. Steelhead (*O. mykiss*) at 16–20°C died at 1.6–1.7 $\text{mg} \cdot \text{L}^{-1}$ in tests by McNeil (1956, cited by Warren and Bouck 1973). The discrepancy between these 2 studies may be stock related since intraspecific differences in DO tolerance have been observed in rainbow trout (Klar et al. 1979). The 4 cutthroat trout stocks in this study had incipient lethal limits that fell between these 2 reported ranges. Hepworth et al. (1999) indicated that cutthroat trout survived overwinter in a reservoir whereas rainbow trout did not. Controlled studies comparing rainbow trout and cutthroat trout stocks are needed to better define these DO tolerance differences.

In DO studies with other salmonids, Katz et al. (1959) noted that resting juvenile chinook salmon (*Oncorhynchus tshawytscha*) mortality at 20°C occurred at 1.4–1.9 $\text{mg} \cdot \text{L}^{-1}$ in 24-hour tests. At 10°C, Klyashtorin (1975) reported

lower threshold values for chinook salmon (1.6 mg · L⁻¹, 19.5 mm Hg), sockeye salmon (*O. nerka*; 1.4 mg · L⁻¹, 19.0 mm Hg), coho salmon (*O. kisutch*; 1.4 mg · L⁻¹), and arctic char (*Salvelinus alpinus*; 1.4 mg · L⁻¹). Burdick et al. (1954) noted mortality of individual brook trout occurred at 1.15–3.40 mg O₂ · L⁻¹ and individual rainbow trout occurred at 0.81–2.47 mg O₂ · L⁻¹, depending upon the temperature. Tests by Burdick et al. (1954) and Klyashtorin (1975) were conducted using the sealed-vessel method, which can lead to underestimation of actual lethal levels (Doudoroff and Shumway 1970). Shepard (1955) noted that brook trout held at 9°C all survived 1.9 mg · L⁻¹ (17% saturation) for 5 days, but died at concentrations below this.

The literature on the effect of size upon tolerance to low DO has been contradictory. Shepard (1955) reported that small fish died more quickly than large fish. Wells (1913) and Keys (1931) observed similar results, but it was not evident in our study. Similarly, no correlation between size and resistance time to low DO was observed by Alabaster et al. (1957) in studies with rainbow trout and perch (*Perca fluviatilis*). Doudoroff and Shumway (1970) reviewed several studies and also found inconsistencies in the effect of size upon DO tolerance.

Overall, results indicated differences in water quality tolerance among the cutthroat trout stocks tested, especially to high temperature and salinity. These differences accentuate the importance of preserving the genetic diversity of the individual stocks for greater flexibility in fisheries management and stock survival. These adaptations may make the southern Bonneville stock a better candidate for stocking in waters of marginal temperature or salinity than the other stocks tested.

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