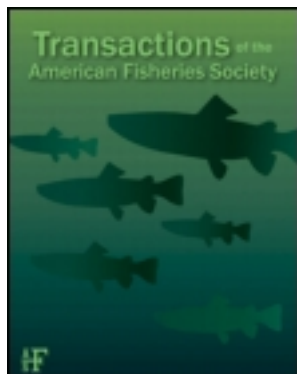


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Relationship between Fish Size and Upper Thermal Tolerance

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ARTICLE

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Abstract

Using critical thermal maximum (CTMax) tests, we examined the relationship between upper temperature tolerances and fish size (fry–adult or subadult lengths) of rainbow trout *Oncorhynchus mykiss* (41–200-mm TL), Apache trout *O. gilae apache* (40–220-mm TL), largemouth bass *Micropterus salmoides* (72–266-mm TL), Nile tilapia *Oreochromis niloticus* (35–206-mm TL), channel catfish *Ictalurus punctatus* (62–264 mm-TL), and Rio Grande cutthroat trout *O. clarkii virginalis* (36–181-mm TL). Rainbow trout and Apache trout were acclimated at 18°C, Rio Grande cutthroat trout were acclimated at 14°C, and Nile tilapia, largemouth bass, and channel catfish were acclimated at 25°C, all for 14 d. Critical thermal maximum temperatures were estimated and data were analyzed using simple linear regression. There was no significant relationship ($P > 0.05$) between thermal tolerance and length for Nile tilapia ($P = 0.33$), channel catfish ($P = 0.55$), rainbow trout ($P = 0.76$), or largemouth bass ($P = 0.93$) for the length ranges we tested. There was a significant negative relationship between thermal tolerance and length for Rio Grande cutthroat trout ($R^2 = 0.412$, $P < 0.001$) and Apache trout ($R^2 = 0.1374$, $P = 0.028$); however, the difference was less than 1°C across all lengths of Apache trout tested and about 1.3°C across all lengths of Rio Grande cutthroat trout tested. Because there was either no or at most a slight relationship between upper thermal tolerance and size, management and research decisions based on upper thermal tolerance should be similar for the range of sizes within each species we tested. However, the different sizes we tested only encompassed life stages ranging from fry to adult/subadult, so thermal tolerance of eggs, alevins, and larger adults should also be considered before making management decisions affecting an entire species.

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Rapid global climate change (Solomon et al. 2007), livestock grazing (Platts 1991; Trimble 1994), removal of riparian cover (Ringle and Hall 1975; Johnson and Jones 2000), and rapid urbanization (LeBlanc et al. 1997) are contributing to increased stream temperatures worldwide, and stream temperatures may be changing at a rate too rapid for many fish species to adapt. Therefore, knowledge of thermal tolerance of a fish species is important so managers can understand how changing stream temperature profiles will affect a particular species. Knowledge of a species' thermal requirements will also help managers select courses of action that give a species the best chance to survive and thrive in their native habitat.

The critical thermal maximum (CTMax) test (Cowles and Bogert 1944; Becker and Genoway 1979) has been widely used to assess and compare thermal tolerance of fish. This test is simple and rapid, and entails heating water that contains a fish until the fish reaches a predetermined endpoint (i.e., unable to remain upright for 30 s). End points of CTMax include initial and final loss of equilibrium (which is the temperature at which the failure of the righting response occurs), onset of spasms, and death (defined by the cessation of opercular movement; Becker and Genoway 1979; Rutledge and Beitingner 1989; Lutterschmidt and Hutchison 1997; Carveth et al. 2006). Final loss of equilibrium or the loss of the righting response is biologically significant because at this stage, fish are unable to escape conditions that will eventually lead to their death (Beitingner et al. 2000). This endpoint is also the most commonly used for assessing the CTMax of fish (Becker and Genoway 1979; Lutterschmidt and Hutchison 1997).

The CTMax test does not mimic thermal regimes experienced by fish in the environment, where temperature changes are typically slower and fish are exposed to high temperatures over longer time periods (Selong et al. 2001). Therefore, it tends to overestimate what the fish can endure over an extended time in the wild. However, the CTMax test is effective for comparing relative tolerance of different fishes and has been successfully used for this purpose in many studies (Becker and Genoway 1979; Beitingner et al. 2000).

Currently, little information exists describing the relationship between life stage or size and thermal tolerance of a given species. Preferences for specific water temperatures can vary among different-sized fish within a species (Kwain and McCauley 1978; McCauley and Huggins 1979; Spotila et al. 1979; Morita et al. 2010), but less is known about whether thermal tolerance varies by size. For example, although small rainbow trout were shown to prefer warmer water than larger rainbow trout, this does not imply a difference in thermal tolerance exists among sizes (Kwain and McCauley 1978). Therefore, variation in thermal tolerance among sizes must be known to evaluate overall thermal tolerance for a species. Furthermore, if a body of water approaches the thermal limit for a given species, it is critical to know if all sizes have a similar thermal tolerance to evaluate the risk of elevated temperatures to all life stages. We evaluated tolerance of a range of different-sized fish, encom-

passing life stages from fry to adult or subadult of five different fish species, to determine if fish size is important when estimating thermal tolerance of a species. We selected an assemblage of fish that included both warmwater and coldwater species that were available in a wide range of sizes. These species represented a variety of threatened and endangered fishes, important North American sport fishes and cultured fishes, and fishes that can develop nuisance populations. We tested Apache trout *Oncorhynchus gilae apache*, rainbow trout *O. mykiss*, Rio Grande cutthroat trout *O. clarkii virginialis*, largemouth bass *Micropterus salmoides*, Nile tilapia *Oreochromis niloticus*, and channel catfish *Ictalurus punctatus*. In addition to providing valuable information for species restoration efforts, these data will allow those interested in studying thermal tolerance of a species to utilize the most sensitive life stage to determine tolerance.

METHODS

Tests were conducted at the following locations: rainbow trout at the Arizona Game and Fish Department (AZGFD) Bubbling Ponds Fish Hatchery in Cornville, Arizona; Rio Grande cutthroat trout at New Mexico State University, Las Cruces, New Mexico; all other species at the University of Arizona, Tucson, Arizona. Rainbow trout (41–200-mm TL; $n = 40$) were held in 1,389-L, 152-cm-diameter circular tanks filled to just over 1,000 L. Biofilters, constructed in 121-L plastic garbage cans, were established 3 weeks before fish were placed in tanks. In the biofilter, water upflowed through 0.05 m³ of Kaldness biofilter media (Aquatic Eco-Systems, Apopka, Florida) and two layers of reticulated filter foam at about 1,900 L/h, providing both biological and mechanical filtration. Once water was chilled to 18°C, rainbow trout were divided by size-groups into mesh baskets placed within the tanks. The mesh baskets effectively separated fish into three to four different size-groups, allowing for water exchange and minimizing interactions among different-sized fish. Fish were kept on a 12 h light: 12 h dark photoperiod and acclimated for at least 14 d, and they were fed Silver Cup crumbled salmon–trout number 3 (Murray, Utah) to satiation every day except 24 h before CTMax tests. Nets were placed over the tank to prevent fish from jumping out of the tank. Water quality was analyzed daily for pH, nitrite, nitrate, and ammonia with an API water quality testing kit (Mars Fishcare, Chalfont, Pennsylvania).

After the acclimation period, 40 rainbow trout were randomly selected for each thermal tolerance test. Each fish was caught with a dip net and quickly placed in a beaker or stainless steel stock pot, depending on fish size. For each trial, fish were allowed to acclimate for approximately 5 min to reduce the effects of the stress on thermal response. Each container sat on 1-cm square plastic grating in a stainless steel water bath heated by Fisher Scientific 645-cm² hot plates. Air diffusers were placed in the water bath and in beakers for smaller fish, and stock pots or clear acrylic tanks for the larger fish to facilitate

water mixing and provide oxygen for fish during the experiments. Fisher Scientific digital thermometers were placed in each container, and plastic grating was placed over the top to prevent fish from jumping out. Digital thermometers were calibrated using an ISO thermometer. Temperature was increased at $0.3^{\circ}\text{C}/\text{min} \pm 0.2^{\circ}\text{C}$ ($18^{\circ}\text{C}/\text{h}$) as recommended by Beitinger et al. (2000). Temperatures were recorded each minute until fish finally lost equilibrium (i.e., inability to remain upright for 30 s; temperature reported was that at the beginning of the 30-s period). Final loss of equilibrium was used as the endpoint for each trial as it is the most commonly used endpoint for fish (Smale and Rabeni 1995; Bennett and Beitinger 1997; Selong et al. 2001; Carveth et al. 2006). After each experimental endpoint was reached, total length of fish was measured and fish were placed in another tank to recover.

Other species were tested following the same procedures as above, except for differences in acclimation temperatures. Rio Grande cutthroat trout were acclimated to 14°C , Apache trout and rainbow trout to 18°C , and all other species to 25°C . Acclimation temperatures were selected to fall within the range of those used in previous studies, typically around the midpoint and always far below the eventual CTMax. Lengths and sample sizes tested were as follows: Apache trout, 40–220-mm TL and $n = 40$; largemouth bass, 72–266-mm TL and $n = 40$; Nile tilapia, 35–206-mm TL and $n = 40$; channel catfish, 62–264-mm TL and $n = 40$, and Rio Grande cutthroat trout, 36–181-mm TL and $n = 49$. All fish were obtained from hatchery sources: Apache trout from AZGFD; Nile tilapia from the Environmental Research Lab, University of Arizona; channel catfish and largemouth bass from Brown's Fish Farm (Pima, Arizona); and Rio Grande cutthroat trout from the New Mexico Game and Fish Department. Once all tests were completed, fish size (TL) was regressed against upper thermal tolerance for each species to identify relationships between size and upper temperature tolerance. We hypothesized that there would be no significant relationship between CTMax and total length. Linear regression analysis (Stata release 11.0 [Academic] 1985–2009) was used to determine if a significant relationship ($\alpha = 0.05$) existed between total length (mm) and CTMax ($^{\circ}\text{C}$) for each species.

RESULTS

There were no detectable relationships between upper thermal tolerance and total length for largemouth bass ($R^2 = 0.0002$, $P = 0.93$), Nile tilapia ($R^2 = 0.025$, $P = 0.33$), rainbow trout ($R^2 = 0.0026$, $P = 0.76$), and channel catfish ($R^2 = 0.0096$, $P = 0.55$; Figure 1). For Apache trout, there was a significant, yet small negative relationship ($R^2 = 0.1374$, $P = 0.028$; Figure 1) between total length and upper thermal tolerance. For Rio Grande cutthroat trout, there was also a significant negative relationship between total length and upper thermal tolerance ($R^2 = 0.412$, $P < 0.001$; Figure 1). However, the difference in tolerance between largest and smallest sizes tested was 0.8°C for Apache trout and 1.3°C for Rio Grande cutthroat trout. Fur-

thermore, only 14% of the variability in thermal tolerance for Apache trout and less than 42% for Rio Grande cutthroat trout can be explained by size.

DISCUSSION

The CTMax test was effective for measuring the relationship between life stage and thermal tolerance for the species we tested. The CTMax test is not intended to mimic environmental conditions similar to longer-term tests, such as the acclimated chronic exposure method (Zale 1984; Selong et al. 2001). The CTMax procedure is meant to be a rapid means to determine the relative ability of a fish to tolerate high temperatures (Becker and Genoway 1979; Selong et al. 2001; Carveth et al. 2006). Final loss of equilibrium was the only endpoint examined in this experiment and is the most widely used endpoint in CTMax tests (Smale and Rabeni 1995; Lutterschmidt and Hutchison 1997; Currie et al. 1998; Beitinger et al. 2000; Selong et al. 2001; Carveth et al. 2006). Final loss of equilibrium may be more useful than death or other endpoints because it marks a point at which a fish no longer has the capacity to escape conditions that will lead to its death (Beitinger et al. 2000). Using a test that employs a quick rate of change prevents acclimation to changing temperatures (Lutterschmidt and Hutchison 1997).

The range in regressed CTMax values we obtained for the various species from the regression of CTMax versus total length were within $1\text{--}2^{\circ}\text{C}$ of those reported by others testing the same species using similar acclimation temperatures, rates of change and a loss-of-equilibrium endpoint (Beitinger et al. 2000). For largemouth bass in our study, CTMax ranged from 35.0°C to 35.4°C , compared with 36.3°C for largemouth bass acclimated at 26°C and a rate of change of $0.017^{\circ}\text{C}/\text{min}$ in a study by Smale and Rabeni (1995). For channel catfish in our study, CTMax ranged from 39.9°C to 40.0°C , while Currie et al. (1998), using the same acclimation temperature and rate of change, obtained a CTMax of 38.7°C . For Rio Grande cutthroat trout in our study, CTMax ranged from 28.6°C to 29.8°C , while Heath (1963) found that CTMax of coastal cutthroat trout *O. clarkii clarkii* acclimated to the same temperature (14°C) but under a rate of change of $0.4^{\circ}\text{C}/\text{min}$ was 29.1°C . Apache trout CTMax ranged from 29.7°C to 30.5°C in our study, but in Lee and Rinne (1980) it was 29.4°C with an acclimation temperature of 20°C and a rate of change of 0.02. Rainbow trout CTMax in our study was high ($31.2\text{--}31.2^{\circ}\text{C}$) compared with those of other similar studies. For rainbow trout acclimated to 20°C with a $0.3^{\circ}\text{C}/\text{min}$ and $0.02^{\circ}\text{C}/\text{min}$ rate of change, CTMax was 29.8°C (Currie et al. 1998) and 29.4°C (Lee and Rinne 1980), respectively. Nile tilapia CTMax in our study ($40.3\text{--}40.5^{\circ}\text{C}$) was somewhat lower than that reported in Denzer (1968), where fish acclimated to 29°C with a $0.1^{\circ}\text{C}/\text{min}$ rate of change had a CTMax of 42°C .

We found no significant relationship between life stages encompassing fry to subadult/adult and thermal tolerance for rainbow trout, Nile tilapia, channel catfish, or largemouth bass.

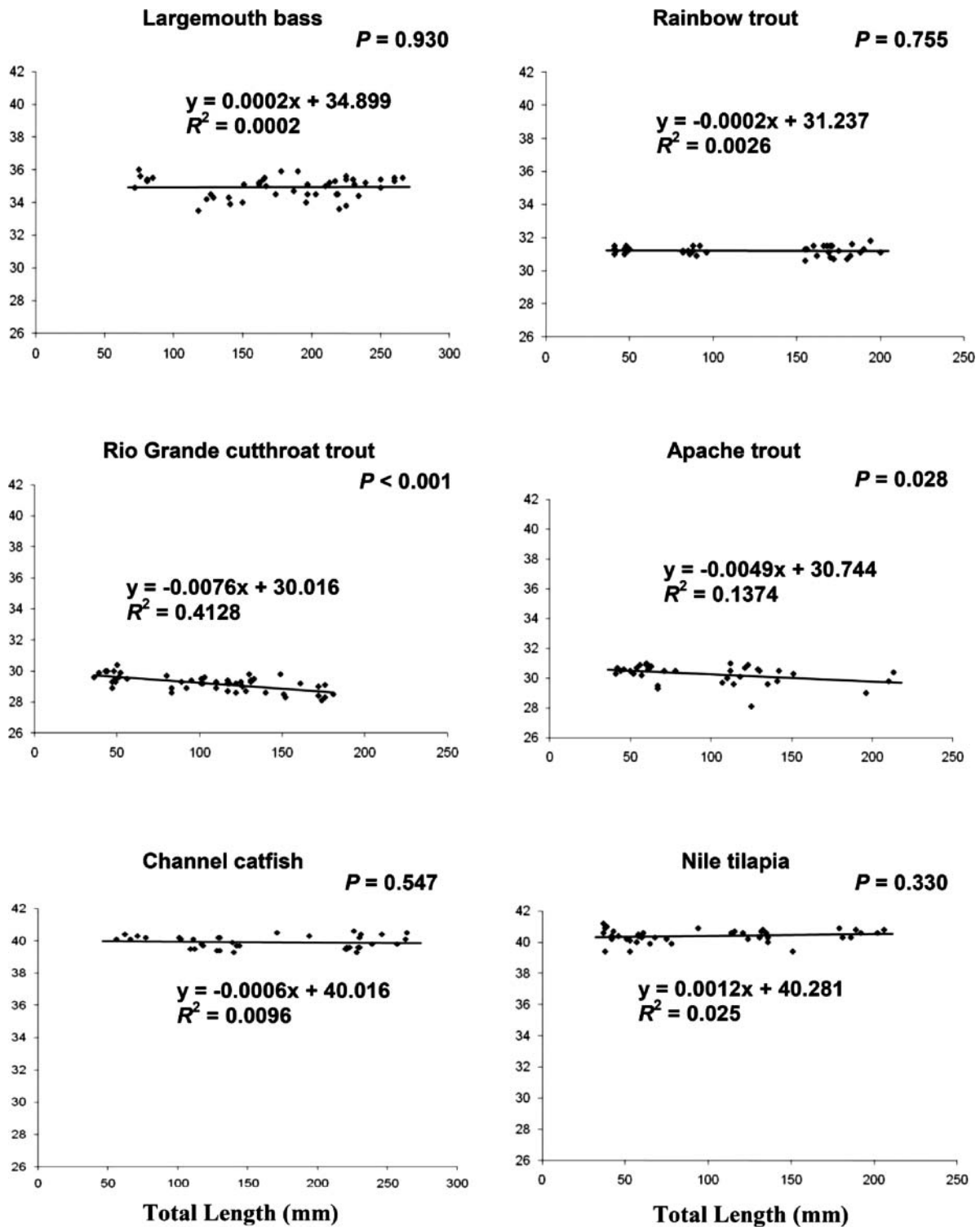


FIGURE 1. Critical thermal maximum for six freshwater species in relation to total length. Acclimation temperatures are as follows: Rio Grande cutthroat trout, 14°C; Apache trout and rainbow trout, 18°C; all other species, 25°C.

Upper temperature tolerances of different life stages of fishes have been evaluated. However, tests on various-sized fish of a species have typically been conducted in different studies that use unequal rates of heating, different acclimation temperatures, and dissimilar tolerance tests, making results difficult to compare. The few tests conducted on various-sized fish where results could be compared reached similar conclusions to ours. Wagner et al. (2001) tested upper thermal tolerance of four stocks of cutthroat trout and found no differences among fish with average weights ranging from 0.7 to 2.9 g. Ospina and Mora (2004) found little variation in the CTMax and critical thermal minimum (CTMin) from juvenile to adult sizes of seven tropical reef fish species.

In contrast, a small negative relationship existed between size and thermal tolerance for Apache trout and Rio Grande cutthroat trout. Selong et al. (2001) noted that juvenile salmonids are the most vulnerable life stage to summer stream temperature increases due to anthropogenic causes. Juvenile Apache trout have been shown to select shallower and faster water than adults (Kitcheyan 1999; Cantrell et al. 2005). Apache trout fry were found in miniature pools in runs or in shallow areas at the edge of pools (Wada 1991). Since shallow water will be most affected by ambient temperature and anthropogenic influences, the smallest fish, which are more likely to occupy these environments, would benefit from having a slightly higher thermal tolerance than adults.

There are some limitations to our study. Due to availability, we were only able to test fish that ranged from fry to small adults or subadults (fish from age 0 to 2+). Although our findings can only be applied to the sizes and species tested, they suggest temperature tolerance may not differ substantially among different-sized fish of the same species. We did not test temperature tolerance of eggs, sac fry, or large adults. Temperature tolerances obtained from CTMax and egg hatching trials can be difficult to compare, especially when temperature tolerances are similar. Eggs of some of the coldwater species we tested do not tolerate temperatures as high as fishes (Wagner et al. 2006; Recsetar 2011), but comparisons between adults and egg temperature tolerance are less clear for warmwater fishes (Kelley 1968; Rana 1990). Further research on how the temperature tolerance of eggs, sac fry, and large adults compares with the life stages we tested would be beneficial.

The CTMax assumes all fish sizes and species are affected at the same rate. Although the rapid rate of heating eliminates acclimation of a fish during the test, it fails to account for differences in body mass or surface area to volume ratio that may produce longer lag times between water temperature and body temperature in larger fish. Smaller fish have a higher surface area-to-volume ratio than large fish and could be affected by rapidly increasing temperatures sooner than larger fish, thus succumbing to loss of equilibrium earlier. However, a relatively slower rate of temperature increase, such as we used in our experiment (e.g., 0.3°C/min), is thought to minimize effects of a smaller body size heating faster than a larger body size (Becker

and Genoway 1979). Lutterschmidt and Hutchison (1997) found no significant lag time between water temperature and body temperature in different-sized bluegill *Lepomis macrochirus* up to 165 g when the heating rate was 1.0°C/min. Cox (1974) found that large bluegill (mean TL = 140 mm) lost equilibrium at lower temperatures than small bluegill (mean TL = 73 mm), but large bluegill ceased opercular beating at higher temperatures than small bluegill. He concluded that his results did not follow a pattern that suggested body temperature lagged behind water temperature.

Our fish were obtained from hatchery sources, and some differences may exist between the results we obtained and those that would be obtained using wild fish. Evidence of differences in temperature tolerance between wild and hatchery fishes of a specific species is mixed. Scope of activity for hatchery and wild rainbow trout was similar at 15°C and 20°C, but was significantly higher for wild fish at 25°C (Dickson and Kramer 1971). Higher temperature tolerance is suspected in domesticated Atlantic salmon versus wild individuals (Gross 1998), but wild brook trout *Salvelinus fontinalis* had higher temperature tolerance than hatchery stocks (Vincent 1960). Kaya (1978) found few differences in upper temperature tolerances in wild rainbow trout from the Firehole River, Wyoming, and two hatchery strains.

In conclusion, our results suggest that upper thermal tolerance varies little from fry to adult for the species we tested. However, the slightly higher thermal tolerance demonstrated by smaller Apache trout and Rio Grande cutthroat trout may allow the smallest individuals to better survive somewhat higher water temperatures that commonly occur in shallow stream margins they inhabit. Further research on large adults, sac fry, and eggs is important to evaluate how thermal tolerance varies for all life stages of a species. If thermal tolerance varies little by size in other fish species, small size-classes could be used for further thermal tolerance testing. These fish would be less expensive, more convenient to hold and transport, and easier to handle.

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