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THERMAL REQUIREMENTS OF THE BONYTAIL (*GILA ELEGANS*): APPLICATION TO PROPAGATION AND THERMAL-REGIME MANAGEMENT OF RIVERS OF THE COLORADO RIVER BASIN

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Abstract—We performed experimental trials on hatchery-reared juvenile bonytails (*Gila elegans*) using the acclimated-chronic-exposure method. Bonytails were exposed to 8–30°C for 112 days to determine effects on growth, condition factor, composition of body, and survival. Survival was ≥98% for all treatments. The predicted temperature was 25.9°C for maximum gain in weight and 14.2°C for zero gain. Temperatures <14°C depressed growth, 14–20°C provided incremental growth, and 22–26°C allowed accelerated growth. We hypothesize that temperatures during propagation and seasonal temperatures of rivers that are 22–26°C, or both, would maximize growth of juveniles and might promote higher survival because bonytails would be less vulnerable to predation, and have greater energy reserves and increased metabolic efficiency.

Resumen—Subadultos de la carpa elegante (*Gila elegans*) criados en cautiverio fueron sometidos a pruebas experimentales utilizando el método de aclimatación y exposición crónica. Utilizamos exposiciones entre 8 y 30°C con una duración de 112 días para determinar los efectos en el crecimiento, condición, composición corporal, y sobrevivencia. La sobrevivencia fue ≥98% en todos los tratamientos. Las temperaturas predichas para obtener crecimiento de peso máximo y de cero fueron de 25.9°C y 14.2°C, respectivamente. Temperaturas <14°C impidieron el crecimiento, las entre 14 y 20°C incrementaron el crecimiento gradual, mientras que las entre 22–26°C aceleraron el crecimiento. Proponemos la hipótesis de que las temperaturas durante la propagación y las temperaturas estacionales de los ríos entre 22–26°C, o ambas, pueden maximizar el crecimiento de los juveniles y pueden promover más alta sobrevivencia porque las carpas elegantes serán menos vulnerables a ala depredación, y tendrán más reservas energéticas e incrementarán su eficiencia metabólica.

The bonytail (*Gila elegans*) is endemic to the Colorado River Basin and once inhabited the large, warm-water rivers of the basin (United States Fish and Wildlife Service, 1984, 2002*a*). Altered hydro-regimes and reduction in floodplains occurring in the era of dam building in the early 1900s reduced habitat available to bonytails, size of populations, and historical range (Minckley and Deacon, 1968; Holden and Stalnaker, 1970; United States Fish and Wildlife Service, 2002*a*). A viable wild population might no longer exist and potential for recruitment appears to be limited to bonytails released from propagation programs (Kaeding et al., 1986; Minckley et al., 2003; Bestgen et al., 2008). The bonytail was listed as endangered in 1980 (United States Fish and Wildlife Service, 1984) and remains one of the most imperiled species of fish in the United States.

The Bonytail Recovery Plan (United States Fish and Wildlife Service, 1984) identified factors believed to be responsible for causing declines and outlined actions necessary to recover the species. The two principal limiting factors that prohibit recruitment are altered thermal regimes and predation by nonnative species (Minckley, 1983, 1991; Marsh, 1985; Clarkson and Childs, 2000; Bestgen, 2008). Changes to thermal habitats have occurred both from a direct impact of in-river hypolimnetic releases from dams and a loss of natural inundation of floodplains that historically provided warmer backwater areas. Introduction of nonnative piscivorous species is, in general, a consequence of introductions of sport fish.

Three other endangered species of fish inhabit the Colorado River Basin, the humpback chub *Gila cypha,* Colorado pikeminnow *Ptychocheilus lucius,* and razorback sucker *Xyrauchen texanus* (United States Fish and Wildlife Service, 2002*b*, 2002*c*, 2002*d*). Among native fishes of the Colorado Basin, these three large-bodied species along with the bonytail commonly are referred to as the big-river fishes of the Colorado River (Minckley et al., 2003). Life histories of bonytails and these three sympatric species are similar. Often, the conclusion of a study (or a result from a management action) pertaining to one of these species can be applied to another member of the group. For example, the temperature regime that promotes the life cycle of one species might likely be beneficial to the sympatric group, or the size needed by subadults of one species to avoid early mortality in life from nonnative predation might be similar among species (Minckley et al., 1991; Schooley and Marsh, 2007).

Although research specific to bonytails is limited, researchers have produced a body of literature for the four big-river fishes that demonstrates that alterations of temperature have reduced survival of embryos, reduced rates of growth of larvae and juveniles, and slow growth has increased early-life mortality (Minckley, 1983, 1991; Marsh, 1985; Kaeding and Osmundson, 1988; Clarkson and Childs, 2000; Tyus and Saunders, 2000; Minckley et al., 2003; Schooley and Marsh, 2007). Researchers have further identified that, although temperature has played a significant role in reduction of bonytails and the three other species, temperature alone is not the single limiting factor (Marsh, 1985; Kaeding et al., 1986; United States Fish and Wildlife Service, 2002*a*, 2002*b*, 2002*c*, 2002*d*). Predation by nonnatives is a causative agent in the continued demise of these four species (Minckley et al., 2003; Clarkson et al., 2005; Schooley and Marsh, 2007). The combination of an altered riverscape and interaction of native and nonnative species with competing and nonadapted life histories has led to what appears to be the largest-scaled expansion and displacement of species of fish in a North American river basin (Olden et al., 2006).

The Bonytail Recovery Plan supports use of propagation to prevent extinction and promote recovery (United States Fish and Wildlife Service, 2004). Varying numbers of hatchery-propagated bonytails have been released since 1981 (Hamman, 1982). Unfortunately, low survival has been reported for all attempts to repatriate them into the wild (Minckley et al., 2003; Bestgen, 2008). Managers have suggested that it might be necessary to release bonytails at a size >300 mm to avoid predation. This suggestion is based on the current low survival assessed for smaller (<300 mm) hatchery-released bonytails, and an observed increased survival of larger (≥300 mm) hatchery-stocked and closely related razorback suckers (Schooley and Marsh, 2007; Bestgen et al., 2008; Zelasko et al., 2010). Techniques of propagation that facilitate growth so fish are larger upon release are being developed (e.g., cage culture, improved diet, poly-culture; Sowka and Brunkow, 1999; Henne et al., 2006, 2007). We designed a study that might allow managers to increase growth of bonytails via management of thermal regimes.

Laboratory methods have been used to refine thermal requirements for propagation and to provide guidance for conservation actions designed to improve thermal habitats (e.g., Selong et al., 2001; Kindschi et al., 2008; Kappenman et al., 2009). The objective of our study was to determine thermal requirements of juvenile bonytails. We examined effects of temperature of water on survival, growth, condition factor, and constituents in the body (e.g., proteins, lipids, moisture, and ash) of juveniles across a range of temperatures they might be exposed to in rivers and in propagation programs at hatcheries. Determining optimal thermal regime for bonytails might provide managers of hatcheries the ability to promote increased growth and produce healthier fish more likely to survive in the river, and also provide guidance on thermal habitats to managers of rivers.

Materials and Methods—Our study was conducted at the United States Fish and Wildlife Service Bozeman Fish Technology Center in Bozeman, Gallatin County, Montana. Adult broodstock were spawned at the United States Fish and Wildlife Service Dexter National Fish Hatchery and Technology Center, Chaves County, New Mexico. The Bozeman Fish Technology Center received embryos on 25 March 2008. Embryos were incubated and hatched at 18°C and survival to hatch was >90%. During April–September 2008, bonytails were held in the quarantine facility at Bozeman Fish Technology Center. During the larval-to-juvenile transition, bonytails were maintained at 18°C in circular tanks and fed to excess with a diet of Otohime Marine (BioKyowa; Kyowa Hakko Kogyo Co., Ltd., Cape Girardeau, Missouri), live *Artemia* reared at Bozeman Fish Technology Center from cultured cysts (Argent Laboratories, Redmond, Washington), and lyophilized freeze-dried Cyclop-eeze (Argent Laboratories, Redmond, Washington). Survival of larvae was high (mortality <5–15%) from hatching to transition to exogenous feed. Larvae gradually were transitioned onto a diet of Otohime Marine, size of feed was increased as fish grew, and feed-to-excess rations were maintained. In October, personnel of the United States Fish and Wildlife Service Bozeman Fish Health Center determined that fish were negative for infections by viruses and parasites. Subsequently, in October, juveniles were transferred from the quarantine facility to the containment building at Bozeman Fish Technology Center and held in two 1.8-m circular tanks maintained at 18°C and fed the same diet and rations until transfer to test tanks.

We used the acclimated-chronic-exposure method (Zale, 1984; Selong et al., 2001) to evaluate the effect of a range of temperatures of water on bonytails. The principles of the acclimated-chronic-exposure method, the water-quality parameters of Bozeman Fish Technology Center, and the thermal system have been described (Selong et al., 2001; Kindschi et al., 2008; Kappenman et al., 2009). Our initial holding temperature for juveniles was 18°C and our test temperatures were 8–30°C. Briefly, water was supplied to 12 head tanks at 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, 28, and 30°C. Water from one of 12 head tanks was assigned randomly to each of three tanks, for a total of 36 holding tanks. Thus, three replicates of each treatment were maintained in 75-L rectangular aluminum fish tanks, measuring 122 cm long by 35.5 cm wide by 25 cm deep. Covers were on tanks at all times except during maintenance and periodic observations. Overhead halogen light was adjusted daily to mimic the natural photoperiod for Bozeman, Montana. Flow-through water from the 12 head tanks was supplied at ca. 3 L/min to each of the 36 tanks. Turnover rate in tanks was >2 times/h and was sufficient to maintain adequate levels of dissolved oxygen and to flush metabolites.

On 31 October 2008, 40 age-0 bonytails (ca. 180–200 days post-hatching) were selected randomly from two 1.8-m tanks (temperature of water, 18°C) and placed in each of the 36 tanks (also at 18°C). Stock fish in tanks were 50–90 mm total length and weight was 1.0–3.0 g. Fish were held at 18°C for 10 days during acclimation to the tank and transition of diet. Transition of diet involved a gradual weaning from a diet of Otohime Marine to a diet developed for razorback suckers by F. T. Barrows, United States Department of Agriculture. We transitioned bonytails to the diet of razorback suckers because, among production hatcheries, it is the most commonly used diet for propagating juvenile bonytails. During 3–10 November, fish were fed a 50% mixture of each diet. During 10–22 November, fish were fed a mixture of 25% Otohime Marine and 75% diet of razorback suckers. Beginning 23 November, fish were fed only diet of razorback suckers. No mortality occurred during acclimation to the tank and transition of diet.

On November 10, 12-day ramping began and temperature of water in each head tank was increased or decreased (from 18°C) by ca. 1°C/day until the testing temperature was achieved. On 22 November, all 12 testing temperatures were reached. Dead fish were not replaced during ramping and experimental periods. Mortality was tallied daily and individual dead fish were weighed. During the ramping period, feed was adjusted in 1% increments from 5 to 10% based on weight of fish per tank. We determined that 6% of body weight per tank was needed to ensure fish were fed to excess in all temperatures. During the ramping period and throughout the experiment, we visually monitored uneaten feed and waste daily, and adjusted rations when necessary to ensure fish were fed to excess.

On 24 November (day 1 of experiment), initial batch weights of fish were taken and fish were counted. At the time, we noted that due to a previous counting error, one of the 12°C-tanks had 30 fish. No new fish was placed in that tank and the experiment proceeded with those 30 fish included as a replicate. There was no statistical difference between initial mean weight of fish on day 1 of treatments at the 12 temperatures ($P = 0.125$), and range of means across treatments was 1.8–4.2 g. Mean weight of fish from all tanks was 2.6 g. On 25 November, we initiated feeding at 6% of body weight of fish per tank using the diet developed for razorback suckers. The schedule for cleaning and feeding was 5 days/week. Fish were not fed on weekends or 2 days before a periodic batch-weighing. Feed was dispensed from an automatic belt feeder placed near the head of each test tank. Fish were batch-weighed (±0.01 g) on days 1, 28, 57, 85, and 112. Amount of feed was calculated and adjusted for each tank 2 days after batch-weighing by using the most recent information for weight to calculate amounts of feed. During the final assessment on day 112, batch-weight and final counts of fish were performed on each tank and 20 fish from each tank were weighed (±0.01 g) and measured (total length; mm).

During the experiment, there was no abnormal fluctuation in water-quality parameters. Temperature of water was monitored multiple times daily by visual observation of digital thermometers and recorded at 24-min intervals with data loggers in each of the 12 head tanks. Average temperature from data loggers in test tanks for the entire study varied less than ±0.3°C. Daily fluctuation in temperature in test tanks was less than ±1.0°C. We monitored percentage saturation of dissolved oxygen, total dissolved gases, and nitrogen plus argon using a Common Sensing Model TBO-DL6 meter (Common Sensing, Clark Fork, Idaho). The common sensing unit was placed in one of the 12 individual head boxes, on a 12-day rotation with gas parameters in each head tank logged every 10 min for 24 h. For all treatments throughout the experiment, dissolved oxygen was >6 mg/L and was 82–90% saturation, total dissolved gases was 96–101% saturation, and nitrogen plus argon was 96–101% saturation.

Composition of body (protein, lipid, moisture, and ash) was calculated by means of standard proximate analysis, and was measured at the end of 112 days from three randomly selected fish from each tank (three tanks/treatment). Fish were frozen until analyzed. Samples were thawed partially and homogenized with an equivalent weight of distilled water. Protein was determined by thermal oxidation (Leco TruSpec, Leco Corp., Saint Joseph, Missouri) following method 992.15 of the Association of Official Analytical Chemists (Association of Official Analytical Chemists, 1990). Lipid was measured using a petroleum-ether extraction (Ankom XT 10; Ankom Technology, Macedan, New York). Moisture in tissue was measured by freeze-drying a 2-g sample (Labconco Freezone 12; Labconco Corp., Kansas City, Missouri) until no change in mass occurred, and ash content was determined by heating a 2-g subsample in a muffle furnace (Barnstead/Thermolyne 30400; Barnstead International, Dubuque, Iowa) at 555°C for 12 h.

Analysis of variance (ANOVA) with Bonferroni comparisons of means were used to compare mean gain in weight of individuals among treatments at 112 days, and percentage survival among treatments at 112 days. Arcsine transformation of data was performed to compare percentage survival. Condition factor ($K = \text{body weight}/\text{total length}^3$; Ricker, 1975) and total length were calculated for a random sample of 60 surviving fish (20 fish from each tank for a total of 60 fish from each treatment) on day 112 and compared among treatments by ANOVA with Bonferroni comparisons of means. Rates of growth were calculated as means of absolute daily gain in weight (absolute rate of growth) and specific rate of growth. Absolute rate of growth was calculated according to the formula absolute rate of growth $= (W_2 - W_1)/t$, where W_2 and W_1 are the final (112 days) and initial (1 day) average weights of fish per tank, respectively, and t is the number of days of the experiment (Ricker, 1979). Specific rate of growth (percent increase in weight per day) was calculated for each treatment according to the formula specific rate of growth $= ([\log_e W_2 - \log_e W_1]/t) \times 100$ (Ricker, 1979). Regression analysis was used to determine the temperature for maximum total length, maximum gain in weight, and minimum needed to maintain weight. Constituents of body measured by proximate analysis were compared among treatments by ANOVA with Bonferroni comparisons of means. Arcsine transformation of data was performed to compare percentage of lipids and proteins. The accepted significance level for statistical tests was $\alpha \leq 0.05$. Unless otherwise specified, values are reported as mean ± *SE*. We examined data for growth, survival, and composition of body with additional post-hoc tests including Fisher's protected least-significant difference (Fisher's PLSD) and Scheffé's S-test. We report the conservative results of Bonferroni comparisons because statistically significant differences detected of the effect of temperature would seem to be truly biologically relevant.

TABLE 1—Survival (%), mean final weight per fish, mean gain in weight per fish, and mean proximate analyses (±*SD*) of the bonytail (*Gila elegans*) after 112 days of captive rearing in water at 12 temperatures (three replicates/treatment). In columns for mean gain in weight (g/fish), proteins (%), and lipids (%), values not sharing a common letter within a column differ statistically ($\alpha = 0.05$).

Treatment (°C)	Survival (%)	Mean final weight (g/fish)	Mean gain in weight (g/fish)	Proteins (%)	Lipids (%)	Moisture (%)	Ash (%)
8	99	1.97	–0.15a	15.6 ± 0.2a	8.4 ± 1.1ab	71.4 ± 1.0	3.3 ± 0.0
10	98	2.15	–0.06ab	15.8 ± 0.2ab	8.3 ± 0.9ab	71.4 ± 0.7	3.4 ± 0.1
12	98	2.37	–0.06ac	16.7 ± 0.6bc	9.4 ± 1.2ab	70.0 ± 1.0	3.3 ± 0.1
14	100	2.64	–0.05ad	16.3 ± 0.2ac	9.1 ± 0.7ab	70.1 ± 0.9	3.4 ± 0.2
16	99	2.50	0.09ae	16.3 ± 0.2ac	9.4 ± 1.0ab	69.9 ± 1.0	3.4 ± 0.2
18	100	2.27	0.21af	16.0 ± 0.3ac	9.4 ± 0.5ab	70.1 ± 0.4	3.5 ± 0.2
20	100	2.58	0.35bcdefg	16.0 ± 0.3ac	9.1 ± 0.6ab	70.2 ± 0.4	3.4 ± 0.1
22	100	3.38	0.69gh	16.3 ± 0.3ac	9.5 ± 1.3ab	69.9 ± 1.1	3.5 ± 0.1
24	98	3.03	0.85h	16.6 ± 0.3bc	8.3 ± 0.4ab	70.9 ± 0.3	3.6 ± 0.1
26	100	2.35	0.52efgh	16.2 ± 0.4ac	10.1± 0.4ab	69.4 ± 0.3	3.8 ± 0.1
28	100	2.99	0.55efgh	16.4 ± 0.1ac	10.1 ± 1.0ab	68.9 ± 0.6	3.8 ± 0.1
30	99	2.88	0.53efgh	15.7 ± 0.3a	12.3 ± 0.4b	67.7 ± 0.4	3.6 ± 0.1

RESULTS—Growth of bonytails was affected by temperature. Mean gain in weight (g/fish) differed statistically among treatments at 112 days (Table 1; $P < 0.001$). Mean gain in weight was highest at 24°C, which differed significantly from treatments ≤20°C, but was not statistically different from 22–30°C (Table 1). Increases in mean gain in weight were observed at 16–30°C, with decreases in treatments ≤14°C. Mean gain in weight at 8 and 10°C began to decrease as early as 27 days, and treatments 8, 10, 12, and 14°C showed decreased gains in weight at 55 days. Growth in treatments 8–14°C showed decreases throughout the remainder of the study, and only treatments ≥18°C demonstrated gains in weight at every weighing. Gain in weight always was highest in treatment 24°C at each weighing (Fig. 1). Maximum percentage daily gain in weight was predicted as 0.103%/day at 25.9°C, predicted temperature for zero gain was 14.2°C, and actual recorded means were −0.027–0.124%/day at 8 and 24°C, respectively (Fig. 2a). Maximum gain in weight (g/day) was predicted as 0.006 g/day at 25.9°C, and actual recorded means were −0.001–0.008 g/day at 8 and

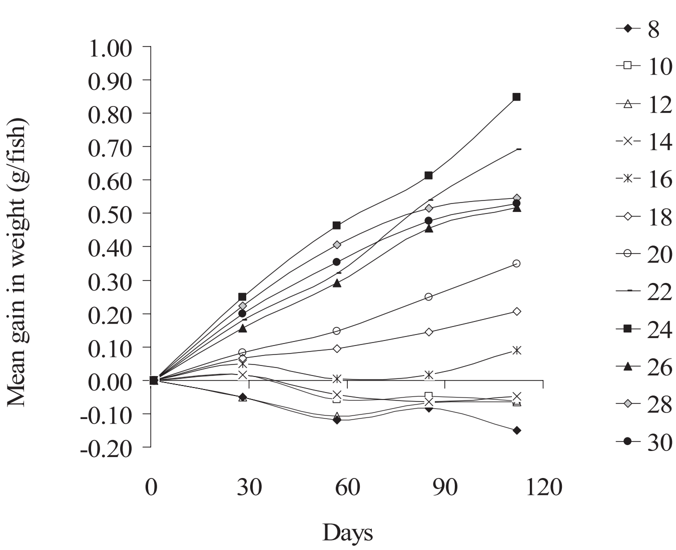

FIG. 1—Growth in mean weight (g/fish) of age-0 juvenile bonytails (*Gila elegans*) after 27, 55, 88, and 112 days of captive rearing at 12 temperatures (8–30°C). Symbols represent mean gain in weight for each treatment connected by smoothed lines.

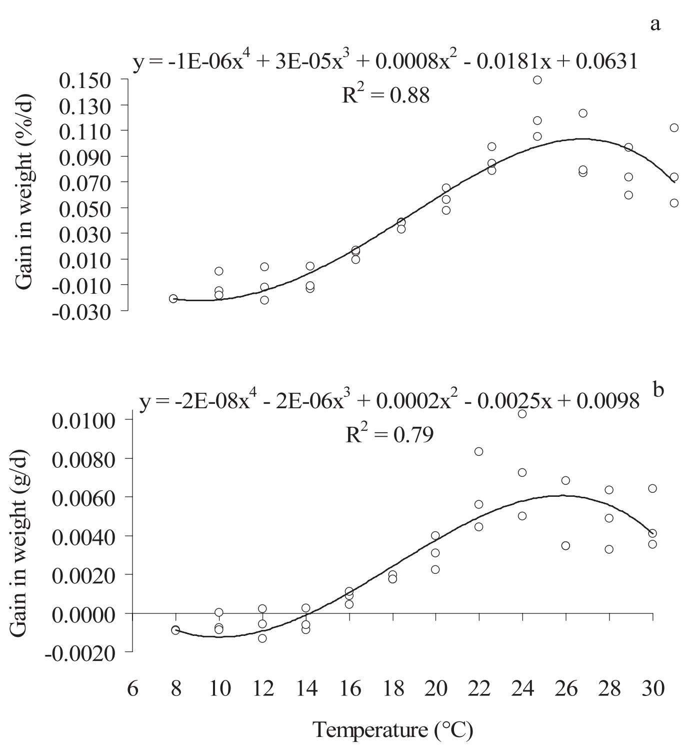

FIG. 2—Growth of age-0 juvenile bonytails (*Gila elegans*) in relation to temperature. Each circle represents mean daily gain in weight of a replicate at 12 treatments (8–30°C; 3 tanks/temperature) during 112 days. Maximum gain in weight predicted by the regression line was a) 0.103%/day and b) 0.006 g/day at 25.9°C.

24°C, respectively (Fig. 2b). Mean total length differed statistically among treatments at 112 days ($P < 0.007$). Treatment 22°C was the only one that differed statistically among treatments. Treatment 22°C was different from treatments 8–18°C but not different from treatments ≥20°C. Regression analyses for growth based on total length predicted that 25.2°C maximized growth in juveniles (Fig. 3).

Growth in our trial appeared to slow when compared to pretrial growth and rate of growth likely was affected by change in diet, transition to tank, and a reduction in daylight. Growth in our study (specific rate of growth, −0.001–0.120%/day) was lower than reported for juveniles of larger size ranges (specific rate of growth, 0.2–0.6%/days; Henne et al., 2006, 2007) and generally lower than growth in two concurrent studies of diet of similarly aged juveniles performed at Bozeman Fish Technology Center (specific rate of growth, 0.1–0.3%/days) and New Mexico State University (specific rate of growth, 0.3–0.5%/days; C. Caldwell, pers. comm.). Variables such as age, palatability of feed, composition of diet (e.g., proteins, lipids), configuration of tank, and density affect rates of growth.

Mean individual condition factor did not differ statistically among treatments at 112 days ($P = 0.731$) and was $65.0–68.6 \times 10^{-7}$. Lipids and proteins varied significantly among treatments (lipids, $P = 0.001$; proteins, $P = 0.002$; Table 1). Percentage of lipids at 30°C was significantly greater than treatments 8, 10, 14, 20, and 24°C, but no other difference was detected among treatments. Lipids showed a low correlative linear relationship with increasing temperatures ($r^2 = 0.33$). Percentage of protein at 8°C differed significantly from 12 and 24°C, but was not different from other treatments. Percentage of proteins at 30°C differed significantly from 12 and 24°C but were not different from other treatments. No other difference between proteins was detected among other treatments. Survival in all treatments (8–30°C) was 98–100% (Table 1). There was no significant difference in mortality among treatments ($P = 0.638$).

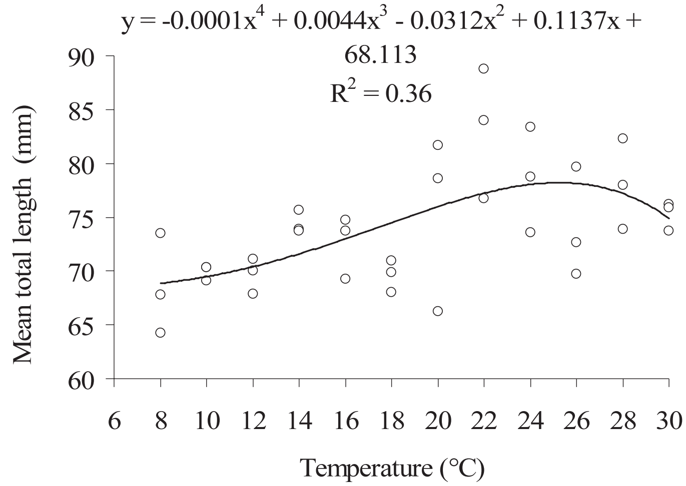

Fig. 3—Mean total length (mm) of age-0 juvenile bonytails (*Gila elegans*) reared for 112 days at 12 temperatures (8–30°C). Each circle represents mean total length of a replicate treatment (3 tanks/temperature).

Discussion—We examined growth of juvenile bonytails in relation to temperature and suggest that the growth-temperature regression curve might be a suitable model for the relative effect of temperature on growth of all big-river fishes of the Colorado River. Our research and the following summary of thermal information (e.g., for the bonytail, Colorado pikeminnow, humpback chub, and razorback sucker) supports a hypothesis that a mutually beneficial thermal regime for big-river fishes exists for the coevolved endangered species. Both practitioners of propagation and managers of rivers might find this information beneficial in aiding recovery of bonytails and the big-river species. Culturists and managers of rivers can use information we provide to maximize growth by controlling temperature of water, and taking advantage of seasonal water temperatures within the ranges we recommend. Near absence of mortality across the temperatures we tested demonstrates that bonytails have adapted to tolerate a wide range of temperatures in rivers. Although bonytails can withstand seasonal cool conditions that exist in riverscapes of the desert Southwest, bonytails, like all of the big-river species, require a corresponding warm summer to grow and survive.

We are not the first to point out thermal similarities among these species of fish. For example, the final preferendum (similar to optimum; Jobling, 1981) estimated for these species using mathematical calculations were 24.2–25.4°C; <1.2°C difference among all species (Bulkley and Pimental, 1983). Our study is unique in that no study of one of the big-river fishes had exposed a species to the incremental range of temperatures as we did with bonytails. Our experiment demonstrated that cold water (<14°C) severely depressed growth, temperatures 14–20°C allowed incremental increased growth, but opportunity for accelerated growth was available only at temperatures >20°C. Our analyses suggest that temperatures for propagation or temperatures of rivers that are 22–26°C would maximize growth of juveniles. Our results are similar to previous thermal studies of bonytails and we demonstrate similarities among big-river fishes. We determined that growth ceased for juvenile bonytails at ≤14.2°C. The threshold for growth for Colorado pikeminnows was ≤13°C (Osmundson, 1987; Kaeding and Osmundson, 1988), humpback chubs ceased growth at ≤12°C (Robinson and Childs, 2001; O. T. Gorman and R. R. VanHoosen, in litt.) and razorback suckers ceased growth at ≤14°C (Clarkson and Childs, 2000; O. T. Gorman and R. R. VanHoosen, in litt.). Further, the optimal temperature we described for bonytails (near 26°C) is similar to the temperature described to maximize growth of these species. The highest growth determined for juvenile Colorado pikeminnows occurred at 25°C (Black and Buckley, 1985), juvenile razorback suckers at 24–25.5°C (Bestgen, 2008; O. T. Gorman and R. R. VanHoosen, in litt.), and juvenile humpback chubs at 24°C (Petersen and Paukert, 2005; O. T. Gorman and R. R. VanHoosen, in litt.). Additional thermal similarities among these species are evident. For example, although upper temperatures tolerated by juveniles or older Colorado pikeminnows and humpback chubs are not available in the literature (using standard methods), both bonytails and razorback suckers have similar upper lethal tolerance (near 39°C) and similar acclimation:response ratios (Carveth et al., 2006).

In bonytails and other fishes, composition of body and condition factor, along with rate of growth are affected by temperature. Bonytails in our 112-day study were able to maintain adequate levels of lipids and a high enough relative condition factor to survive at all temperatures we tested. It is hypothesized that larger fish released from propagation programs might survive at higher rates not only because they are less vulnerable to predation, but also because they have increased metabolic efficiency and greater reserves of energy. Many studies have demonstrated that, in temperate environments, size, condition factor, and lipids play a role in survival of juveniles during their first year (Oliver et al., 1979; Adams et al., 1982; Henderson et al., 1988; Post and Evans, 1989; Shuter and Post, 1990; Thompson et al., 1991). In thermal experiments such as ours, deposition of reserves of energy, as reflected by percentage composition of lipids in the body or by condition factor, can act as an indicator of metabolic thermal optima and thresholds. It is noteworthy that we did not observe a typical dose-response affect of temperature on condition factor or level of lipids in the body in our relatively short-term study. Importantly, lipids were maintained at mean levels >8% in all treatments and >6% in all replicates, and condition factor was maintained at >0.65 in all treatments.

There is little information available for the condition factor or the level of lipids in the body of wild bonytails, and no information is available for the minimum levels needed for survival. The only condition factor and levels of lipids reported are from studies of diet in hatcheries. A condition factor of 0.81–0.83 and levels of lipids ≤25% were observed in hatchery-reared, age-0 bonytails (older and larger than those in our study; Henne et al., 2006). A condition factor of 0.66–0.68 and levels of lipids near 12% were observed in a concurrent study we performed on diet with bonytails from the same origin. These lipid levels (e.g., 12–25%) are within the normal range for fish and representative of typical diet and culture in hatcheries.

To survive, all species of fish must maintain some minimum level of lipids and level of condition (e.g., above a critical threshold) as a reserve of energy. The level of fat (percentage of dry weight) and minimum condition factor required for survival of bonytails appears to be ≥6% and ≥0.65, respectively. Condition factor is relative to species, but comparisons to levels of lipids to other species are possible. The critical lipid level reported for the yellow perch (*Perca flavescens*) was 2.2% (Newsome and Leduc, 1975), 3.2% was the critical level reported for the sand smelt (*Atherena boyeri*; Henderson et al., 1988), and 3–6% was reported critical for the Colorado pikeminnow (Thompson et al., 1991). High content of lipids and a high condition factor might be especially important to survival of native species released from propagation programs into an environment that has been thermally altered and is host to nonnative piscivores fish, i.e., in the Colorado River Basin (Kaeding and Osmundson, 1988; Marsh et al., 2005; Schooley and Marsh, 2007; Bestgen, 2008; Bestgen et al., 2008). Field investigators might wish to incorporate an examination of condition factor and level of lipids in the body across varying seasons from hatchery released and recaptured fish for comparative analyses. Laboratory studies that identify the minimum levels needed for survival may also be useful. The information might provide insight into mechanisms responsible for low survival observed in hatchery-released bonytails.

A reduction in growth of bonytails can be an indicator of thermal stress. Thermal stress that results in reduced intake of feed might also result in lower immune function and an increased risk of developing a disease (Lim and Webster, 2001). The inflection points where growth peaks or ceases might signal a potential for additional negative consequences of a longer thermal exposure. Bonytails at all temperatures might have been eating enough feed to maintain adequate condition and reserves of lipids for the trial period, but mean weight was decreasing below 14°C, suggesting that extended periods below 14°C eventually will result in mortality. Culturists and managers of rivers should consider that bonytails exposed to temperatures <14°C might suffer increased stress, while temperatures >26°C might also promote stress. Ecologists might wish to examine how extended periods of cool temperatures influence reserves of lipids, loss of weight, and immune function of bonytails. Laboratory studies that mimic the time and temperature regimes that hatchery bonytails experience when released into the current modified environment of rivers might be helpful in understanding mechanisms causing overwinter mortality.

The information we present can be used to identify rearing habitats and determine effectiveness of improving thermal habitats with a thermal-control device (e.g., such as the analyses developed for humpback chubs; Petersen and Paukert, 2005; Coggins and Pine, 2010). Many articles have discussed benefits, risks, and feasibility of management actions that might provide suitable thermal habitats for native species of fish in the Colorado River Basin (Kaeding and Osmundson, 1988; Minckley, 1991; Clarkson and Childs, 2000; Petersen and Paukert, 2005;

Coggins and Pine, 2010; Osmundson, 2010; R. T. Muth et al., in litt.). For example, Bestgen (2008) determined that warmer temperatures improved growth of larval razorback suckers and he detailed how increased temperatures of water from a thermal-control device and restoration of floodplain could benefit razorback suckers. Bulkley and Pimental (1983) suggested guidelines for management of rivers that would benefit razorback suckers. We suggest that similar modifications of habitats and thermal guidelines described by previous researchers might promote growth and survival of juvenile bonytails.

The scale of thermal change that has occurred in the mainstem Colorado River is dramatic and might be a factor explaining displacement of bonytails by nonnative rainbow trout *Oncorhynchus mykiss*. Annual temperature in the Colorado River near its confluence with the Little Colorado River (once a likely habitat of bonytails) historically was 2–26°C and now is 8–12°C due to hypolimnetic-released water from dams (Coggins and Pine, 2010). The range of temperatures now present is well below temperatures at which bonytails lost weight in our study, but nearly optimal for rainbow trout exposed to an acclimated-chronic-exposure thermal trial (i.e., 13.1°C optimal; Bear et al., 2007). Conversely, the temperature we found that promoted maximum growth of bonytails (near 26°C) was lethal to 50% (LT50) of rainbow trout in <10 days and lethal to 90% in a 1-month exposure (Bear et al., 2007). Restoring thermal habitats to more natural conditions is likely to provide bonytails a competitive advantage, and significant thermal modifications could be used to control cold-water species.

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