

Critical thermal minima and maxima of three freshwater game-fish species acclimated to constant temperatures

Rebecca J. Currie¹, Wayne A. Bennett² & Thomas L. Beitinger

*Department of Biological Sciences, University of North Texas, P.O. Box 5218, Denton, TX 76203, U.S.A.
(e-mail: beitingr@unt.edu)*

¹*Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, U.S.A.*

²*Department of Biology, University of West Florida, 11000 University Parkway, Pensacola, FL 32514, U.S.A.*

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Synopsis

A total of 120 critical thermal maxima (CT maxima) and 120 critical thermal minima (CT minima) were determined for channel catfish, largemouth bass and rainbow trout acclimated to three constant temperatures: 20, 25 and 30 °C in catfish and bass, and 10, 15 and 20 °C in trout. Highest mean CT maximum and lowest mean CT minimum measured over these acclimation temperatures were 40.3 and 2.7 °C (catfish), 38.5 and 3.2 °C (bass) and 29.8 and ~ 0.0 °C (trout). Temperature tolerance data were precise with standard deviations generally less than 0.5 °C. Channel catfish had the largest thermal tolerance scope of the three species while rainbow trout had the lowest tolerance of high temperatures and the highest tolerance of low temperatures. In all species CT minima and CT maxima were highly significantly linearly related to acclimation temperature. Within each species, slopes relating CT maxima to acclimation temperature were approximately half as large as those relating CT minima to acclimation temperature, suggesting that acclimation temperature has a greater influence on tolerance to low rather than high temperatures. Slopes relating both CT minima and CT maxima to acclimation temperature for the two warm-water species were similar and approximately twice those for the rainbow trout.

Introduction

According to the 'father' of fish environmental physiology, F.E.J. Fry, temperature, heat (*sensu stricto*) can influence fishes in multiple ways. Among these, temperature can 'act as a lethal factor when its effect is to destroy the integrity of the organism' (Fry 1947). Owing to the large number of species and their key role in freshwater and marine ecosystems, a vast literature reports temperature tolerances of fishes. Thermal relations of fishes have been studied for more than 100 years, and many of the earliest studies involved temperature

tolerance (e.g., Heath 1884, Day 1885, Carter 1887, Vernon 1899). Quantitative laboratory studies of temperature tolerance of fishes date from the late 1920's (Hathaway 1927), and escalated during the 1940s and early 1950s with numerous publications by J.R. Brett, F.E.J. Fry, P. Doudoroff and J.S. Hart.

Thermal tolerances of fishes in the laboratory have been quantified by both static (incipient lethal) and dynamic (critical thermal) methods. In the plunge or static technique, a temperature lethal to 50% of a fish sample, the incipient lower or incipient upper lethal temperature (ILLT or IULT), is estimated by plunging groups of fish from various

constant acclimation temperatures into a series of static test temperatures near estimated lower and upper temperature limits. Mortality is recorded over time, and estimates of the temperature tolerated by 50% of the sample for various time intervals are made from a regression of percentage mortality on acclimation temperature (Fry 1947).

In the critical thermal methodology, CTM, fish are subjected to a constant dynamic temperature change until a predefined sublethal endpoint (e.g., loss of equilibrium or muscle spasms) is reached at which locomotory movements become disorganized and an animal loses the ability to escape from conditions which may ultimately lead to its death (Cowles & Bogert 1944). Critical thermal maximum (CT maximum) and minimum (CT minimum) are calculated as the arithmetic mean of the collective thermal points at which the endpoint is reached (Lowe & Vance 1955, Cox 1974). The CTM provides an ecologically relevant lethal index, since fishes in nature may encounter such temperatures either temporally or spatially as acute fluctuations outside of their tolerance limits (Brett 1956, Hutchison 1976).

Huntsman & Sparks (1924) appear to be first to use a modified CTM when they recorded the death point of numerous species of marine fishes and invertebrates exposed to temperature increases of $0.2\text{ }^{\circ}\text{C min}^{-1}$. Sumner & Doudoroff (1938) combined dynamic temperature changes ($0.05\text{ }^{\circ}\text{C min}^{-1}$) with a sublethal endpoint (cessation of respiratory movements) in the longjaw mudsucker, *Gillichthys mirabilis*. These authors noted that this endpoint did not necessarily represent death since many of the fish recovered when returned to cooler water. Nevertheless, Cowles & Bogert (1944) are given credit for originating this methodology and coining the terms CT maximum and CT minimum in their classic paper on desert reptiles. The contemporary CTM definition as it relates to fishes, is usually that of Cox (1974).

Although both CTM and ILT endpoints are quantitatively expressed as a temperature, are determined experimentally with animals acclimated to particular temperatures, and involve time and temperature as major test variables, the two methods do not quantify the same response. The CTM

requires a constant, progressive change of temperature upward or downward from acclimation until physiological disorganization occurs. This method is faster, requires few fish, does not confuse handling stress with thermal stress and approximates natural conditions better than static methods (Bennett & Judd 1992). In contrast, the ILT method features an abrupt transfer to temperatures either above or below acclimation and exposure until lethality occurs, requires a large number of fish, and with the possible exceptions of thermal upwellings and shallow tide pools, does not represent conditions found in nature. Although both methods are suitable to describe temperature tolerance of fishes, Bennett & Beitinger (1997) argue that the ILT results give a physiological view while the CTM yields an ecological perspective.

Ironically, most laboratory tolerance estimates for fishes involve high temperatures, whereas most fish kills in nature are caused by exposure to low temperatures. Although we could find only a few citations of fish kills owing to heat death (e.g., Huntsman 1942, Coulton 1959, Mundahl 1990), the literature contains more than 20 citations (references by request) of death due to low temperatures appearing as early as 1887 (Willcox 1887) and continuing to the present (Bennett & Judd 1992). Two observations combine to help explain this disparity. First, fish gain heat tolerance more rapidly than cold tolerance (see Doudoroff 1942, Brett 1946, Davies 1973) and second, upper temperature tolerances of most fish are well above typical temperatures of their natural habitats (Mundahl 1990).

Not surprisingly, thermal tolerances of fishes vary greatly. For example, off the coast of Belize, large populations of pupfish, *Cyprinodon artifrons*, mosquitofish, *Gambusia yucatanana*, and goldspotted killifish, *Floridichthys carpio* thrive at daily temperatures in excess of $40\text{ }^{\circ}\text{C}$ (Heath et al. 1993). In contrast, Antarctic icefishes, *Trematomus* spp., complete their entire life cycles at temperatures just above $-1.8\text{ }^{\circ}\text{C}$ and die due to excessive heat at temperatures near $6\text{ }^{\circ}\text{C}$ (Somero & DeVries 1967). Sheepshead minnow, *Cyprinodon variegatus*, living in shallow south Texas tide pools experience seasonal water temperature shifts of $40\text{ }^{\circ}\text{C}$ (Bennett & Judd 1992) and in the laboratory survive temper-

ature extremes of < 0 to approximately $45\text{ }^{\circ}\text{C}$ (Bennett & Beitinger 1997).

The objective of this research was to measure CT minima and CT maxima of three game-fish species: largemouth bass, *Micropterus salmoides*, channel catfish, *Ictalurus punctatus*, and rainbow trout, *Oncorhynchus mykiss*, acclimated to three constant temperatures. These species were chosen because they are economically important, widely distributed and are among the top game-fishes in North America.

Methods

Largemouth bass and channel catfish were obtained from Inslee's Fish Farm in Connerville, Oklahoma. All largemouth bass and channel catfish were juveniles approximately 10 cm long and had a mean mass of approximately 15 g. Rainbow trout were purchased from the Crystal Lake Fish Hatchery in Ava, Missouri. Rainbow trout were approximately 6 weeks old, 4 cm in length and had a mean mass of 2 g.

In the laboratory, fish were separated into groups and placed into three 570 l Living Streams (Frigid Units Inc.) for temperature acclimation. Critical thermal minima and maxima were determined for largemouth bass and channel catfish held at constant temperatures of 20.0, 25.0 and 30.0 $^{\circ}\text{C}$ ($\pm 0.1\text{ }^{\circ}\text{C}$) for a minimum of 20 days, and rainbow trout held at 10.0, 15.0 and 20.0 $^{\circ}\text{C}$ ($\pm 0.1\text{ }^{\circ}\text{C}$) for a minimum of 20 days. Constant holding temperatures of 25.0 and 30.0 $^{\circ}\text{C}$ were maintained via Haake thermoregulators. Lower constant holding temperatures, 10.0, 15.0 and 20.0 $^{\circ}\text{C}$, were maintained by Frigid Units Inc. cooling units. All fish were fed several times each day until sated, after which unconsumed feed was removed by vacuum.

Dissolved oxygen ($\pm 0.1\text{ mg l}^{-1}$), conductivity ($\pm 10\text{ }\mu\text{mho cm}^{-2}$), pH (temperature corrected, $\pm 0.1\text{ pH unit}$), temperature ($\pm 0.1\text{ }^{\circ}\text{C}$), total ammonia (NH_4 and NH_3^+ , $\pm 0.1\text{ mg l}^{-1}$) and nitrites ($\text{mg NO}_2\text{ l}^{-1}$ as N, $\pm 0.1\text{ mg l}^{-1}$) were measured daily during the first week of holding and twice weekly thereafter. Dissolved oxygen and conductivity were measured using a YSI Model 54 oxygen meter and a YSI

Model 33 S-C-T meter following standard operating procedures provided by the manufacturer. A Markson Science Inc. Model 88 digital meter was used to monitor pH in the acclimation tanks. Temperature was recorded using a NBS calibrated mercury thermometer. Finally, ammonia and nitrites were measured using a chemical test kit manufactured by Aquarium Systems.

Water was changed in all acclimation tanks four times a week to prevent build-ups of ammonia, nitrates and nitrites. Depending upon the holding temperature, 5 to 20% of the water in each tank was siphoned along with waste materials and replaced with carbon-filtered tap water. The water was treated with a dechlorinator to prevent chlorine poisoning. When conductivity readings began to increase, tank water was replaced with the de-ionized water. The amount of water replaced was adjusted to prevent more than $\pm 1\text{ }^{\circ}\text{C}$ transient change in water temperature. For water temperatures of 15 and 10 $^{\circ}\text{C}$, water was cooled prior to replacement in holding tanks. All three species were kept under a diel LD 12:12 photoperiod. After holding at a particular constant temperature for 20 days, fish were considered to be acclimated to that temperature.

Prior to each temperature tolerance trial, ten fish were randomly selected from an acclimation temperature and placed individually into mesh baskets. The baskets were submerged into the 190 l glass CTM chamber. Water quality variables (see previous discussion for variables, techniques and accuracy) in the CTM chamber were matched to those of the acclimation tank prior to the introduction of fish. Test water was continually mixed and aerated during trials by bubbling air through air stones. Chamber water was cooled by a Blue-M constant flow portable cooling coil during CT minima trials. Three Haake thermoregulators circulated (but did not heat) water across the coil to promote uniform cooling. Water temperatures were increased during CT maxima trials by activating the heating element of one or more circulating thermoregulators. Water temperature was either decreased or increased during CTM trials at a constant rate of $0.3\text{ }^{\circ}\text{C min}^{-1}$. This rate of temperature change fulfills CTM criterion proposed by Becker & Genoway (1979).

Loss of equilibrium (LOE) was the selected end-

point during CTM trials (see Beitinger & McCauley 1990, Bennett & Beitinger 1997, for discussions of CTM endpoint criteria). Loss of equilibrium was defined as failure of a fish to maintain dorso-ventral orientation for at least one minute. Once a fish reached this endpoint, the temperature was immediately measured to ± 0.1 °C with a NBS calibrated mercury thermometer. The fish was removed from its basket, weighed (± 0.5 g), measured (standard length ± 0.1 cm), returned to its prior acclimation temperature and assessed for survival. Temperature change trials continued until LOE was observed in all ten test fish. For each acclimation temperature, two CT maxima and two CT minima trials of 10 fish each were conducted yielding a total of 120 individual measurements for each species.

The CT minima and CT maxima values of each species/acclimation temperature combination were described by parametric statistics. Linear regression was used to test for relationships between temperature tolerance and acclimation temperature. Slopes from these regression models were tested via Student's *t* statistics. Within and among species, differences between/among CT maxima and CT minima values were statistically tested via one-way ANOVA and Student-Newman-Keuls (SNK) multiple range tests. All statistical decisions were made with an α of 0.05.

Results

The critical thermal methodology effectively generated accurate and precise thermal tolerance data for our three test species. Typical CTM trials required approximately 2–3 h to complete. A single trial yielded ten separate data points. The data were statistically precise with standard deviations less than 0.5 °C in a majority (39 of 59, 66%) of trials. During CT maxima trials, LOE was obvious as test fish approached physiological death. During CT minima trials, LOE was not as easily observed, but signs of disorientation appeared in individuals of all three species as temperatures decreased, except rainbow trout acclimated to 10 °C. Other CTM endpoints, specifically the onset of muscle spasms, did not occur in any fish during CT minima trials. Less

than 5% of test fish died during the 24 h observation period subsequent to CTM trials. Most mortalities occurred in fish which were exposed to temperatures beyond their endpoint owing to a delay in returning them to their pretest acclimation temperature.

Channel catfish acclimated to constant temperatures of 20, 25 and 30 °C had CT maxima values (mean \pm SD) of 36.4 ± 0.25 , 38.7 ± 0.36 and 40.3 ± 0.29 °C, and CT minima (mean \pm SD) values of 2.7 ± 0.41 , 6.5 ± 0.40 and 9.8 ± 0.41 °C, respectively. Critical thermal maxima and minima at each acclimation temperature were statistically distinct (SNK, $\alpha = 0.05$). At 20 °C, the temperature tolerance scope (ie., CT maxima – CT minima) was maximum (33.7 °C) and decreased linearly as acclimation temperature increased. Linear relationships between CT minima and CT maxima values separately and acclimation temperature were highly significant, $p < 0.0001$ (Figure 1). The coefficients of determination (R^2) for these regression models indicate that more than 95% of the measured variation in CT maxima and CT minima were accounted for by acclimation temperature. The regression slopes indicate a gain in heat tolerance of 0.40 °C and loss of cold tolerance of 0.71 °C for each 1.0 °C increase in acclimation temperature.

Largemouth bass acclimated to constant temperatures of 20, 25 and 30 °C had CT maxima (mean \pm SD) values of 35.4 ± 0.47 , 36.7 ± 0.59 and 38.5 ± 0.34 °C, respectively. Although the CT maxima at 30 °C was significantly greater than values measured at 20 and 25 °C (SNK $\alpha = 0.05$), CT maxima values at acclimation temperatures of 20 and 25 °C were not significantly different. A SNK multiple range test separated CT minima (mean \pm SD) values of 3.2 ± 0.27 , 7.3 ± 0.52 and 10.7 ± 0.61 °C, measured at acclimation temperatures of 20, 25 and 30 °C, respectively, into three statistically distinct groups. The maximum thermal tolerance scope was 32.2 °C at an acclimation temperature of 20 °C. Simple linear regressions of CT maxima or CT minima values on constant acclimation temperatures yielded highly significant models which accounted for at least 85% of observed variation (Figure 1). The regression slopes indicate that for every 1 °C increase in acclimation temperature, CT maxima

101.3

98.06

95.72

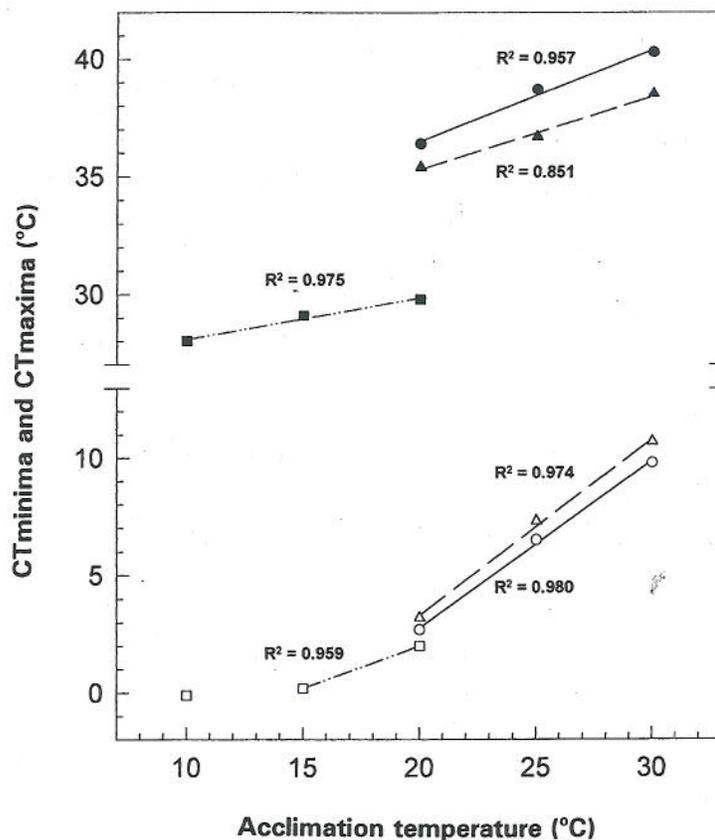


Figure 1. Critical thermal maxima (CT maxima, solid symbols) or critical thermal minima (CT minima, open symbols) regressed on acclimation temperature (AT) for channel catfish (circles), largemouth bass (triangles) and rainbow trout (squares).

Regression models for each of the above listed species were: channel catfish, CT maxima = $28.58 + 0.40$ (AT) and CT minima = $11.36 + 0.71$ (AT); largemouth bass, CT maxima = $28.92 + 0.32$ (AT) and CT minima = $26.23 + 0.18$ (AT); rainbow trout, CT maxima = $26.23 + 0.18$ (AT) and CT minima = $5.31 + 0.36$ (AT).

and CT minima increased by 0.32 °C and 0.76 °C, respectively.

Critical thermal maxima (mean \pm SD) values of 28.0 ± 0.36 , 29.1 ± 0.27 and 29.8 ± 0.36 °C and minima of ~ 0.0 , 0.2 ± 0.16 and 2.0 ± 0.16 °C were measured for rainbow trout acclimated to 10, 15 and 20 °C. Critical thermal minima values for rainbow trout acclimated to 10 °C were recorded as ~ 0.0 °C, because LOE was not observed at 0.0 °C, the lowest temperature attainable in CT minima trials. Critical thermal maxima and minima were significantly distinct at each acclimation temperature (SNK $\alpha = 0.05$). Temperature tolerance scope was maximal, 28.9 °C, at an acclimation temperature of 15 °C. Highly significant linear relationships occurred between acclimation temperature and temperatures at which LOE occurred (Figure 1).

Regression slopes indicate that, for each 1 °C increase in acclimation temperature, the CT maxima of rainbow trout increased by 0.18 °C and the CT minima increased by 0.36 °C.

Channel catfish were more tolerant of both high and low temperatures than largemouth bass. At each of the three constant acclimation temperatures, CT maxima of channel catfish were highly significantly greater than those of largemouth bass (t values from one-tailed, independent t tests at 20, 25 and 30 °C were 8.5, 13.2 and 18.8, respectively; $p < 0.0005$). Similarly, CT minima of channel catfish were highly significantly lower than those of largemouth bass at each acclimation temperature (one-tailed, independent t test, t values at acclimation temperatures of 20, 25 and 30 °C were 4.2, 5.0, 5.8 respectively; $p < 0.0005$). The small standard devia-

tions and relatively large sample size of each group ($n = 20$) combined to generate large t values and hence, small probabilities.

At 20 °C, the only acclimation temperature common to all three species, rainbow trout had significantly lower CT maxima and CT minima than either channel catfish or largemouth bass (one-way ANOVA followed by SNK multiple range test with $\alpha = 0.05$). Channel catfish had the highest CT maximum, 36.4 °C, which was approximately 1.0 and 6.6 °C higher than CT maxima of largemouth bass and rainbow trout, respectively. At this acclimation temperature, rainbow trout had the smallest CT minimum, 2.0 °C, which was 1.2 and 0.7 °C lower than CT minima for largemouth bass and channel catfish, respectively.

All nine intraspecific and interspecific comparisons of regression slopes relating temperature tolerance and acclimation temperature were statistically significant (all comparisons, $t > 2.37$, $p < 0.02$). Slopes relating CT minima and acclimation temperature for each of the three species were approximately twice those relating CT maxima and acclimation temperature. CT maxima and CT minima slopes of channel catfish and largemouth bass were nearly twice those measured for rainbow trout. Although similar, CT minima and CT maxima slopes for largemouth bass and channel catfish were significantly different. The difference in CT minima and CT maxima between these two species begins at 0.5 and 1.0 °C at an acclimation temperature of 20 °C and increases to 0.9 and 1.8 °C for fish acclimated to 30 °C. As a consequence, the thermal tolerance of catfish is 1.5 °C greater than that of bass at an acclimation temperature of 20 °C and nearly 3 °C greater at an acclimation temperature of 30 °C. These apparently small differences in slope allow catfish to tolerate temperature ranges 5 to 10% greater than those of largemouth bass over this range of acclimation temperatures.

Discussion

Of the three species tested, channel catfish were tolerant of the widest range of temperatures. A review of the literature revealed three papers and one in

press manuscript in which CT maxima values have been reported for channel catfish (Table 1). Over a range of acclimation temperatures of 12 to 32 °C, Cheetham et al. (1976) found a linear increase from 34.5 to 41 °C in CT maxima of immature channel catfish. At a single acclimation temperature of 22.7 °C, Reutter & Herdendorf (1976) reported a CT maximum of 38.0 °C for this species. Finally, in studies in our laboratory, control channel catfish acclimated to 20 °C had a CT maximum of 38.0 °C (Watenpaugh et al. 1985) and Bennett et al. (1997) reported CT maxima values of 30.9 to 42.1 °C in juvenile catfish acclimated to four temperatures between 10 and 35 °C, respectively. Critical thermal maxima in all of these studies are extremely similar to the CT maxima values of 36.4, 38.7 and 40.3 °C for catfish acclimated to 20, 25 and 30 °C, respectively, generated in our research.

Hart (1952) and Allen & Strawn (1967) reported a range of 30.3 to 37.8 °C in IULTs of channel catfish acclimated to six temperatures between 15 and 34 °C. At similar acclimation temperatures, IULTs are approximately 3 °C lower than CT maxima. This consistent difference between IULT and CT maxima is a result of differences between static and dynamic temperature tolerance methods. Comparisons of these two methods for estimating temperature tolerance have been provided by Fry (1947), Hutchison (1976), Kilgour & McCauley (1986), Bennett & Judd (1992), and Bennett & Beitinger (1997).

Hart (1952) found that channel catfish acclimated at three temperatures between 15 and 30 °C had respective IULTs of 0.0 to 6.0 °C; however, published research reporting CT minima of channel catfish were not found. Relative to high temperature tolerance, little research has dealt with cold tolerance (Beitinger & McCauley 1990). The CT minima generated by our research are the only reported values for channel catfish. Channel catfish acclimated to 20, 25 and 30 °C had mean CT minima values of 2.7, 6.5 and 9.8 °C. If the regression model generated for channel catfish acclimated over a 20 to 30 °C range of acclimation temperatures holds at lower temperatures, we predict a CT minima approaching 0.0 °C for channel catfish acclimated to about 16 °C.

We found only three studies which measured

temperature tolerance in largemouth bass exposed to dynamic changes in temperatures (Table 2). Smith & Scott (1975) measured CT maxima of 36.7 and 40.1 °C in immature largemouth bass acclimated to 20 and 28 °C, respectively. These values are 1.4 and 2.2 °C higher than CT maxima values interpolated from our CT maxima regression model for largemouth bass acclimated to the same temperatures. The larger CT maxima values reported by Smith & Scott (1975) are likely the result of selection for increased thermal tolerance in their fish, since they were captured from Par Pond on the Savannah River Plant (Aiken, South Carolina). Par Pond receives an extreme thermal input from the operation of a plutonium-producing nuclear reac-

tor. Surface water temperatures at the heated end of Par Pond generally range between 30 and 40 °C during the summer and 20 to 30 °C in winter (Holland et al. 1974). Some fishes living in thermal discharges, e.g., bluegill, *Lepomis macrochirus*, have evolved higher thermal tolerance (Holland et al. 1974). Our data support the conclusions of Smith & Scott (1975) that the largemouth bass in their study have an increased tolerance of high temperatures relative to largemouth bass from other locations.

Two additional studies (Guest 1985, Fields et al. 1987) attempted to determine if Florida largemouth bass, *Micropterus salmoides floridanus*, have different temperature tolerances than northern largemouth bass, *M. s. salmoides*. This question was first

Table 1. Summary of laboratory temperature tolerance data for channel catfish. Statistics listed for CTM are mean \pm one standard deviation (sample size).

T _{acclim} °C	Method	Endpoint	Time or rate	Lethal value °C	Reference
Upper temperature tolerance					
15 ¹	IULT	death	~ 24 h	30.3	Hart (1952)
20 ¹	IULT	death	~ 24 h	32.8	Hart (1952)
25 ¹	IULT	death	~ 24 h	33.5	Hart (1952)
20 ²	IULT	death	~ 24 h	32.7	Hart (1952)
25 ²	IULT	death	~ 24 h	33.5	Hart (1952)
26	IULT	death	121 h	36.6	Allen & Strawn (1967)
30	IULT	death	121 h	37.3	Allen & Strawn (1967)
34	IULT	death	121 h	37.8	Allen & Strawn (1967)
22.7	CTMax	LOE	-	38.0	Reutter & Herdendorf (1976)
12	CTMax	LOE	1.0 °C min ⁻¹	34.5 \pm 0.53 (12) ³	Cheetham et al. (1976)
16	CTMax	LOE	1.0 °C min ⁻¹	34.2 \pm 0.74 (12) ³	Cheetman et al. (1976)
20	CTMax	LOE	1.0 °C min ⁻¹	35.5 \pm 0.38 (12) ³	Cheetman et al. (1976)
24	CTMax	LOE	1.0 °C min ⁻¹	37.5 \pm 0.52 (12) ³	Cheetham et al. (1976)
28	CTMax	LOE	1.0 °C min ⁻²	39.2 \pm 0.58 (12) ³	Cheetham et al. (1976)
32	CTMax	LOE	1.0 °C min ⁻¹	41.0 \pm 0.31 (12) ³	Cheetham et al. (1976)
36 ⁴	-	-	-	-	Cheetham et al. (1976)
20	CTMax	LOE	0.3 °C min ⁻¹	38.0 \pm 0.39 (20)	Watenpaugh et al. (1995)
10	CTMax	LOE	0.15 °C min ⁻¹	30.9 \pm 0.61 (10)	Bennett et al. (1987)
20	CTMax	LOE	0.15 °C min ⁻¹	35.8 \pm 0.47 (10)	Bennett et al. (1997)
30	CTMax	LOE	0.15 °C min ⁻¹	40.1 \pm 0.66 (10)	Bennett et al. (1997)
35	CTMax	LOE	0.15 °C min ⁻¹	42.1 \pm 0.25 (10)	Bennett et al. (1997)
Lower temperature tolerance					
15 ¹	ILLT	death	~ 24 h	0.0	Hart (1952)
20 ¹	ILLT	death	~ 24 h	2.5	Hart (1952)
30 ¹	ILLT	death	~ 24 h	6.0	Hart (1952)
20 ²	ILLT	death	~ 24 h	4.7	Hart (1952)

¹ Source: Florida.

² Source: Ontario.

³ Estimated from Figure 1, Cheetham et al. (1976).

⁴ All fish died during acclimation period.

Table 2. Summary of laboratory temperature tolerance data for largemouth bass. Statistics listed for CTM are mean \pm one standard deviation (sample size).

T_{acclim} °C	Method	Endpoint	Time or rate	Lethal value °C	Reference
Upper temperature tolerance					
10 ¹	TL ₅₀	death	24 h	28.0	Hathaway (1927)
22-23	TL ₅₀	death	24 h	32.2	Hathaway (1927)
30 ²	TL ₅₀	death	24 h	35.2	Hathaway (1927)
20 ³	IULT	death	~ 24 h	32.5	Hart (1952)
25 ³	IULT	death	~ 24 h	34.5	Hart (1952)
30 ³	IULT	death	~ 24 h	36.4	Hart (1952)
30 ⁴	IULT	death	~ 24 h	36.4	Hart (1952)
20 ⁵	IULT	death	~ 24 h	31.8	Hart (1952)
25 ⁵	IULT	death	~ 24 h	32.7	Hart (1952)
30 ⁵	IULT	death	~ 24 h	33.7	Hart (1952)
20-21	IULT	death	24 h	28.9	Black (1953)
25-31 ⁶	IULT	death	48 h	35.6	Cvancara et al. (1976)
20	CTMax	LOE	1 °C min ⁻¹	36.7 \pm 0.76 (40)	Smith & Scott (1975)
28	CTMax	LOE	1 °C min ⁻¹	40.1 \pm 1.33 (40)	Smith & Scott (1975)
30 or 36 ⁷	CLMax ¹⁰	death	1 °C day ⁻¹	38.9-39.8	Guest (1985)
30 or 36 ⁸	CLMax ¹⁰	death	1 °C day ⁻¹	38.2-39.4	Guest (1985)
8 ⁹	CTMax	death	0.2 °C min ⁻¹	29.2 \pm 1.36 (10)	Fields et al. (1985)
16 ⁹	CTMax	death	0.2 °C min ⁻¹	33.6 \pm 0.87 (10)	Fields et al. (1985)
24 ⁹	CTMax	death	0.2 °C min ⁻¹	36.5 \pm 0.51 (10)	Fields et al. (1985)
32 ⁹	CTMax	death	0.2 °C min ⁻¹	40.9 \pm 0.40 (10)	Fields et al. (1985)
8 ⁸	CTMax	death	0.2 °C min ⁻¹	30.4 \pm 0.97 (10)	Fields et al. (1985)
16 ⁸	CTMax	death	0.2 °C min ⁻¹	34.1 \pm 0.48 (10)	Fields et al. (1985)
24 ⁸	CTMax	death	0.2 °C min ⁻¹	37.5 \pm 0.64 (10)	Fields et al. (1985)
32 ⁸	CTMax	death	0.2 °C min ⁻¹	41.8 \pm 0.38 (10)	Fields et al. (1985)
32 ⁹	CLMax ¹⁰	death	1 °C day ⁻¹	37.3 \pm 0.60 (10)	Fields et al. (1985)
32 ⁸	CLMax ¹⁰	death	1 °C day ⁻¹	39.2 \pm 0.64 (10)	Fields et al. (1985)
Lower temperature tolerance					
20 ³	ILLT	death	° 24 h	5.5	Hart (1952)
30 ³	ILLT	death	° 24 h	11.8	Hart (1952)
20 ⁵	ILLT	death	° 24 h	5.2	Hart (1952)
25 ⁵	ILLT	death	° 24 h	7.0	Hart (1952)
30 ⁵	ILLT	death	° 24 h	10.5	Hart (1952)
10 or 20 ⁷	CLMin ¹¹	death	1 °C day ⁻¹	< 1.5-3.0	Guest (1985)
10 or 20 ⁸	CLMin ¹¹	death	1 °C day ⁻¹	< 1.5-4.0	Guest (1985)

¹ Transferred from 20 to 10 °C for 16 days.

² Transferred from 20 to 30 °C for 4 days.

³ Source: Ontario.

⁴ Source: Tennessee.

⁵ Source: Florida.

⁶ Mississippi River water temperature at capture.

⁷ Source: Northern U.S.

⁸ Source: Florida.

⁹ Source: Wisconsin.

¹⁰ CLmax = (chronic lethal maximum), temperature at which death occurred when heated 1.0 °C day⁻¹.

¹¹ CLmin = (chronic lethal minimum), temperature at which death occurred when cooled 1.0 °C day⁻¹.

investigated in Hart's (1952) classic study of morphological and physiological variation among fishes. Of the ten species studied by Hart (1952) only the common shiner, *Luxilus* (= *Notropis*) *cornutus*, western mosquitofish, *Gambusia affinis* bluegill and largemouth bass showed appreciable geographic differences in IULTs. Paradoxically, Hart (1952) found that largemouth bass from Ontario withstood higher temperatures than the bass from Florida. Interestingly, IULTs of largemouth bass from Knoxville, Tennessee resembled those of Ontario largemouth bass and not those from Florida.

In Guest's (1985) study, upper and lower temperature tolerances were determined for both northern and Florida largemouth bass populations exposed to a chronic temperature change of $1.0\text{ }^{\circ}\text{C day}^{-1}$, with death as the endpoint. Neither the rate nor the endpoint meet CTM criteria. Surprisingly, all size groups of northern largemouth bass were more tolerant of both lower and higher temperatures than corresponding size groups of Florida largemouth bass. Although the upper lethal temperatures of northern largemouth bass acclimated to 30 and 36 $^{\circ}\text{C}$ were greater than four similar sized groups of Florida largemouth bass, actual differences in mean tolerance values ranged from only 0.2 to 0.7 $^{\circ}\text{C}$. The eight mean upper temperature tolerance values ranged from 38.2 to 39.8 $^{\circ}\text{C}$ (Table 2).

In the most comprehensive comparison of upper lethal temperature tolerance in northern and Florida largemouth bass, Fields et al. (1987) collected data which contradicted those of both Hart (1952) and Guest (1985). At each of four different constant acclimation temperatures (ranging between 8 and 32 $^{\circ}\text{C}$) and a heating rate of $0.2\text{ }^{\circ}\text{C min}^{-1}$ and death as the endpoint), Florida largemouth bass had higher temperature tolerances than largemouth bass from Wisconsin (Table 2). Also when acclimated to 32 $^{\circ}\text{C}$ and exposed to chronic heating ($1.0\text{ }^{\circ}\text{C day}^{-1}$), the mean death point of Florida largemouth bass was nearly 2 $^{\circ}\text{C}$ higher than that of the northern subspecies. Comparing the CT maxima of largemouth bass in our study to those of Field's (1987) suggests that our sample of largemouth bass came from the northern subspecies.

Other reported IULTs for largemouth bass include Hathaway (1927), Black (1953) and Cvancara

et al. (1977); see Table 2. It is noteworthy that a majority of the IULTs reported in Table 2 are about 2 to 4 $^{\circ}\text{C}$ lower than in CT maxima values, which further corroborates an explanation based on the methodological differences between dynamic and static temperature tolerance estimation.

Similar to channel catfish, we found no published CT minima values for largemouth bass. Hence, our values of 3.2, 7.3 and 10.7 $^{\circ}\text{C}$ at acclimation temperatures of 20, 25 and 30 $^{\circ}\text{C}$ represent the only CT minima data available for this species. If our CT minima-acclimation temperature regression model holds at lower temperatures, it predicts that largemouth bass would have a CT minima of 0.0 $^{\circ}\text{C}$ when acclimated to approximately 15.6 $^{\circ}\text{C}$.

In eight separate comparisons, Guest (1985) reported that the mean low temperature death point following chronic cooling of northern largemouth bass were lower than those of similarly acclimated Florida largemouth bass; however, these comparisons may have been confounded by seasonal effects. Unexpectedly in this study, mean lower lethal temperatures were not significantly different at acclimation temperatures of 10 and 20 $^{\circ}\text{C}$ for either subspecies.

Also, Hart (1952) reported ILLT for largemouth bass from two locations, acclimated to temperatures between 20 and 30 $^{\circ}\text{C}$ (Table 2). The ILLT values for Ontario and Florida largemouth bass were not as different as the IULT values, and were about 1 to 2 $^{\circ}\text{C}$ higher than our CT minima at the same acclimation temperatures.

The literature contains more temperature tolerance data for rainbow trout than either channel catfish or largemouth bass. We found 12 published papers reporting temperature tolerance in rainbow trout (Table 3) with Black (1953) apparently the first. Several of these studies included only one acclimation temperature, and all but one measured only upper temperature tolerance.

Our CT maxima values of 28.0, 29.1 and 29.8 $^{\circ}\text{C}$ for rainbow trout acclimated to temperatures of 10, 15 and 20 $^{\circ}\text{C}$ are within 0.5 $^{\circ}\text{C}$ of CT maxima previously published by Lee & Rinne (1980) and Strange et al. (1993) for rainbow trout acclimated to the same temperatures (Table 3). Lee & Rinne (1980) concluded that these upper temperature tolerances

Table 3. Summary of laboratory temperature tolerance data for rainbow trout.

T _{acclim} °C	Method	Endpoint	Time or rate	Lethal value °C			Reference
Upper temperature tolerance							
11	IULT	death	24 h	24.0			Black (1953)
18	IULT	death	24 h	26.5			Alabaster & Welcomme (1962)
20	IULT	death	< 24 h	27.0			Craigie (1963)
6	IULT	death	24 h	24.3			Alabaster (1964)
15	IULT	death	24 h	25.9			Alabaster (1964)
20	IULT	death	24 h	26.7			Alabaster (1964)
15	IULT	death	96 h	25–26 ¹			Bidgood & Berst (1969)
- ²	- ³	death	168 h	25.0			Cherry et al. (1977)
16	IULT	death	101 h	25.6			Hokansen et al. (1977)
5	IULT	death	168 h	23.7	25.0	23.2	Kaya (1978) ⁴
9	IULT	death	168 h	24.2	25.2	24.7	Kaya (1978) ⁴
13	IULT	death	168 h	25.2	25.2	24.7	Kaya (1978) ⁴
17	IULT	death	168 h	25.7	25.7	25.2	Kaya (1978) ⁴
21	IULT	death	168 h	26.2	26.2	25.7	Kaya (1978) ⁴
24.5	IULT	death	168 h	26.2	26.2	26.2	Kaya (1978) ⁴
4	IULT	death	24, 48, 96 h	22.8	22.7	22.6	Threader & Houston (1983) ⁵
8	IULT	death	24, 48, 96 h	24.1	24.1	24.0	Threader & Houston (1983) ⁵
12	IULT	death	24, 48, 96 h	24.6	24.5	24.5	Threader & Houston (1983) ⁵
16	IULT	death	24, 48, 96 h	25.4	25.3	25.1	Threader & Houston (1983) ⁵
20	IULT	death	24, 48, 96 h	25.9	25.7	25.5	Threader & Houston (1983) ⁵
10	CTMax	LOE	0.02 °C min ⁻¹	28.45 ± 0.28 (5)			Lee & Rinne (1980)
20	CTMax	LOE	0.02 °C min ⁻¹	29.35 ± 0.19 (5)			Lee & Rinne (1980)
15	CTMax	LOE	0.3 °C min ⁻¹	29.40 ± 0.59 (55)			Strange et al. (1993)
Lower temperature tolerance							
10	ILLT	death	96 h	0.5			Becker et al. (1977)
15	ILLT	death	96 h	1.4			Becker et al. (1977)
20	ILLT	death	96 h	3.3			Becker et al. (1977)
10	CTMin	LOE ₅₀	0.3 °C min ⁻¹	- ⁶			Becker et al. (1977)
15	CTMin	LOE ₅₀	0.3 °C min ⁻¹	0.7			Becker et al. (1977)
20	CTMin	LOE ₅₀	0.3 °C min ⁻¹	2.1			Becker et al. (1977)
10	CTMin	LOE ₅₀	0.17 °C min ⁻¹	- ⁶			Becker et al. (1977)
15	CTMin	LOE ₅₀	0.17 °C min ⁻¹	0.2			Becker et al. (1977)
20	CTMin	LOE ₅₀	0.17 °C min ⁻¹	1.5			Becker et al. (1977)
10	CTMin	LOE ₅₀	0.083 °C min ⁻¹	- ⁶			Becker et al. (1977)
15	CTMin	LOE ₅₀	0.083 °C min ⁻¹	< 0.1			Becker et al. (1977)
20	CTMin	LOE ₅₀	0.083 °C min ⁻¹	1.2			Becker et al. (1977)
10	CTMin	LOE ₅₀	0.05 °C min ⁻¹	- ⁶			Becker et al. (1977)
15	CTMin	LOE ₅₀	0.05 °C min ⁻¹	< 0.1			Becker et al. (1977)
20	CTMin	LOE ₅₀	0.05 °C min ⁻¹	1.3			Becker et al. (1977)
10	CTMin	LOE ₅₀	0.016 °C min ⁻¹	- ⁶			Becker et al. (1977)
15	CTMin	LOE ₅₀	0.016 °C min ⁻¹	- ⁶			Becker et al. (1977)
20	CTMin	LOE ₅₀	0.016 °C min ⁻¹	0.9			Becker et al. (1977)

¹ IULTs for trout from four widely separated Great Lakes watersheds.² not reported.³ highest temperature survived for 7 days following exposure to 1 °C day⁻¹ increase.⁴ IULTs for three different populations of trout.⁵ IULTs measured at times of 24, 48 and 96 h, respectively.⁶ LOE₅₀ was not observed; LOE₅₀ < 0.0 °C.

(28 to 29 °C) were high enough to allow rainbow trout to be introduced into the southwestern United States.

The most comprehensive study on upper temperature tolerance of rainbow trout is that of Kaya (1978) who measured static 168 h IULTs in young-of-the-year and juvenile rainbow trout collected from three sources and acclimated to six different constant temperatures between 5 and 24.5 °C (Table 3). Kaya (1978) concluded that the similarity in IULTs of rainbow trout inhabiting and reproducing in the heated waters of the lower Firehole River (Yellowstone National Park) to trout from two hatcheries indicated that these fish had not developed increased tolerance to high temperatures. From these data, Kaya (1978) computed a 168 h ultimate IULT of 26.6 °C which is about 3 °C lower than the highest CT maximum measured for this species in our study and those of Lee & Rinne (1980) and Strange et al. (1993).

Low temperature tolerance data of rainbow trout are more limited probably because these fish commonly inhabit waters that seasonally reach 0.0 °C or lower, and hence, little interest exists concerning their ability to tolerate cold temperatures. Rainbow trout in our study acclimated to 10, 15 and 20 °C had CT minima of ~ 0.0, 0.2 and 2.0 °C. Loss of equilibrium was not observed in fish acclimated to 10 °C suggesting that their CT minimum would be below 0.0 °C which allows them to survive temperatures in waters that are ice covered.

The most complete picture of rainbow trout low temperature tolerance is provided by Becker et al. (1977) who measured CT minima reported as LOE₅₀ (the temperature at which 50% of a sample lost equilibrium) at five different rates of temperature decrease for rainbow trout acclimated to 10, 15 and 20 °C. Becker et al. (1977) estimated CT minima of < 0.0, 0.7 and 2.0 °C for rainbow trout acclimated at 10, 15 and 20 °C and exposed to a 0.3 °C min⁻¹ rate of temperature change. These values are nearly identical to ours (< 0.0, 0.2 and 2.0 °C). At slower rates of temperature decrease (0.167, 0.083, 0.05 and 0.0167 °C min⁻¹) rainbow trout had lower CT minima, suggesting that fish may have gained low temperature tolerance acclimation during the trials. We found no published reports of ILLT for rainbow trout.

In addition to establishing lethal limits for the game fishes studied, our interspecies CT minima and CT maxima comparisons allow us to interpret thermal limiting effects as they relate to the fishes' distribution in nature. Of the two warm-water species, channel catfish was more tolerant to both high and low temperatures than largemouth bass. In fact, channel catfish had a CT maxima 1.8 °C higher and a CT minima 0.5 °C lower than those of largemouth bass when both species were acclimated to 30 and 20 °C, respectively. These tolerance differences result in about a 7% difference in overall tolerance scope, and the increase is reflected in the larger zoogeographic range for channel catfish compared to largemouth bass (Robison & Buchanan 1982). Not surprisingly, rainbow trout had the lowest tolerance of high and highest tolerance of low temperatures among these three species. This result is consistent with the more northern distribution of this species.

It is possible that some of the observed differences in temperature tolerance between rainbow trout and the other two species is related to size (age) differences, since rainbow trout in our research were considerably smaller than either channel catfish or largemouth bass. Only a few studies have examined the effects of either ontogeny or scaling of fishes on temperature tolerance, e.g. Paladino & Spotila (1978) and Guest (1985). We found no studies examining these effects on temperature tolerance of rainbow trout. Hence, the similarity of CT maxima of rainbow trout in our study and those of Strange et al. (1993) and Lee & Rinne (1980), where fish varied in length from 4 to 20 cm, suggest that at least over this size range, upper temperature tolerance of rainbow trout is quite consistent.

The effect of acclimation temperature on temperature tolerances is reflected mathematically by the magnitude of the slopes relating these two variables. As acclimation temperature increased, both CT maxima and CT minima increased in all three species. The former represents a gain in heat tolerance and the latter, a loss of cold tolerance. Gain in heat tolerance and loss of cold tolerance were different both intraspecifically and interspecifically. It is noteworthy that over the 10 °C temperature range studied, slopes relating acclimation temper-

ature to CT minima are approximately twice those relating acclimation temperature to CT maxima for each of the three species. For example, CT maxima in rainbow trout increased 0.18 °C for each 1 °C increase in acclimation temperature, while CT minima decreased 0.36 °C for each 1 °C decrease in acclimation temperature. Equivalent values for channel catfish and largemouth bass are 0.40 and 0.71 °C, and 0.32 and 0.76 °C. This consistent trend suggests that changes in acclimation temperature have a greater effect on low temperature tolerance than tolerance of high temperatures.

In general, it appears that acclimation temperature has a larger effect on changes in upper temperature tolerance in fishes with wider temperature tolerances, i.e., more eurythermal species. Channel catfish and largemouth bass gained heat tolerance, i.e., increased CT maxima, by approximately 0.40 and 0.32 °C, respectively, for each 1 °C increase in acclimation temperature. This gain in heat tolerance is consistent with previous studies of warmwater fishes. Slopes relating upper temperature tolerance (either IULT or CT maxima) to acclimation temperature in brown bullhead, *Ictalurus nebulosus*, is 0.31 °C (Brett 1944), goldfish, *Carassius auratus*, is 0.33 °C (Fry et al. 1942), 0.46 °C in fathead minnows, *Pimephales promelas* (Richards & Beiting 1995), and 0.28 °C in sheepshead minnow, *Cyprinodon variegatus* (Bennett & Beiting 1997). In contrast, coldwater species including salmonids have far smaller slopes relating heat gain and acclimation temperature. Our slope for rainbow trout relating CT maxima and acclimation temperature, 0.18 °C, is consistent with values of 0.14 °C for brook charr, *Salvelinus fontinalis* (Fry et al. 1946), 0.12 °C for chum salmon, *Oncorhynchus keta* (Brett 1952) and approximately 0.2 °C in sockeye salmon, *O. nerka* (Brett 1952). A study comparing the rates of gain of heat tolerance in these two groups would be interesting; one could hypothesize that since the slopes for rainbow trout are smaller, they should be able to reacclimate more rapidly than species with larger slopes relating tolerance and acclimation temperature. By minimizing CT maxima differences across their thermal acclimation range (only a 1.8 °C difference between 10 and 20 °C in our data), rainbow trout retain nearly maximal heat tolerance

regardless of ambient temperatures. This thermal mode has an obvious benefit to fishes such as salmonids that are likely to encounter near lethal high temperatures.

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