Comparison of Upper Thermal Tolerances of Native and Nonnative Fish Species in Arizona

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Abstract.—We used a lethal thermal method to estimate the upper thermal tolerances of 11 native and 7 nonnative fish species found throughout southern Arizona. Fish were acclimated to 25°C and 30°C. For all species tested, an increase in acclimation temperature resulted in a higher thermal tolerance value. Among the species acclimated to 25°C, desert pupfish *Cyprinodon macularius*, western mosquitofish *Gambusia affinis*, and Gila topminnow *Poeciliopsis occidentalis* were most tolerant to high temperature. Speckled dace *Rhinichthys osculus*, spikedace *Meda fulgida*, and loach minnow *R. cobitis* were least tolerant. Many native species demonstrated a limited ability to extend their upper temperature tolerances via acclimation. Our data suggest that several native species may be sensitive to increasing annual and large daily temperature fluctuations in Arizona's streams and rivers. Although southwestern native fishes were previously believed to be tolerant to high temperature due to their evolution in desert environments, this study suggests that many of these fishes are less tolerant than previously thought. In addition, many fishes introduced from the eastern United States had higher temperature tolerances than some of the native desert species tested. Increases in stream temperatures in Arizona could reduce the habitat available for native fishes and therefore may favor those nonnative species with higher thermal tolerances.

Deterioration in the quality of streams in the southwestern United States over the past 100 years has resulted in the decline or complete loss of many unique and ecologically sensitive endemic fish species. Causes for reductions in stream quality include introductions of exotic organisms and novel diseases, permanent changes in stream velocity and volume, deterioration of water quality, and alteration of habitat (Lowe et al. 1967; Moyle et al. 1986; Rinne et al. 1986; Douglas et al. 1994). In particular, rising water temperatures have become a concern, compelling fisheries managers to evaluate the effects of increasing water temperatures on fish health and survival (Barber et al. 1970; Poole and Berman 2001; Chatterjee et al. 2004).

Arizona stream temperatures are influenced primarily by groundwater and snowmelt. Declines in both have led to reductions in stream volume (Deacon et al. 1987), which combined with loss of riparian vegetation, can result in increased daily and annual temperature fluctuations (Swift and Messer 1971; Ebersole et al. 2001; USGS 2005). Consequently, temperatures in degraded streams are now more likely to be influenced by atmospheric temperature. Others have found stream temperatures to be correlated with ambient air temperatures (Morrill et al. 2005). From 1907 to 2006, mean annual air temperature in Arizona rose by 1.5°C (NOAA 2006).

It is well known that small changes in water temperature can have considerable consequences for freshwater fishes (Morgan et al. 2001), affecting a wide variety of life history, behavioral, and physiological responses (Brett 1956; Myrick and Cech 2000; Lass and Spaak 2003). The thermal tolerance of an organism is influenced by many biotic and abiotic factors; acclimation temperature and thermal history are among the most important (Lutterschmidt and Hutchison 1997b; Beitinger et al. 2000; Chung 2001). Water temperature has been described as an important environmental resource, and fish often compete for favorable temperatures (Magnuson et al. 1979). A temperature increase beyond the optimal range for any species can influence the capacity to function properly (Crawshaw 1977). Elevated temperature can diminish swimming ability in fishes (MacNutt et al. 2004) and can result in poor body condition by reducing cardiac performance and limiting the amount of available oxygen (Brett 1956; Fry 1967; Crawshaw 1977). Temperature can influence metabolic activities and have lasting effects on behavior, such as predator avoidance, migration, and spawning (Reynolds 1977).

Across North America, incidences of heat death in fishes are becoming more common (Bailey 1955; Zimmerman and Kucera 1977; Matthews et al. 1982; Mundahl 1990; Castleberry and Cech 1992). Mortalities related to high water temperatures are thought to occur frequently in Arizona, particularly in stagnant

shallow waters with high ambient temperatures and direct sun exposure. Summer temperatures ranging from 35.0°C to 40.3°C have been recorded frequently in small Arizona streams (Deacon and Minckley 1974; USGS 2005). Existing research suggests that these temperatures approach the upper thermal tolerances of some native fishes of the southwestern United States (John 1964; Lowe and Heath 1969).

Because most evolved in a desert environment, Arizona native fishes are considered to be tolerant to high temperature; however, little data are available to support this idea. Available information is limited to field observations and a small number of laboratory studies (John 1964; Lowe and Heath 1969; Minckley and Barber 1971; Deacon and Minckley 1974). Field observations are often unreliable, as it is difficult to ascertain whether a fish died because of high temperatures or other environmental factors. Under natural conditions, many nonthermal factors can interfere with thermal responses, making an estimate of thermal tolerance obtained in the field less accurate. Laboratory results derived by a variety of methods are often ambiguous and difficult to interpret due to differences in acclimation temperatures, heating rates, undefined behavioral endpoints, and other factors (Lutterschmidt and Hutchison 1997b). This often makes it difficult to compare the thermal tolerances of fish species among studies. Lethal limits typically are comparable only when repeated when tests are run under similar conditions and similar acclimation temperatures are used (Brett 1956). Therefore, the objectives of this research were to use a lethal thermal method (LTM) to estimate and compare the upper thermal tolerances of 11 native and 7 nonnative freshwater fishes found throughout Arizona.

Methods

Fish collection.—The 11 native and 7 nonnative fish species used in our study included those found mainly in warmwater streams (Table 1). We used small seine nets (1.6-mm mesh) to collect wild fish in the spring and summer of 2003 and 2004 from Aravaipa Creek, Bonita Creek, San Pedro River, Verde River, and Buenos Aires National Wildlife Refuge stock tanks. We collected fish of similar total lengths (TL, 30–70 mm); however, fathead minnow, yellow bullheads, bluegills, and green sunfish measured 80–116 mm TL. Gila topminnow and Gila chub were artificially propagated at the University of Arizona. Razorback suckers and bonytails were propagated at the Willow Beach National Fish Hatchery, Arizona. All species were treated for *Ichthyophthirius multifiliis* with a 3% formaldehyde solution (Quick Cure; Aquarium Prod-

ucts, Glen Burnie, Maryland) for at least 10 d upon arrival to the laboratory.

When possible, we limited tests to summer so that photoperiod and time of capture would be similar among tests. Long photoperiods are typically associated with increased heat tolerance (Fry 1967; Lutterschmidt and Hutchison 1997b).

Acclimation and LTM.—The critical thermal method (CTM), as described by Becker and Genoway (1979), is the most common method used to quantify fish tolerance to extreme high and low temperatures. In a CTM test, temperature is increased or decreased at a constant linear rate until a predefined sublethal endpoint is reached. The CTM provides a standard for evaluating the thermal requirements of an organism and is often used to make comparisons among species (Lutterschmidt and Hutchison 1997b). The CTM is a preferred method in the field of thermal ecology because of the small number of animals needed and the short time required to complete a test. The use of similar acclimation temperatures and heating rates also facilitates comparisons of data from several studies. However, because nonlethal endpoints can be subjective and are inconsistent among studies, we used a LTM, which was adapted from Becker and Genoway (1979). The LTM is similar to the CTM method except fish are followed to temperature at death instead of stopping tests at a nonlethal endpoint. Using the LTM, we generated three sublethal estimates and one lethal estimate of thermal tolerance for each fish. These endpoints were as follows: (1) initial loss of equilibrium, which is the temperature at which first loss of equilibrium occurs (Rajaguru 2002); (2) final loss of equilibrium, or the temperature at which the failure of righting response occurs (Becker and Genoway 1979; Rutledge and Beitinger 1989; Smale and Rabeni 1995); (3) temperature before death, where fish are experiencing no movement but flaring opercula (Beitinger et al. 2000); and (4) death, which is defined as the cessation of opercular movement (Becker and Genoway 1979).

We found no evidence that the upper thermal tolerance of fish is affected by low-concentration formalin treatments. However, to avoid affecting the experiment by the initial formaldehyde prophylactic treatment, we held fish for at least 14 d posttreatment during the acclimation period before testing. We used 200-W Ebo-Jager aquarium heaters to maintain 10–12 fish of each species in well-aerated, rectangular, 75-L glass aquaria at 25 ± 0.1°C and at 30 ± 0.1°C (mean ± 95% confidence interval). Acclimation to a temperature can take from a few days (MacNutt et al. 2004; Ospina and Mora 2004) to 30 d (Bennett and Beitinger 1997). We chose these acclimation temper-

TABLE 1.—Native and nonnative Arizona fishes acclimated to 25°C or 30°C and subjected to lethal thermal maximum tests (* = nonnative; $n \geq 12$ fish/species). Temperatures are reported for four endpoint initial loss of equilibrium (ILOE), final loss of equilibrium (FLOE), flaring opercula (FO), and death (DE). Confidence intervals (95%) are indicated for each value.

Species	Acclimation at 25°C				Acclimation at 30°C			
	ILOE	FLOE	FO	D	ILOE	FLOE	FO	D
Desert pupfish *Cyprinodon macularius*	40.0 ± 0.3	40.0 ± 0.3	41.4 ± 0.3	41.8 ± 0.2	41.3 ± 0.3	42.0 ± 0.3	42.4 ± 0.2	42.7 ± 0.3
Western mosquitofish *Gambusia affinis**	39.5 ± 0.3	39.5 ± 0.3	40.5 ± 0.2	40.7 ± 0.2	41.4 ± 0.8	41.7 ± 0.3	42.1 ± 0.4	42.1 ± 0.4
Gila topminnow *Poeciliopsis occidentalis*	38.4 ± 0.4	38.4 ± 0.4	39.4 ± 0.3	39.4 ± 0.3	41.1 ± 0.4	41.3 ± 0.6	41.5 ± 0.3	42.1 ± 0.3
Red shiner *Cyprinella lutrensis**	37.6 ± 0.6	37.6 ± 0.6	39.3 ± 0.1	39.5 ± 0.3	39.7 ± 0.3	40.4 ± 0.6	40.6 ± 0.2	40.9 ± 0.2
Yellow bullhead *Ameiurus natalis**	38.0 ± 0.4	38.0 ± 0.4	39.2 ± 1.3	39.8 ± 0.9				
Largemouth bass *Micropterus salmoides**	37.8 ± 0.3	37.8 ± 0.3	38.8 ± 0.4	39.1 ± 0.4				
Longfin dace *Agosia chrysogaster*	38.2 ± 0.1	38.2 ± 0.1	38.7 ± 0.1	38.9 ± 0.1	40.5 ± 0.2	40.8 ± 0.2	40.9 ± 0.1	41.1 ± 0.1
Razorback sucker *Xyrauchen texanus*	36.7 ± 0.2	36.7 ± 0.2	38.5 ± 0.1	39.1 ± 0.2	39.1 ± 0.3	39.8 ± 0.2	40.2 ± 0.2	40.3 ± 0.1
Green sunfish *Lepomis cyanellus**	37.4 ± 0.5	37.4 ± 0.5	38.4 ± 0.3	39.3 ± 0.2	40.2 ± 0.5	40.7 ± 0.2	41.1 ± 0.2	41.5 ± 0.2
Bonytail *Gila elegans*	37.2 ± 0.4	37.2 ± 0.4	38.2 ± 0.4	38.7 ± 0.4	39.0 ± 0.3	39.5 ± 0.3	39.9 ± 0.2	40.2 ± 0.2
Gila chub *Gila intermedia*	37.0 ± 0.2	37.0 ± 0.2	37.9 ± 0.3	38.3 ± 0.2	38.1 ± 0.3	38.5 ± 0.3	38.7 ± 0.4	39.0 ± 0.3
Roundtail chub *Gila robusta*	36.6 ± 0.1	36.6 ± 0.1	37.5 ± 0.3	38.0 ± 0.3				
Bluegill *L. macrochirus**	35.8 ± 0.4	35.8 ± 0.4	37.2 ± 0.4	37.3 ± 0.3	38.7 ± 0.3	39.1 ± 0.2	39.4 ± 0.2	39.6 ± 0.2
Spikedace *Meda fulgida*	34.7 ± 0.5	34.7 ± 0.5	37.0 ± 0.3	37.0 ± 0.4	36.9 ± 0.7	38.2 ± 0.5	38.8 ± 0.4	39.1 ± 0.3
Fathead minnow *Pimephales promelas**	36.1 ± 1.2	36.1 ± 1.2	36.5 ± 1.2	36.9 ± 1.1				
Desert sucker *Catostomus clarkii*	35.1 ± 0.3	35.1 ± 0.4	36.5 ± 0.2	36.9 ± 0.2	36.7 ± 0.8	37.0 ± 0.4	37.3 ± 0.4	37.6 ± 0.2
Loach minnow *Rhinichthys cobitis*	35.3 ± 0.2	35.3 ± 0.2	36.4 ± 0.1	36.5 ± 0.1	36.1 ± 0.3	36.4 ± 0.3	36.5 ± 0.4	36.8 ± 0.5
Speckled dace *R. osculus*	34.4 ± 0.4	34.4 ± 0.4	35.9 ± 0.2	36.0 ± 0.4	35.8 ± 0.6	36.9 ± 0.1	37.0 ± 0.1	36.9 ± 0.3

atures because they are often encountered in streams throughout southern Arizona and are commonly cited in the literature (Beitinger et al. 2000). Due to the limited availability of the desired size-class in the rivers that we sampled, fathead minnow, largemouth bass, and yellow bullheads were tested only at 25°C. Large windows in the laboratory provided natural light cycles. We fed fish daily to satiation with a combination of brine shrimp *Artemia* spp., daphnia *Daphnia* spp., bloodworms *Chironomus* spp., spirulina *Arthrospira platensis*, and tropical fish food flakes. Diet composition was varied by species. We used a siphon to remove unconsumed food every other day. We also removed approximately 20% of the tank water three to four times per week and replaced it with dechlorinated (Stress Coat; Aquarium Pharmaceuticals, Inc., Chalfont, Pennsylvania) tap water to prevent the accumulation of ammonia, nitrates, and nitrites. Small water changes ensured that water temperature fluctuated less than 1.0°C each day. We tested water quality, including pH, nitrite, nitrate, alkalinity, and hardness with aquarium test strips. Fish were fasted for 24 h before testing.

In each trial, we tested four fish per species (a total of at least 12 fish/species). Each fish was randomly selected from the holding tank and placed in a 1-L beaker filled with water from the acclimation tank. We placed four beakers in a 42-cm × 28-cm × 11-cm metal basin filled with water. Beakers were elevated on a metal grate, which allowed water flow to reach all sides of the beakers. A powerhead (Model Rio 1100;

TAAM, Inc., Camarillo, California) was placed in the basin to mix the water.

Once a fish was placed in the test beaker, the temperature within the beaker was maintained at the acclimation temperature for 30 min to minimize handling stress. We used portable aerators and air stones within each beaker to keep test water continually mixed and aerated. Once a testing period commenced, the basin was placed on a Fisher Scientific (Hampton, New Hampshire) 120-V, 5.4-A hot plate, and temperature was increased at a constant rate of 0.3°C/min, as is recommended for small-bodied fishes (Beitinger et al. 2000). We adjusted settings on the hot plate at predetermined intervals to ensure a linear rate of change. Rate of change did not vary by more than 0.2°C/min within a given test. We tested each species using a minimum of three trials to account for any variation caused by slight differences in rates of change between each test. During each experiment, one person observed the fish while a second person recorded data and maintained correct hot plate settings. After the fish died, we weighed and measured each individual.

Data analyses.—We tested whether thermal tolerance values within species differed significantly among trials due to small differences in rates of change. One-way analysis of variance (ANOVA) determined that there were no significant effects of trial for each species. Therefore, a mean value (number of replicates $\geq$ 12) was calculated for each species tested at each acclimation temperature for all four endpoints.

We used ANOVA with a Tukey post hoc analysis of honestly significant differences to test for differences in

variability among the four endpoints for all species combined ($\alpha = 0.05$). The most precise endpoint was selected for use in all subsequent statistical analyses. We then tested for differences in effect of acclimation temperature within species by use of two-sample t-tests, and an ANOVA with a Tukey post hoc analysis of honestly significant differences was used to test for differences in temperature tolerances among species. Analyses were conducted with JMP version 4.0.4 (SAS 2001).

The acclimation response ratio (ARR) estimates the ability of fish to alter upper thermal tolerance values with changing acclimation temperature (Claussen 1977). We calculated the ARR for each species by taking the difference between the endpoint at each acclimation temperature (25°C and 30°C) and then dividing by the difference in the acclimation temperatures ($\Delta T = 5$°C).

Results

We were able to successfully assess the lethal thermal tolerances of all 18 species tested. For all species, there was no significant difference between trials (ANOVA: $P > 0.05$). Intraspecific data were pooled and mean values were calculated. The most precise endpoint (Table 1) was flaring opercula (SE = 0.36°C), followed by temperature at death (SE = 0.41°C), final loss of equilibrium (SE = 0.53°C), and initial loss of equilibrium (SE = 0.54°C). Loss of equilibrium, a widely cited endpoint, was not easily observed in some species, and signs of disorientation varied greatly by species. Therefore, we used flaring opercula as the endpoint in all subsequent statistical analysis and to rank the relative thermal tolerances of all species.

Flaring opercula values ranged from 41.4 ± 0.3°C (mean ± 95% confidence interval) for desert pupfish to 35.9°C ± 0.2°C for speckled dace when acclimated at 25°C. Comparison of flaring opercula values indicated a strong difference among species (ANOVA: $F = 138.4$, $P < 0.0001$) for both acclimation temperatures. Overall, tolerance did not seem to be grouped by taxa. Cyprinids comprised the largest family tested and had the widest tolerance, ranging from the lowest (18th) to the fourth-highest tolerance among the 18 species tested. The most abundant nonnative species found throughout Arizona comprised four of the top six positions with respect to thermal tolerance, all surviving temperatures close to or above 40°C.

Within species, there was a significant increase in thermal tolerance as acclimation temperature was increased (two-sample t-tests: $P < 0.0001$) for all species. Average mean increase with acclimation temperature was 1.43 ± 0.4°C.

The ability of fish to thermally acclimate varied greatly among species (Figure 1). Acclimation response ratios varied greatly within the cyprinid family, ranging from 0.02 for loach minnow to 0.5 for green sunfish.

Discussion

The LTM provided a precise measure of upper thermal tolerance for all species tested. We employed a quick rate of change to minimize the lag time between water temperature and internal body temperature of the fish as well to minimize the opportunity for fish to reacclimate to changing temperature. A thermal tolerance test that utilizes such a fast rate of change is not a test meant to mimic natural conditions but to demonstrate relative differences in the ability to withstand high temperature among species. Under natural conditions, stream temperatures rise at a slower rate than that used in this study, sometimes taking 12 h to increase by 5–10°C (<0.01°C/min). Fish typically are exposed to heterogeneous thermal environments, and latency in body temperature change during exposure to high temperatures affords the organism time to escape potentially lethal conditions (Beitinger et al. 1977). For this reason, CTM tests typically overshoot the tolerance of fish in the wild by 3–4°C (Beitinger et al. 2000; Selong et al. 2001), and our LTM results could be expected to exceed upper lethal temperatures by a similar amount. Consequently, our results would not accurately reflect temperatures that these species can withstand in the wild unless temperatures in the wild increase at a similar rate to the ones used in this study; however, they are a good measure of relative tolerance among species.

There has been much concern expressed over the choice of endpoints for acute thermal tolerance tests (see Lutterschmidt and Hutchison 1997b and Beitinger et al. 2000 for a complete review). Researchers often incorrectly define or fail to report the endpoints used in their tests, often creating confusion because of the large number of potential endpoints. For this reason, we chose to test and report four of the most commonly cited endpoints. According to Beitinger et al. (2000), final loss of equilibrium is an ecologically significant endpoint because the fish loses its ability to escape conditions that will ultimately lead to death. Final loss of equilibrium is the most widely cited CTM endpoint (Mundahl 1990; Smale and Rabeni 1995; Benfey et al. 1997; Currie et al. 1998; Diaz and Buckle 1999; Selong et al. 2001) and, as most fish recover once placed into cooler water, is the most logical endpoint when testing endangered and threatened species. However, initial
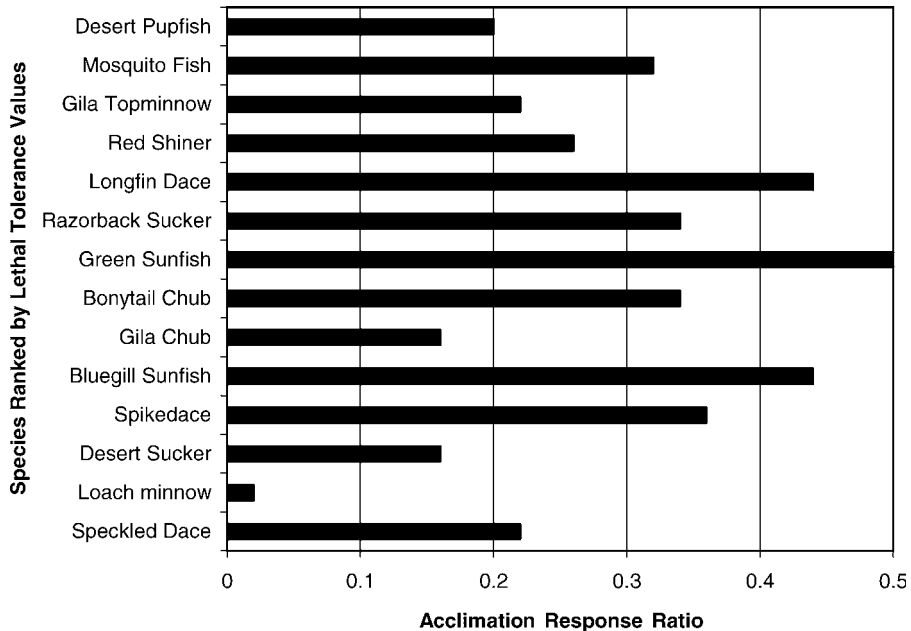
FIGURE 1.—Acclimation response ratios (ARRs) for native and nonnative Arizona fishes acclimated at 25°C and 30°C. Low ARR values indicate a limited ability to alter thermal tolerance with changing acclimation temperature. Species are ranked from highest (desert pupfish) to lowest thermal tolerance (speckled dace) based on the flaring opercula endpoint of the lethal thermal method. Largemouth bass, yellow bullheads, roundtail chub, and fathead minnow are not shown, as they were not acclimated at 30°C.

and final losses of equilibrium were the least statistically precise endpoints we tested. All fish experienced loss of equilibrium, but signs were subtler in some species, specifically loach minnow and yellow bullheads, which remained on the bottom of the beaker for the majority of the test period. Several species demonstrated obvious disorientation only when prodded with a glass rod. In a similar study conducted by Lutterschmidt and Hutchison (1997a), loss of equilibrium had significantly more variance than another endpoint, the onset of spasms. The species we used did not consistently experience the onset of spasms and this endpoint was not recorded. Final loss of equilibrium and death were more precise endpoints than initial loss of equilibrium. However, flaring opercula, a lethal endpoint, was the most precise endpoint and was the most consistent among all species. For this reason, we used the flaring opercula endpoint to rank the thermal tolerances of the species we tested. We recommend that flaring opercula be reported as the endpoint in lethal tests.

During the acclimation period in thermal tolerance studies, fish are often held in the same tank (Watenbaugh and Beitinger 1985; Currie et al. 1998; Novinger and Coon 2000; Rajaguru 2002; Chatterjee et al. 2004; MacNutt et al. 2004); in some cases, authors do not describe how the acclimation process took place (Diaz and Buckle 1999; Chung 2001). Holding fish in the same tank and then moving each to an individual beaker for the tests could be considered pseudoreplication because all fish are acclimated under the same conditions before the tests. However, due to equipment limitations, it is often impossible to place hundreds of fish in individual acclimation tanks over a lengthy acclimation period. We tried to minimize potential pseudoreplication by splitting individual fish among several acclimation tanks; however, we could not completely eliminate it. Because each fish was transferred singly to a beaker to undergo temperature increases, we defined each fish as a replicate.

This study suggests that the thermal tolerances of some cyprinid species approached the tolerance of the desert pupfish. Although Brett (1956) concluded that ictalurids have the highest tolerance and cyprinids have intermediate tolerance, we found that thermal tolerance was not grouped by taxa. Desert pupfish were most tolerant to high temperature, and their upper lethal tolerance reached 42.4 ± 0.2°C when acclimated to 30°C. Tolerance to extremely high temperature is common among cyprinodonts (see Beitinger et al. 2000), and these fishes typically inhabit water with high temperatures. Desert pupfish can live at 38.9°C

and exhibit discomfort and death at 40.6°C (Deacon and Minckley 1974). Using the same acclimation temperature as in our study, Lowe and Heath (1969) determined the CTM for desert pupfish to be 42 ± 0.3°C (mean ± SD). Speckled dace had the lowest tolerance (35.8 ± 0.6°C). John (1964) reported a maximum thermal tolerance of 33°C for speckled dace in the wild; however, in his study, fish were not acclimated to a constant temperature, and fluctuations of 10–15°C occurred before testing.

Although previously studied, several nonnative species were included in our tests to ensure that endpoint values were estimated for fish collected in Arizona. Our results were consistent with other studies. Red shiners ranked within the top 5 of the 18 species tested in this study and are known to successfully cope with extreme pH, salinity, and temperature (Matthews and Hill 1977). King et al. (1985) reported that red shiners experience loss of equilibrium at 36.5–38.0°C (SD = 0.41°C) when acclimated at 25°C. Similarly, loss of equilibrium was reported at 39.6 ± 0.23°C (mean ± SD) when red shiners from a Texas population were acclimated at 30°C (Rutledge and Beitinger 1989). The red shiner has become a notorious invader throughout streams in Arizona and has been cited in the decline of threatened spikedace and loach minnow (USFWS 1991a, 1991b). Red shiners are able to persist in environments that have been rendered inhospitable for many native fishes (Douglas et al. 1994) and can tolerate thermal shock at high and low temperatures (Matthews and Hill 1977). Data for other nonnative species were also consistent with our findings. Currie et al. (1998) reported a CTM value of 36.7 ± 0.59°C (mean ± SD) for largemouth bass from Oklahoma acclimated at 25°C at a rate of change of 0.3°C/min. Similar consistencies exist for western mosquitofish from an Arizona State University population (Otto 1973). Among the nonnative species we tested, thermal tolerance values were consistent for fish collected from different regions. This provides us with some confidence that results from different studies can be compared when similar rates of change are used.

Temperature tolerance acclimation is the process of reestablishing internal homeostasis, allowing for survival in heterogeneous thermal environments. Stauffer et al. (1984) demonstrated that cyprinids possess a greater ability to acclimate to changing temperature than do salmonids. Although the difference in acclimation temperature in this study was only 5°C, among the 18 species we studied there was a large amount of variability in the ability to extend upper thermal tolerance limits by acclimation to the higher 30°C temperature. A limited ability for temperature

tolerance acclimation indicates that the realized tolerance of a species is similar to the fundamental tolerance, regardless of the acclimation temperature (Beitinger and Bennett 2000). Those fishes that had low ARR values (e.g., loach minnow, desert suckers, desert pupfish, and Gila chub) have fundamental upper thermal tolerances that cannot be extended much by increasing acclimation temperature. Species with high ARR values (e.g., bluegills, green sunfish, and longfin dace) might be able to increase their upper thermal tolerances even more with increasing acclimation temperature.

Overall, our results indicate that native cyprinids were less tolerant to high temperature than nonnative cyprinids and centrarchids, suggesting that these nonnative species may have an advantage at high temperature. Evolutionary history was cited as the reason for the success of the arroyo chub *Gila orcuttii* in displacing the native Mojave tui chub *Gila bicolor mohavensis* (Castleberry and Cech 1986). Due to their evolution under fluctuating environmental conditions, including temperature, arroyo chub are better adapted for dealing with fluctuating environmental conditions in the Mojave River, California. Changing thermal regimes throughout Arizona may be negatively impacting native species by exposing native fishes to temperature fluctuations outside of their tolerance range and favoring some of the more heat-tolerant nonnative species. Historically, desert streams and rivers experienced small daily and annual temperature fluctuations. Anthropogenic alteration of stream channels and riparian areas have increased the amount of exposed surface area and increased the amount of solar radiation reaching the stream, resulting in substantially elevated water temperatures (Dickerson and Vinyard 1999). Today, stream temperatures throughout Arizona regularly reach 34–35°C in summer (USGS 2005); in the past, temperatures as high as 40.3°C were recorded during July and August (Deacon and Minckley 1974). Although present surface temperatures may be similar to past surface temperatures, the cooler, deeper water that was once available as a buffer from high temperature has now diminished (John 1964; Deacon and Minckley 1974).

In summary, our results report the relative thermal tolerances of many previously untested desert fish species. Although southwestern native fishes were previously believed to be tolerant to high temperature owing to their evolution in desert environments, this study suggests that many of these fishes are less tolerant than previously thought. In addition, many fishes introduced from the eastern United States had higher temperature tolerances than some of the native desert species we tested. Increasing stream tempera-

tures in Arizona could be reducing the habitat available for native fishes and favoring those nonnative species with higher thermal tolerances.

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