

Temperature Effects of Hypolimnial-Release Dams on Early Life Stages of Colorado River Basin Big-River Fishes

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Declines of native big-river fishes of the Colorado River Basin, southwestern United States, have been attributed in part to emplacement of hypolimnial-release dams. Lowered spring-summer tailwater temperatures inhibit spawning and embryonic development, depress swimming performance and growth, and reduce survival of early life stages. We examined effects of three temperatures (10 C, 14 C, 20 C) on aspects of growth, development, and physiology of larval and early juvenile life stages of *Xyrauchen texanus* (Razorback Sucker), *Catostomus latipinnis* (Flannelmouth Sucker), *Gila cypha* (Humpback Chub), and *Ptychocheilus lucius* (Colorado Squawfish) in the laboratory. Lengths, weights, and specific growth rates of all species were significantly lower at 10 C and 14 C than at 20 C, and time to transformation from larval to juvenile life stage was delayed at colder temperatures. Transfer of fishes from 20 C to 10 C (simulating transport from warm tributaries to cold tailwaters) caused loss of equilibrium in youngest life stages. All these effects increase exposure of larvae to existing sources of mortality. Conservation of the big-river species in hypolimnial-release tailwaters will require thermal modification of dam discharges to lessen detrimental effects of cold water temperatures. Because such action may also benefit nonindigenous biota, recovery of the native fauna may ultimately depend upon implementation of comprehensive (and likely expensive) control measures against nonnative species.

MAINSTEM and major tributary rivers of the Colorado River basin, western United States, have been altered by more than a dozen major dams. These dams have contributed to declines and endangerment of indigenous, "big-river" fishes (those that range throughout the system in larger streams; Minckley et al., 1986) by blocking migration routes (Holden, 1979), and altering temperature, discharge, and sediment-transport patterns (Holden, 1979). The latter changes disrupted physical processes that created and maintained conditions necessary for reproduction and survival of the big-river ichthyofauna. In addition, lentic habitats created upstream from dams and the downstream hydrographic changes facilitated establishment of nonindigenous aquatic organisms that negatively impacted native fishes (Moyle et al., 1986; Minckley, 1991).

Hypolimnial-release dams in the basin especially affected big-river fishes through depression of spring-summer tailwater temperatures. Low temperatures (< 15 C) inhibit gonadal maturation, spawning (Holden and Stalnaker, 1975; Minckley, 1991) and embryonic development (Hamman, 1982; Marsh, 1985) of these species. In studies of *Ptychocheilus lucius* (Colorado Squawfish), low temperatures depressed growth and swimming performance of juveniles (Black and Bulkley, 1985; Bestgen, 1996; Childs and Clarkson, 1996) and caused behavioral

changes and mortality in larvae due to cold shock (Berry, 1988). A host of other negative life-history impacts may accrue to Colorado River basin warmwater native fishes caused by rearing in cold temperatures, including increased early life mortality and decreased survival to sexual maturity (Kaeding and Osmundson, 1988), reduced condition, lipid stores, and body size that result in elevated overwinter mortality for young-of-year fishes (Thompson et al., 1991) and lowered fecundity (McAda and Wydoski, 1983).

Changes to the native big-river ichthyofauna downstream from hypolimnial-release dams are well documented and appear in large part a response to depressed spring-summer water temperatures. For example, the 1962 closure and subsequent operation of Flaming Gorge Dam on Green River, Utah, lowered spring-summer tailwater temperatures to near 6 C from a previous range of 7–21 C (Vanicek et al., 1970). Several native species including *Gila robusta* (Roundtail Chub), *Rhinichthys osculus* (Speckled Dace), and federally endangered *P. lucius*, *G. cypha* (Humpback Chub), *G. elegans* (Bonytail), and possibly *Xyrauchen texanus* (Razorback Sucker) ostensibly disappeared from uppermost portions of the 104-km tailwater reach above Yampa River following dam closure (Vanicek et al., 1970; for discussion of *Gila* spp. in this reach, see Holden, 1991), a result likely hastened by a

preimpoundment poisoning operation in 1962 (Vanicek and Kramer, 1969; Holden, 1991). In addition, no reproduction by any native species was observed in the reach below the dam to Yampa River during years with high spring-summer flows and concomitant low water temperatures (Vanicek et al., 1970). Following warming of spring-summer tailwater temperatures to highs near 13 C after retrofit of Flaming Gorge Dam with temperature controls in 1978, reproduction by many native fishes was restored in the lower reach (P. B. Holden and L. W. Crist, unpubl.).

In the Colorado River and tributaries between Glen Canyon Dam and Lake Mead, Arizona (the Grand Canyon system), *P. lucius*, *G. robusta*, and *G. elegans* were extirpated following lowering of spring-summer tailwater temperatures to near 10 C after completion of Glen Canyon Dam in 1963 (Minckley, 1991). *Gila cypha* distribution in the Colorado River contracted (R. Valdez and R. J. Ryel, unpubl.), and *X. texanus* is extremely rare and functionally extirpated, with no evidence of reproduction. Mainstem reproduction by *Catostomus latipinnis* (Flannelmouth Sucker) also has been reduced or eliminated (Weiss, 1993). Most successful reproduction by remaining native fishes in the Grand Canyon system now occurs only in tributaries (Kaeding and Zimmerman, 1983; Schmidt et al., 1998). Glen Canyon Dam is now being considered for modification to allow release of warmer epilimnetic water for benefit of native fishes.

We investigated effects of depressed water temperature on Colorado River Basin big-river fishes by examining certain growth, physiological, and developmental responses of early life stage *X. texanus*, *C. latipinnis*, *G. cypha*, and *P. lucius* in the laboratory. Quantification of temperature impacts will identify management implications of temperature depression and enhance development of management options to assist conservation and recovery of this imperiled ichthyofauna.

MATERIALS AND METHODS

Temperature experiments were conducted at Bubbling Ponds State Hatchery near Cornville, Arizona. Water was from a pathogen-free artesian well at 18.6 C, 7.6 pH, 366 μ S/cm specific conductance, and 4.3–7.3 mg/L dissolved oxygen.

Culture.—Gametes of *G. cypha* were collected 26–27 April 1993, from pituitary-injected, manually stripped fish caught in the lower Little Col-

orado River, Grand Canyon, Arizona. Fertilized eggs were incubated 1–3 days on screens floating in 19-liter buckets filled with aerated, desilted river water. Water temperatures in the buckets, which were partially submerged in the river, ranged from 16 C to 21 C. Following transport to Bubbling Ponds Hatchery, embryos were acclimated to ambient 18.6 C water over 90 min and treated daily with 1667 ppm formalin for 15 min as prophylaxis against fungus during further incubation in Heath trays. Larvae were transferred to shallow troughs of through-flowing 18.6 C water until swim-up and transferred to aquaria at 20 ± 0.5 C. Larvae were fed *Artemia salinus* nauplii, zooplankton from hatchery ponds, and Bio-Kyowa commercial feed ad libitum three times daily. Beginning 2–4 weeks following swim-up, larvae and juveniles were fed commercial trout feed of progressively larger sizes as needed.

Hatchery broodstock *P. lucius* was spawned 20 May 1993, and embryos were incubated in hatching jars in 18.6 C water. Newly hatched larvae were transferred to flow-through troughs at 18.6 C for a few days prior to 90 min acclimation to 20 ± 0.5 C aquaria. Feeding was as described for *G. cypha*.

Embryos from *X. texanus* broodstock were cultured at 18–21 C in Heath trays at Dexter National Fish Hatchery in Dexter, New Mexico, and hatched 8–9 March 1994. Swim-up larvae were air-transported to Bubbling Ponds Hatchery and acclimated to 20 ± 0.5 C aquarium water over 90 min. Feeding (five times daily) and other treatments were identical to those for *G. cypha*, except that zooplankton was not provided.

Catostomus latipinnis gametes were taken from naturally ripe, manually stripped fish caught in Colorado River near Lee's Ferry, Arizona, on 14 May 1995. River temperature at time of collection was 12 C. Embryos were placed in a sealed bag filled with river water and oxygen, transported to Bubbling Ponds Hatchery, and acclimated to 18.6 C water over 90 min.

Embryos were incubated in hatching jars at 18.6 C and treated once with 0.025% betadine in a 10-min bath to control aquatic fungi. Young hatched 21–22 May, and larvae were acclimated to aquaria at 20 ± 0.5 C as described for other species. Larvae were fed ad libitum five times daily as described for *X. texanus*.

Growth experiments.—Experimental temperatures of 10, 14, and 20 C were selected to simulate spring-summer reproductive and rearing conditions extant in the mainstem and major Colorado River tributaries. Although variable, tail-

water temperatures below unmodified hypolimnial-release dams in the basin are near 10 C year-round, whereas spring-summer temperatures in river reaches unaffected by dams approach 20 C (U.S. Geological Survey records). Our 14 C experimental temperature simulated mixing of tributary and mainstem tailwater flows or eddy return channels and other low-velocity "backwater" habitats in tailwater reaches that may warm above mainchannel temperatures.

Because early life stage fishes may drift (Berry, 1988; Robinson et al., 1998), be transported via flood (R. Valdez and Ryel, R. J. unpubl.), or actively disperse from spawning streams into tailwater reaches, we examined temperature effects on three age groups (7 days, 14 days, and 41 days posthatch) of each species to evaluate effects of differential timing of entrance to cold tailwaters from warm tributaries.

Eighteen 38-liter aquaria were individually supplied with recirculating hatchery water inside the temperature-controlled lab under natural light conditions supplemented with illumination from wide spectrum fluorescent lights during daytime. Two one-quarter-hp chillers equipped with mechanical, biological, and chemical filters were connected to two sets of six aquaria maintained at 10 ± 0.5 C and 14 ± 0.5 C, respectively. A third set of six aquaria was supplied with ambient 20 ± 0.5 C water but was otherwise treated identically. Temperatures in each aquarium were monitored daily with max/min thermometers.

Growth experiments were initiated with 6–8-day (hence age 7-day), 13–15-day (hence age 14-day), and 39–43-day (hence age 41-day) post-hatch groups of each species. Swim-up (7-day) larvae were acclimated to 20 C for a minimum of 24 h prior to initiation of experiments, whereas older age groups were reared at this temperature. Between 50 and 100 fish from each experimental group were transferred to aquaria maintained at experimental (10 C, 14 C) and control (20 C) temperatures.

Fish ($n = 5$ –23 unless fewer fish remained on last sampling date) were sampled from each aquarium by fine-meshed dip net and weighed and measured [total length (TL)]. Because of a limited availability of *G. cypha*, an attempt was made to return individuals to experimental aquaria alive following collection of data. *Gila cypha* were anesthetized in 125 mg/L MS-222, placed on blotter paper for 5 sec, weighed and measured, and returned to respective aquaria. Age 7-day and age 14-day *G. cypha* groups were weighed to the nearest 0.1 mg and measured to

the nearest 0.1 mm; fish in the age 41-day *G. cypha* group were weighed to the nearest 0.01 g.

Samples of *P. lucius*, *C. latipinnis*, and *X. texanus* were sacrificed and preserved in 10% formalin prior to collection of length and weight data (no corrections for shrinkage). Fish were blotted 5 sec and weighed (nearest 0.1 mg) and measured (nearest 0.1 mm).

Development.—We microscopically examined all preserved specimens of *C. latipinnis* and *X. texanus* to determine transformation from larval to juvenile stages. For *X. texanus* and *C. latipinnis*, D. E. Snyder and R. Muth (unpubl.) reported that total lengths at loss of the preanal finfold coincided with lengths at transformation, and rarely were finfolds lost without concomitant acquisition of the adult complement of fin rays. We therefore used presence/absence of the preanal finfold as the single determinant of life stage. For *G. cypha* and *P. lucius*, we considered total lengths at loss of finfolds (D. E. Snyder, unpubl.) as representative of size at transformation. We assessed time to transformation for these species by comparing experimental replicate mean lengths to D. E. Snyder's (unpubl.) reported lengths at loss of finfolds.

Temperature shock.—Thermal-shock experiments, to simulate conditions experienced by fishes entering cold tailwaters from warm tributaries, were conducted on young *G. cypha* (5–7-day and 11–13-day posthatch), *X. texanus* (7–9-day, 11–13-day, and 42–43-day posthatch), and *C. latipinnis* (7–8-day, 14–15-day, and 42–43-day posthatch). Culture and rearing were as described for growth experiments. Fishes were acclimated to 20 C water over 24 h. One to three replicates of 20–100 fish each were then transferred separately to aquaria at the following temperatures: 10 ± 0.5 C, 12 ± 0.5 C, and 14 ± 0.5 C. Replicate controls at 20 ± 0.5 C for all groups were handled in like manner. Fish behavior was observed intensively for several minutes following initiation of each treatment and thereafter for 1-min periods at various intervals over 1–5 h.

Analyses.—The Levene test determined that variances of length and weight data (and transformations) within species-age-temperature groups were not homogeneous. We employed the non-parametric Kruskal-Wallis (K-W) test to compare mean ranks of untransformed lengths and weights across experimental temperatures for each species and age group at each sampling date. Significance levels were adjusted for multiple tests with the Bonferroni sequentially rejective multiple test procedure of Holm (1979).

Replicate data for *X. texanus* and *C. latipinnis* were pooled for analyses, whereas analyses of *G. cypha* and *P. lucius* compared ranks of replicate means (individual data were lost after data summarization). Posthoc multiple comparisons of length and weight statistics across temperatures within each species and age at each sampling date were made using procedures of Zar (1984: 199–201).

We computed specific growth rate (SGR; percent increase in body weight per day) for each species-age-temperature-replicate mean weight as $100 \times [(\log_e \text{ final weight} - \log_e \text{ initial weight}) / \text{days}]$. Kruskal-Wallis tests were used to compare SGRs across temperatures and ages within species. When null hypotheses were rejected (corrected for multiple tests), nonparametric posthoc multiple comparisons were made using procedures of Zar (1984).

RESULTS

Growth.—Plots of mean lengths (Fig. 1) and weights (Fig. 2) over time for each species-age group show enhanced growth with increasing temperature. The flat period of *P. lucius* growth between days 42 and 59 coincided with an outbreak of costiasis.

Comparisons of lengths and weights across temperatures for each *X. texanus* and *C. latipinnis* age group and sample date showed significant differences among mean ranks, with exceptions of age 14-day *X. texanus* for length at day 2, age 41-day *X. texanus* for length and weight at days 10 and 24, and age 41-day *C. latipinnis* for length and weight at day 35 (Tables 1–2).

Tests of replicate mean length and weight comparisons across temperatures for *G. cypha* and *P. lucius* were significant for each sampling date, with the exception of the 24-day comparisons of length and weight for *P. lucius*. Corrections for multiple tests rendered all test probabilities nonsignificant for these two species.

Kruskal-Wallis tests revealed significant differences in SGR among sampling dates, temperatures, and ages for all species. A nonparametric multiple comparison test (Zar, 1984) showed that mean ranks of SGRs were significantly different among all temperature comparisons and that SGR ranks of age-7 and age-14 groups differed from those of age-41 fish but were not different from each other. Plots of mean SGR for age groups of each species over time are shown in Figure 3.

Development.—As determined by presence/absence of the preanal finfold, smallest juvenile *X. texanus* in our experiments was 23.7 mm TL,

and largest larva was 28.7 mm. Respective *C. latipinnis* lengths were 27.0 mm and 30.5 mm. Total lengths at transformation from larva to juvenile are 27–30 mm for *X. texanus* and 28–29 mm (rarely to 31 mm) for *C. latipinnis* (D. E. Snyder and R. Muth, unpubl.). Length at time of finfold absorption for *G. cypha* is reported as 26–27 mm, and 25 mm (rarely 24 mm) for *P. lucius* (D. E. Snyder, unpubl.).

Transformation from larva to juvenile was first observed in age 7-day *X. texanus* 57 days following commencement of temperature experiments at 20 C (30% of sample), and all fish reared at 20 C transformed by day 126. In contrast, no age 7-day *X. texanus* had transformed by day 126 at 14 C or 10 C (maximum TL = 22.0 mm and 14.2 mm, respectively). Ten percent of the sample of age 14-day *X. texanus* reared at 20 C were juveniles on day 51 (all transformed by day 120), but all fish remained in larval stage by day 120 for 14 C and 10 C groups (maximum TL = 24.1 mm and 20.0 mm, respectively). Juvenile *X. texanus* in the age 41-day group were first observed in the day 63 sample at 20 C (65% of sample) and by day 128 at 14 C (30% of sample), but none had transformed by day 128 at 10 C (maximum TL = 25.6 mm).

Juveniles were first observed 59 days following commencement of temperature experiments at 20 C (70% of sample) in the age 7-day *C. latipinnis* group, and all had transformed by day 91. First observance of juveniles in samples of age 7-day *C. latipinnis* reared at 14 C was day 91 (40% of sample), but no fish reared at 10 C had transformed by that time (maximum TL = 21.3 mm). First detection of age 14-day *C. latipinnis* juveniles was in the day 63 sample at both 20 C (80% of sample) and 14 C (10% of sample), but all 10 C fish remained larvae by day 92 (maximum TL = 25.4 mm). All age 41-day *C. latipinnis* samples contained juveniles by day 35 at all experimental temperatures (63% at 20 C, 63% at 14 C, 50% at 10 C), but only at 20 C did all fish complete transformation by day 64.

Based on replicate mean length data, “average” age 41-day *G. cypha* larvae transformed to juvenile stage by day 14 at 20 C (mean TL = 28.6 mm), by day 43 at 14 C (mean TL = 30.3 mm), and some by day 93 at 10 C (mean TL = 26.0). No *G. cypha* larvae from any temperature group transformed to juvenile in the short-duration trials for age 7-day and age 14-day groups. “Average” time to transformation for age 14-day *P. lucius* occurred by day 42 at 20 C (mean TL = 26.6 mm) but not by 92 days at 14 C and 10 C (mean TL = 20.1 mm and 11.7 mm, respectively).

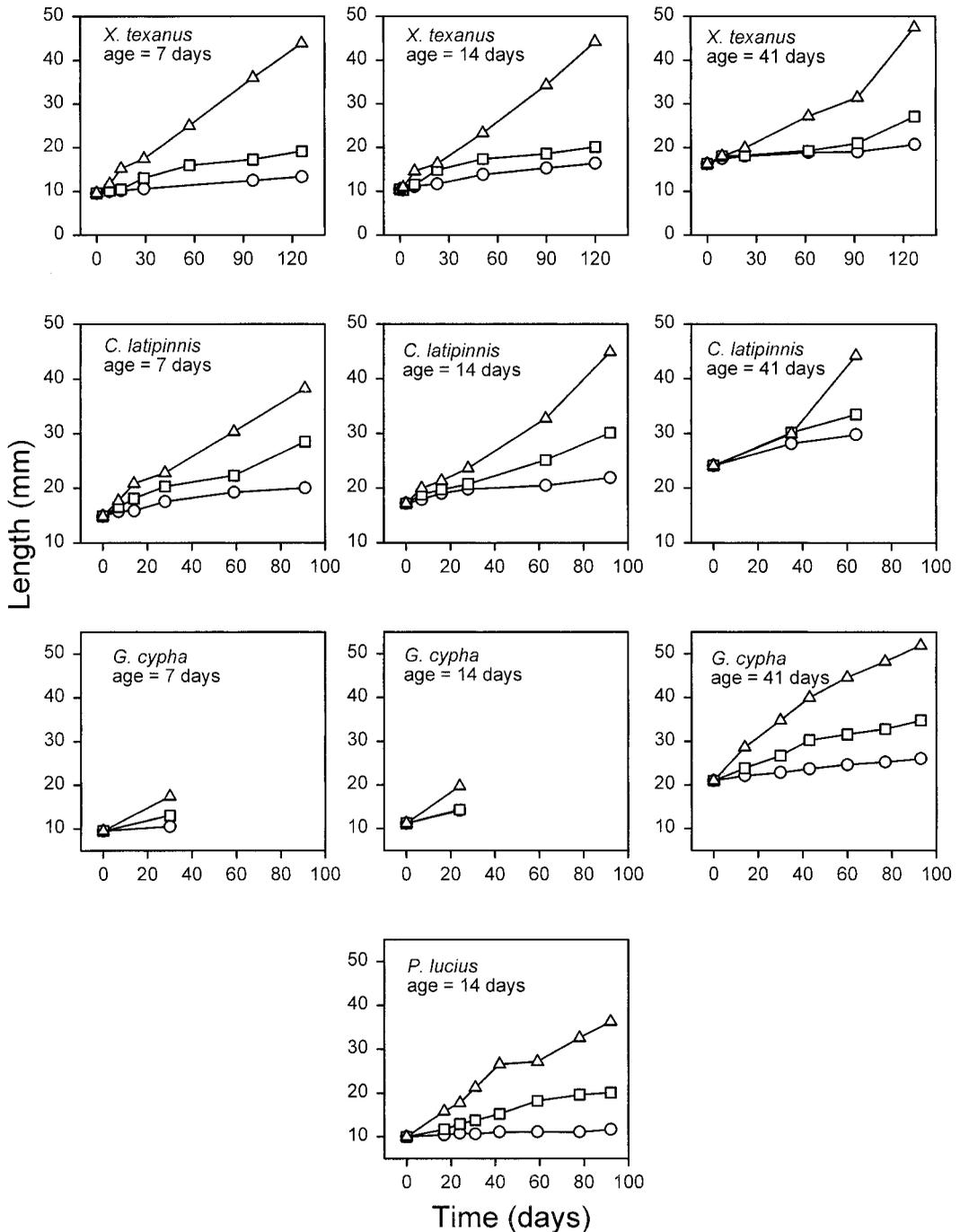


Fig. 1. Changes in length (TL) over time of early life stage big-river fishes reared at three temperatures. Points represent mean responses of each species; ages are days posthatch at initiation of experiment. Circles denote 10 C, squares 14 C, and triangles 20 C.

Temperature shock.—There were no noticeable differences in behaviors among replicate tanks for any species, age, or temperature combination in temperature shock tests. All 5–7 day *G.*

cypha larvae transferred from 20 C to 10 C immediately entered “cold coma,” a condition characterized by an inability to maintain equilibrium and position in the water column (Cou-

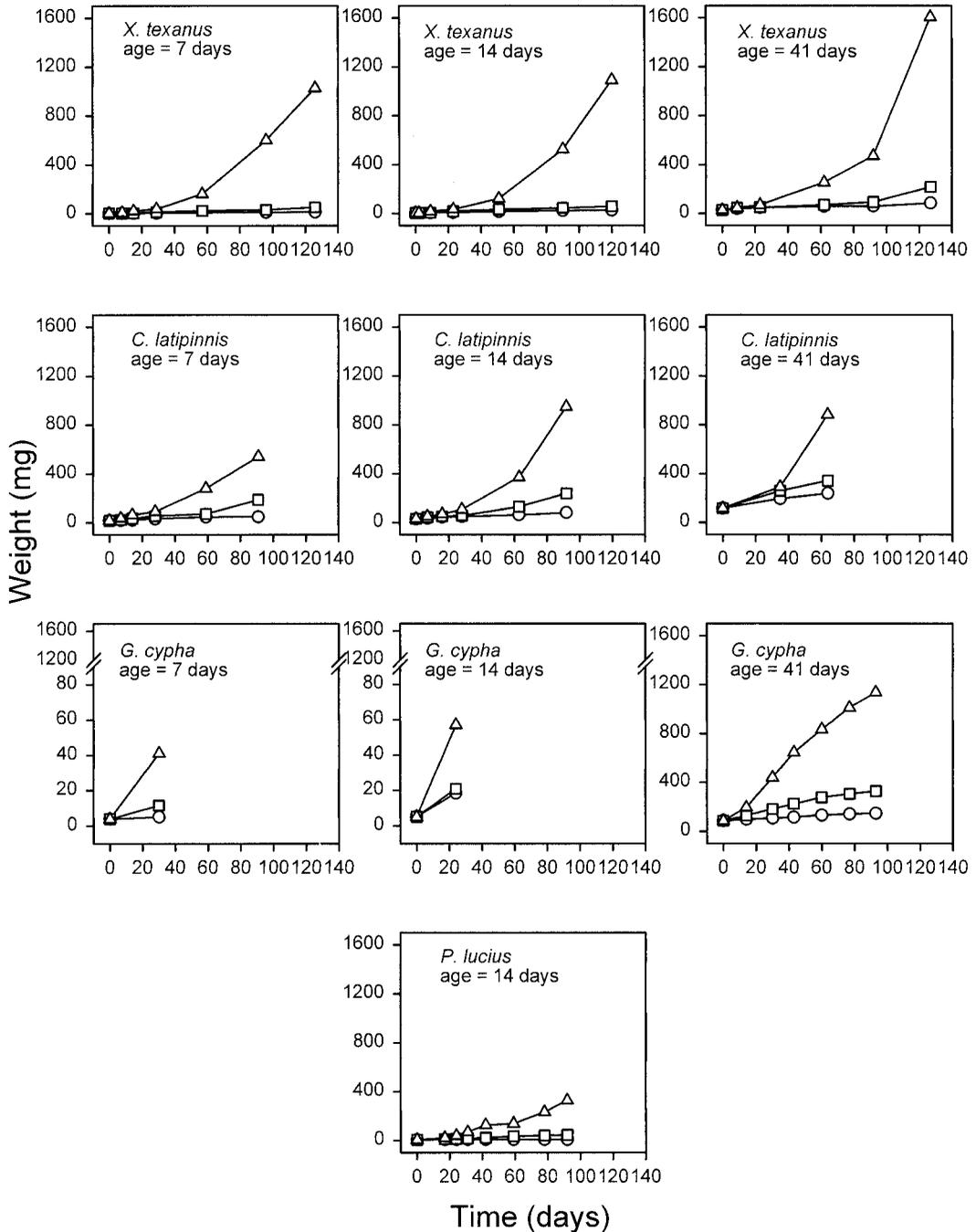


Fig. 2. Changes in weight over time of early life stage big-river fishes reared at three temperatures. Points represent mean responses of each species; ages are days posthatch at initiation of experiment. Circles denote 10 C, squares 14 C, and triangles 20 C. Note the y-axis scale breaks for age-7 and age-14 *Gila cypha*.

tant et al., 1974). Fish drifted in the slow current provided from water inflow to the tank until settling to the bottom, where they remained immobile for approximately 90 min. Over the next 60 min, they regained their ability to swim

in the water column but appeared lethargic compared to 20 C control groups. *Gila cypha* larvae transferred from 20 C to 12 C became lethargic but did not lose their ability to remain in the water column. No behavioral effects were

TABLE 1. MULTIPLE COMPARISONS OF LENGTH AND WEIGHT MEAN RANKS (POOLED REPLICATES) ACROSS THREE TEMPERATURES OF THREE AGES (7, 14, AND 41 DAYS POSTHATCH AT INITIATION OF EXPERIMENT) OF EARLY LIFE STAGE *Xyrauchen texanus*. Day is days past initiation of experiment. Superscript denotes comparisons that were not significant ($\alpha > 0.05$) when adjusted for multiple comparisons.

Age	Day	Length			Weight			N
		10 C	14 C	20 C	10 C	14 C	20 C	
7	8	19.58 ^a	23.80 ^a	48.13	20.95 ^a	20.80 ^a	49.75	60
	15	18.63 ^a	22.38 ^a	50.50	13.90 ^a	27.10 ^a	50.50	60
	29	10.50	31.13	49.88	10.50	31.70	49.30	60
	57	—	10.55	30.45	—	10.50	30.50	40
	96	10.55	30.45	50.50	10.50	30.50	50.50	60
	126	4.00 ^a	13.50 ^a	25.00	4.00 ^a	13.50 ^a	25.00	30
14	2	25.65 ^a	25.30 ^a	40.55 ^a	20.25 ^a	27.90 ^a	43.35	60
	9	17.73 ^a	24.13 ^a	49.65	17.60 ^a	24.17 ^a	49.72	60
	23	12.10	34.72 ^a	44.67 ^a	12.35	34.67 ^a	44.47 ^a	60
	51	11.35	30.88	49.28	11.40	31.05	49.05	60
	90	11.90	29.10	50.50	12.40	28.60	50.50	60
	120	11.10	29.90	46.50	11.32	29.67	46.50	52
41	10	25.60 ^a	33.72 ^a	32.17 ^a	24.98 ^a	34.28 ^a	32.25 ^a	60
	24	25.10 ^a	27.88 ^a	38.53 ^a	25.55 ^a	27.83 ^a	38.13 ^a	60
	63	19.73 ^a	22.17 ^a	49.60	18.10 ^a	24.20 ^a	49.20	60
	93	18.17 ^a	26.85 ^a	46.47	18.70 ^a	26.77 ^a	46.03	60
	128	11.43	29.83	50.25	11.55	29.70	50.25	60

noted for 5–7 day chub larvae transferred from 20 C to 14 C.

Eleven- to 13-day *G. cypha* larvae transferred from 20 C to 10 C also entered cold coma but regained normal behavior after 15 min. No other treatment groups (20 C to 12 C or 20 C to 14 C) at this age exhibited obvious adverse behavioral effects. No *G. cypha* mortality occurred under any treatment over the 4-h observation periods.

For the catostomids, only 7–9-day *X. texanus*

and 7–8-day *C. latipinnis* larvae subjected to temperature shock from 20 C to 10 C appeared to enter cold coma. This condition lasted for 30–60 sec and 5–10 sec for *X. texanus* and *C. latipinnis*, respectively. Thereafter, larvae of both species periodically “rested” on the aquarium bottom for 5–10 sec at intervals that increased over time. This behavior was also apparent at higher temperatures, including controls, for both species, but resting times were on the order of 1–3 sec. No definitive cold coma behavior

TABLE 2. MULTIPLE COMPARISONS OF LENGTH AND WEIGHT MEAN RANKS (POOLED REPLICATES) ACROSS THREE TEMPERATURES OF THREE AGES (7, 14, AND 41 DAYS POSTHATCH AT INITIATION OF EXPERIMENT) OF EARLY LIFE STAGE *Catostomus latipinnis*. Day is days past initiation of experiment. Superscript denotes comparisons that were not significant ($\alpha > 0.05$) when adjusted for multiple comparisons.

Age	Day	Length			Weight			N	
		10 C	14 C	20 C	10 C	14 C	20 C		
7	7	11.48	29.67	50.35	11.10	29.95	50.45	60	
	14	10.50	30.50	50.50	10.50	30.50	50.50	60	
	28	10.57	32.35	48.58	10.50	32.55	48.45	60	
	59	10.50	31.00	50.00	10.50	30.60	50.40	60	
	91	10.50	31.83	49.17	10.75	31.55	49.20	60	
	14	7	13.48	27.85	50.17	12.38	31.58	47.55	60
14	16	14.57 ^a	27.73 ^a	49.20	15.60 ^a	28.05 ^a	47.85	60	
	28	15.43	28.65	47.42	16.30 ^a	25.77 ^a	49.42	60	
	63	11.75	32.33	47.42	11.60	32.25	47.65	60	
	92	10.80	30.90	49.80	11.02	30.83	49.65	60	
	41	35	14.45 ^a	19.15 ^a	12.90 ^a	14.60 ^a	19.20 ^a	12.70 ^a	30
		64	8.20 ^a	14.30 ^a	24.00	8.50 ^a	14.20 ^{ab}	23.80 ^b	30

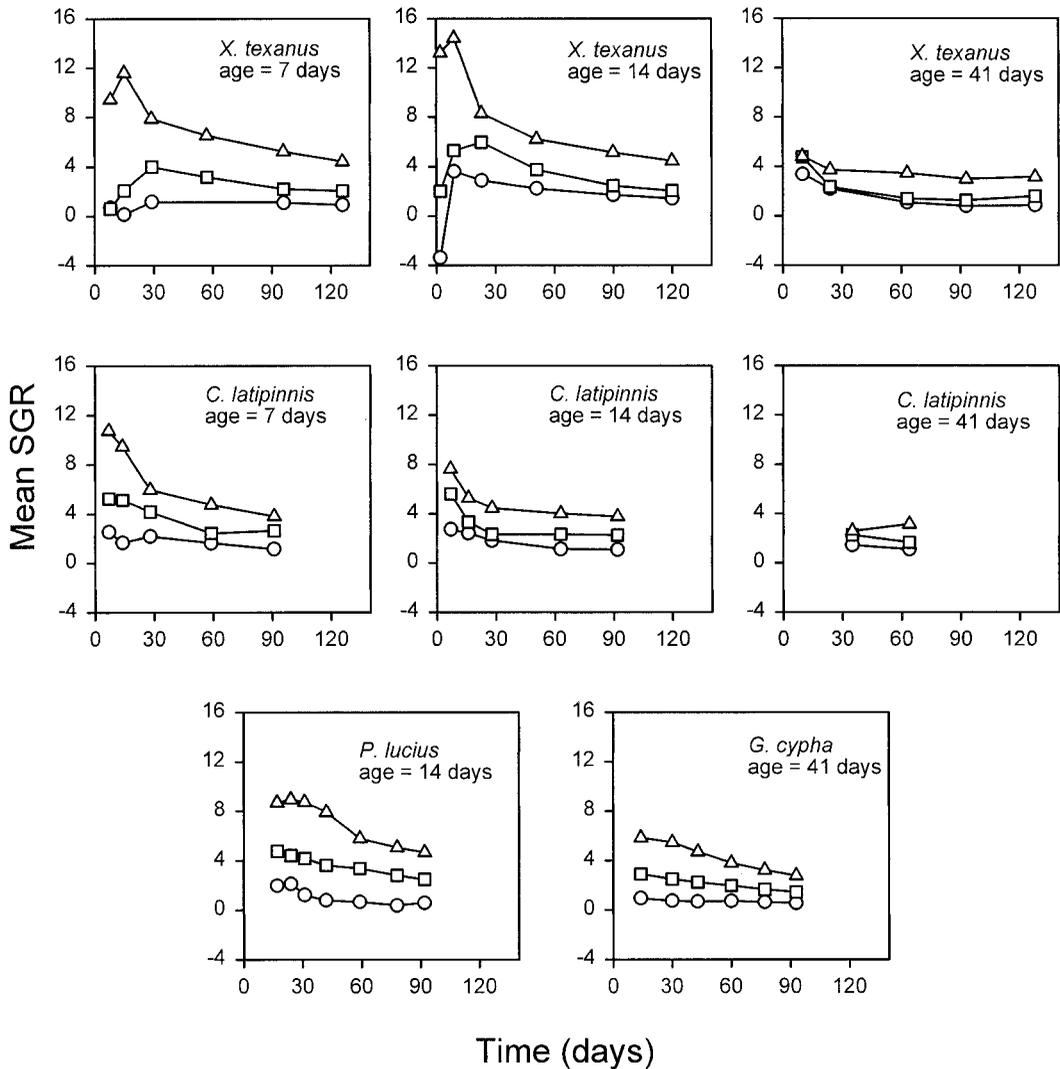


Fig. 3. Mean specific growth rate (SGR) of early life stage big-river fishes reared at three temperatures. Ages are days posthatch at initiation of experiment. Circles denote 10 C, squares 14 C, and triangles 20 C.

occurred at 12 C or 14 C at this age for either species nor with older ages of either species. Swimming behaviors, however, were lethargic at all treatment temperatures for all ages. No mortality attributed to temperature effects occurred in any *X. texanus* or *C. latipinnis* temperature shock experiment.

DISCUSSION

Field observation (Miller, 1961; Vanicek et al., 1970; Kaeding and Zimmerman, 1983), laboratory experimentation (Marsh, 1985; Berry, 1988; Thompson et al., 1991; and others), and simulation (Kaeding and Osmundson, 1988) convincingly demonstrate the negative effects of

cold water temperature (< 15 C) on life-history parameters of native fishes of the Colorado River basin. Our results also suggest adverse effects of low temperature on early life stage growth and development are similar across the species examined. Physiological/behavioral effects (as determined by cold shock experiments) are less consistent.

Our research quantified the effects of water temperature on growth of early life stage big-river fishes: (1) mean ranks of SGR were significantly lower at both 10 C and 14 C compared to 20 C controls on all sampling dates and in all age comparisons; and (2) for *X. texanus* and *C. latipinnis*, mean ranks of length and weight were significantly different across experimental

temperatures, sample dates, and ages (except for the earliest comparisons of some older age groups). Failure to detect similar length and weight differences in *P. lucius* and *G. cypha* was presumably a result of small sample size resulting from analysis of only replicate means. We conclude that lowered water temperature had the same effect on both catostomids and cyprinids.

Our results and those of Berry (1988) suggest early larval stages of some species (*G. cypha*, *P. lucius*) enter cold coma for periods of 5–90 min upon entering cold waters, at least when experiencing the most extreme temperature changes (e.g., from 20 C or higher to 10 C or lower). Some direct mortality is possible (Berry, 1988). With smaller temperature differences (e.g., from 20 C to 12 C), some cold coma may occur in larvae, activity levels may be reduced, and other physiological/behavioral changes may be evident (see also Berry, 1988). At moderate temperature differences (e.g., from 20 C to 14 C), we noted few or no short-term effects. Older larval and postlarval fishes did not exhibit any apparent physiological/behavioral effects (except lethargy) at any temperature change (see also Berry, 1988). Research on other warmwater species has also shown that behavioral changes are lessened with smaller temperature differences (Speakman and Kenkel, 1972; Griffith, 1978; Burton et al., 1979) and with older fish (Pitkow, 1960; Nickum, 1966).

Effects of entering cold coma in the Colorado River system are potentially severe. Predation rates may be increased (Coutant et al., 1974), and physical damage and death may occur from abrasion against substrates, entrainment in high current velocities and turbulence, or from burial if fish settle on the substrate.

Early life stage big-river fishes that enter cold tailwaters become exposed to essentially perpetual near-winter temperature conditions, with resultant severe growth depression that negatively acts upon numerous life-history parameters, as previously noted. Our experiments showed delays in transformation from larva to juvenile at lower temperatures, in some cases extending the larval stage through an entire season or more. Delays in transformation lengthen exposure to existing sources of mortality such as food scarcity (Papoulias and Minckley, 1990, 1992), hydrological disturbance (Robinson et al., 1998), predation (Ruppert et al., 1993), parasitism (Clarkson et al., 1997), or other factors (Houde, 1987).

These findings suggest that, short of dam removal, more flexible dam operations (especially warming of discharges) are needed to conserve

populations of Colorado River basin big-river fishes in hypolimnial-release tailwaters. Effects of tailwater warming via modification of Flaming Gorge Dam resulted in immediate positive response by native fishes (P. B. Holden and L. W. Crist, unpubl.). Although tailwater reaches may not provide all environmental elements required for successful completion of lifecycles of some of the big-river species, they should not be disregarded in recovery efforts, especially given the deteriorating or tenuous status of many of these fishes in other river reaches (Lanigan and Tyus, 1989; Minckley et al., 1989; Osmundson and Burnham, 1998).

Kaeding and Osmundson (1988), Minckley (1991), Childs and Clarkson (1996), and others cautioned that increasing tailwater temperatures to benefit warmwater native fishes may also advantage nonnative aquatic biota, perhaps to the detriment of the former. Absent such modification, however, big-river species will likely continue to decline and disappear from tailwater reaches, as exemplified by the trend in Grand Canyon (Minckley, 1991; Weiss, 1993; R. Valdez and R. J. Ryel, unpubl.). Thermal modification of tailwaters is the only way to alleviate the known restriction by cold water temperatures to successful spawning, embryo incubation, and larval growth of warmwater native fishes. In concert with provision of more natural (pre-dam) hydrological release patterns, we believe expansion of nonnative fish populations can be minimized to the relative benefit of natives. Should operational changes result in expansion of nonnative populations to the increased detriment of natives, a return to full hypolimnetic discharge temperatures could largely reset the system to its former state, albeit with continued deterioration of native fish stocks.

Resolution of conflicts between native and nonnative species interactions likely will require basinwide implementation of innovative activities that have not yet been seriously considered. These should include routine provision of high-magnitude floods to destabilize nonindigenous fish populations (Minckley and Meffe, 1987; Tyus and Karp, 1989), development of new taxon-specific ichthyocides, segregation of native and nonnative (sport) fisheries, and education of the public about the ecological consequences of transfaunations and values of native communities. Stopgap measures such as acquisition of instream flows or increased hatchery production and repatriation of native fishes may slow or stop declines, but recovery of the big-river native ichthyofauna of the Colorado River Basin may ultimately depend upon implementation of

more comprehensive (and expensive) control measures against nonnative fishes.

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