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Juvenile Growth of Native Fishes in the Little Colorado River and in a Thermally Modified Portion of the Colorado River

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Abstract.—We estimated juvenile growth rates of four native fish species using the von Bertalanffy growth equation and length data from fish captured during 1991–1994 in the Little Colorado River, a tributary to the Colorado River in Arizona in the Grand Canyon. We compared growth rates to water temperatures for all four species and modeled the effects of warming the Colorado River (through a proposed retrofit of Glen Canyon Dam) on the growth of age-0 emigrants from the tributary. Juvenile growth rates in the Little Colorado River were fastest for flannelmouth sucker *Catostomus latipinnis*, slowest for speckled dace *Rhinichthys osculus*, and intermediate for humpback chub *Gila cypha* and bluehead sucker *Catostomus discobolus*. Growth rates for each species were positively correlated with water temperature; flannelmouth sucker exhibited the strongest relationship, followed by speckled dace, humpback chub, and bluehead sucker. Our model indicates that native fish immigrating into the cold Colorado River (8–12°C) from the relatively warm Little Colorado River during their first 3 months of life will grow very little by the end of their first year. According to other studies, older, larger fish that disperse into the Colorado River are more likely to survive than those that migrate as larvae. Growth, and possibly survival, of native fish larvae that drift from tributaries into the Colorado River could be increased if water released from Glen Canyon Dam is warmed during the period of larval drift.

Dams and dam operations can change the suitability of downstream riverine habitat for native fishes (Ward and Stanford 1979; Stanford et al. 1996). One change involves alteration of the thermal regime. For example, in the Colorado River between Glen Canyon Dam and Lake Mead, hypolimnetic releases from the dam result in relatively constant cold (7–12°C; mean, 10.5°C) year-round temperatures in the tailwater (Stanford and Ward 1991; Stevens et al. 1997).

Of eight indigenous species, only four remain (humpback chub *Gila cypha*, flannelmouth sucker *Catostomus latipinnis*, bluehead sucker *Catostomus discobolus*, and speckled dace *Rhinichthys osculus*), and main-stem reproduction appears to be uncommon for humpback chub and the sucker species (Schmidt et al. 1998); the extent of speckled dace spawning in the main stem is unknown. In contrast, all four native species reproduce, feed, and grow in tributary streams, of which the Little Colorado River (124 km below the Glen Canyon Dam) is the most important. Water temperatures in the Little Colorado River resemble those of the Colorado River before the dam was built (predam; Figure 1). The native fishes spawn primarily in spring through early summer, and the young rear in the tributary streams. However, some young immigrate (by both passive and active movement) into the Colorado River during the summer (Robinson et al. 1998), when main-stem temperatures are 9°C colder than in the Little Colorado River (Kaeding and Zimmerman 1983; Figure 1). Growth of these migrants probably decreases substantially on entering the Colorado River (Clarkson and Childs 2000). In addition, the mortality of larval native fishes transported into the Colorado River probably increases because of the physiological effects of cold water temperatures (Clarkson and Childs 2000; Taniguchi and Nakano 2000), such as less ability to avoid predation, less competitive ability, and less foraging efficiency. It also seems probable that fish entering the Colorado River early in the summer will grow more slowly (Clarkson and Childs 2000) and attain a smaller size by end of their first year than will same-age fish that enter later in the summer. These smaller fish probably experience greater mortality rates than larger individuals do, because of their poorer competitive ability (Fausch and White 1986; Elliott 1994; Post et al. 1999; Taniguchi and Nakano 2000) and poorer ability to avoid predation (Werner and Gilliam 1984; Rice et al. 1987; Luecke et al. 1990).

Historically, water temperatures in the predam Colorado River in Grand Canyon have ranged from near freezing in December and January to approximately 26°C in July and August and are typ-

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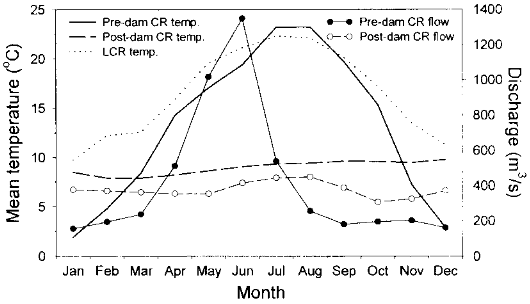

FIGURE 1.—Mean monthly temperatures and flows in the predam (1950–1962) and postdam (1990–1997) Colorado River (CR) at Lees Ferry (U.S. Geological Survey gauging station 099380000) and mean monthly temperatures in the Little Colorado River (LCR; 1991–1994, 0.6 km above the mouth), Arizona. Main-stem temperatures near the Little Colorado River during summer are approximately 2.5°C warmer than those at Lees Ferry.

ically above 17°C from May through September (Kaeding and Zimmerman 1983), when native fish reproduce and larvae disperse from tributaries. It may be possible to restore the predam thermal regime to the Colorado River by way of warming releases from Glen Canyon Dam (USFWS 1994; USDI 1999). Knowledge of age-0 growth rates of native fishes in relation to temperature is therefore necessary to make decisions regarding implementation and operation of a temperature modification structure. Here we present growth data for the four native species through the juvenile stage in the Little Colorado River and present evidence that properly timed warming of the main-stem Colorado River during the spring and summer can allow immigrant juvenile fishes to grow to larger sizes than they would in an unmodified Colorado River.

Methods

We sampled fish monthly from May 1991 through June 1994. We sampled four consecutive days during the first half of each month except during May through June, when we sampled daily. We sampled the lower 14 km of the Little Colorado River above the mouth, primarily in the vicinity of 1.9 and 10.5 km above the mouth. Fish were captured at locations that could be effectively sampled with seines (2–5 m long × 1–1.5 m high with 1.6- or 3.2-mm mesh), dip nets (0.5-mm mesh), and cylindrical minnow traps (0.8-mm mesh). All fish captured were identified as to species, measured for total length (mm), and weighed (g) when possible. Colorado River flow data (mean daily flows) were acquired from the U.S. Geological Survey (gauging station 099380000). Water temperature data (mean daily temperatures) were obtained from the U.S. Department of Interior, Grand Canyon Monitoring and Research Center, Flagstaff, Arizona.

Analysis.—We used data collected during the first 2 weeks of each month to analyze length frequencies. We used FiSAT (FAO 1996) computer software to model species growth based on the von Bertalanffy growth function, expressed as follows:

$$l_t = L_\infty \cdot [1 - e^{-K(t - t_0)}]$$

where l_t = length at time t, L_∞ = asymptotic length, K = the curvature parameter, t = a given time or age, and t_0 = the age fish would have had at length zero if they had always grown according to the growth equation (FAO 1996). For each species we followed FiSAT (FAO 1996) procedures to estimate population parameters, using the direct fit of length-frequency data. We first constructed Powell–Wetherall plots to estimate L_∞. We then used Shepard's method to scan K values, using the above L_∞. Next, we input a range of possible K and L_∞ values, conducted a response surface analysis, and selected the K and L_∞ values resulting in the greatest R_n (goodness-of-fit index). We input the generated K and L_∞ values into Electronic Length Frequency Analysis (ELEPHAN 1; FAO 1996) software to generate a von Bertalanffy growth curve. If the curve did not appear to fit the data, we modified the values of the input parameters and reran the analysis. We also used an automated search routine to let the computer find the best combination of parameters (best fit of the curve = greatest R_n).

Based on the final von Bertalanffy growth equations, we used ELEPHAN 1 to generate length-at-age data for each species through the juvenile stage (1991–1993). We used the generated length data and 1991 Little Colorado River temperature data to assess the effects of water temperature on growth of juvenile fish. For each species we calculated actual daily growth rates, $(\mathrm{TL}_{t+1} - \mathrm{TL}_t)/(d_{t+1} - d_t)$, where TL = total length at times t and $t + 1$, and d = day at times t and $t + 1$. We then calculated mean monthly growth rates based on daily growth rates from the 16th of one month to the 15th of the next month. We also calculated mean monthly water temperature (mean of daily temperatures from the 16th of one month through the 15th of the next month). We used a curve-fitting routine in SPSS (version 8.0; SPSS 1998) to evaluate the best mathematical relationship of temperature and growth; data used were from May

TABLE 1.—Von Bertalanffy growth equation parameters estimated using FiSAT for Little Colorado River native fishes. Parameters are as follows: L_∞ = asymptotic length, K = curvature parameter, C = amplitude of seasonal growth oscillation, WP = winter point (time of year when growth rate is slowest), and R_n = goodness-of-fit index.

		Parameter				
Species	N	L_∞ (mm)	K	C	WP	R_n
Humpback chub	2,947	360	0.245	0.960	0.090	0.281
Speckled dace	2,835	110	1.200	0.950	0.100	0.208
Flannelmouth sucker	178	450	0.310	0.900	0.070	0.269
Bluehead sucker	2,563	260	0.370	0.900	0.210	0.449

1991 through April 1992. For all four species we chose linear regression as the best model (it typically had the greatest correlation coefficient). We used analysis of covariance (ANCOVA) to assess whether age-0 growth rates differed among species and whether the effect of temperature on growth rate differed among species.

TABLE 2.—Length (mm) at age estimated from von Bertalanffy growth equations for four native fish species in the Little Colorado River, Arizona, through age 2. Species hatch predominantly in May and June. Small sample sizes resulted in length-at-age estimates only through 19 months for flannelmouth sucker.

		Species			
Age (year)	Month	Humpback chub	Speckled dace	Bluehead sucker	Flannel-mouth sucker
0	May	9		9	
	Jun	19	8	15	11
	Jul	31	25	23	25
	Aug	44	40	35	46
	Sep	56	52	48	64
	Oct	65	60	59	77
	Nov	71	66	70	86
	Dec	75	68	77	91
1	Jan	76	69	81	93
	Feb	76	70	83	94
	Mar	77	70	84	96
	Apr	80	72	85	101
	May	85	75	87	111
	Jun	93	80	90	124
	Jul	102	84	97	138
	Aug	113	89	105	
	Sep	122	93	113	
	Oct	129	95	121	
	Nov	134	97	128	
	Dec	137	97	133	
2	Jan	138	98	136	
	Feb	138	98	138	
	Mar	138	98	138	
	Apr	141	99	139	
	May	145	99	140	
	Jun	151	101	143	
	Jul	158	102	147	
	Aug	166	104	153	
	Sep	174	105	159	
	Oct	179	106	164	
	Nov	183	106	169	
	Dec	185	106	173	

On the basis of the relationship of growth to water temperature, we modeled the effect of warming the Colorado River on growth of age-0 immigrant native fishes. We plotted von Bertalanffy growth curves derived from length-frequencies of the Little Colorado River fish. On the same graph we plotted lines that represented growth of fish immigrating, at two different dates (May 15 and July 15), into a cold (May–December 1991 river temperatures) or warmed (17.5°C) Colorado River. The size of the fish at the three dates (output of ELEPHAN 1) represented the length of the fish during each of the first 3 months of life. The temperature at which growth rates were equal to zero was solved mathematically from the regression equations of temperature versus growth rate, and growth rates were set equal to zero for lower temperatures. To assess how the duration of a warming period might affect the growth of young-of-year native fish, we modeled growth through age 0 for fish exposed to a 90- or 120-d warming period.

Results

Of the four von Bertalanffy growth models, that for bluehead sucker had the best fit (Table 1). Age-0 growth rates differed among species (df = 3,26; $F = 3.454$; $P = 0.03$) and were fastest for flannelmouth sucker ($b = 0.42$ mm/d, SE = 0.05) and slowest for speckled dace ($b = 0.28$ mm/d, SE = 0.04), with humpback chub ($b = 0.29$ mm/d, SE = 0.04) and bluehead sucker ($b = 0.32$ mm/d, SE = 0.01) exhibiting intermediate rates. By 12 months of age, estimated lengths of humpback chub and bluehead suckers were similar (85 and 87 mm TL, respectively), whereas speckled dace were estimated to be 80 mm long and flannelmouth suckers were 124 mm (Table 2).

Growth rates of juvenile native fish were highly and significantly correlated with water temperature (Table 3). ANCOVA indicated that the relationship between temperature and growth rates differed among species (df = 3,34; $F = 6.66$; $P = 0.001$) with flannelmouth suckers exhibiting the strongest

TABLE 3.—Linear regression equations describing the association between temperature (T) and growth (G = mm/d) of native fishes from hatching (May or June 1991) to mid-age-1 (April 1992) in the Little Colorado River, Arizona.

Species	Equation	r	SE of slope	df	F	P
Humpback chub	$G = -0.403 + 0.037T$	0.98	0.002	1,9	249.47	<0.001
Speckled dace	$G = -0.511 + 0.044T$	0.96	0.005	1,8	86.13	<0.001
Flannelmouth sucker	$G = -0.604 + 0.056T$	0.98	0.004	1,8	197.75	<0.001
Bluehead sucker	$G = -0.210 + 0.026T$	0.78	0.007	1,9	13.69	0.005

relationship (greatest slope) followed by speckled dace, humpback chub, and bluehead suckers. Estimated temperatures below which growth rates equaled zero were 10.9°C for humpback chub, 11.6°C for speckled dace, 10.8°C for flannelmouth suckers, and 8.1°C for bluehead suckers. Mean monthly temperatures in the Colorado River from May through December 1991 were 10.2°C (range, 9.0–10.9°C).

Fish size at the end of age 0 depended on the timing and duration of the warming period (Figure 2). May immigrants (humpback chub and bluehead suckers) attained similar lengths at end of age 0, regardless of timing of the warming period, because all were exposed to the same duration of warming. Fish that immigrated in June or July (all four species) had a broader range of possible lengths at end of age 0, because they could ex-

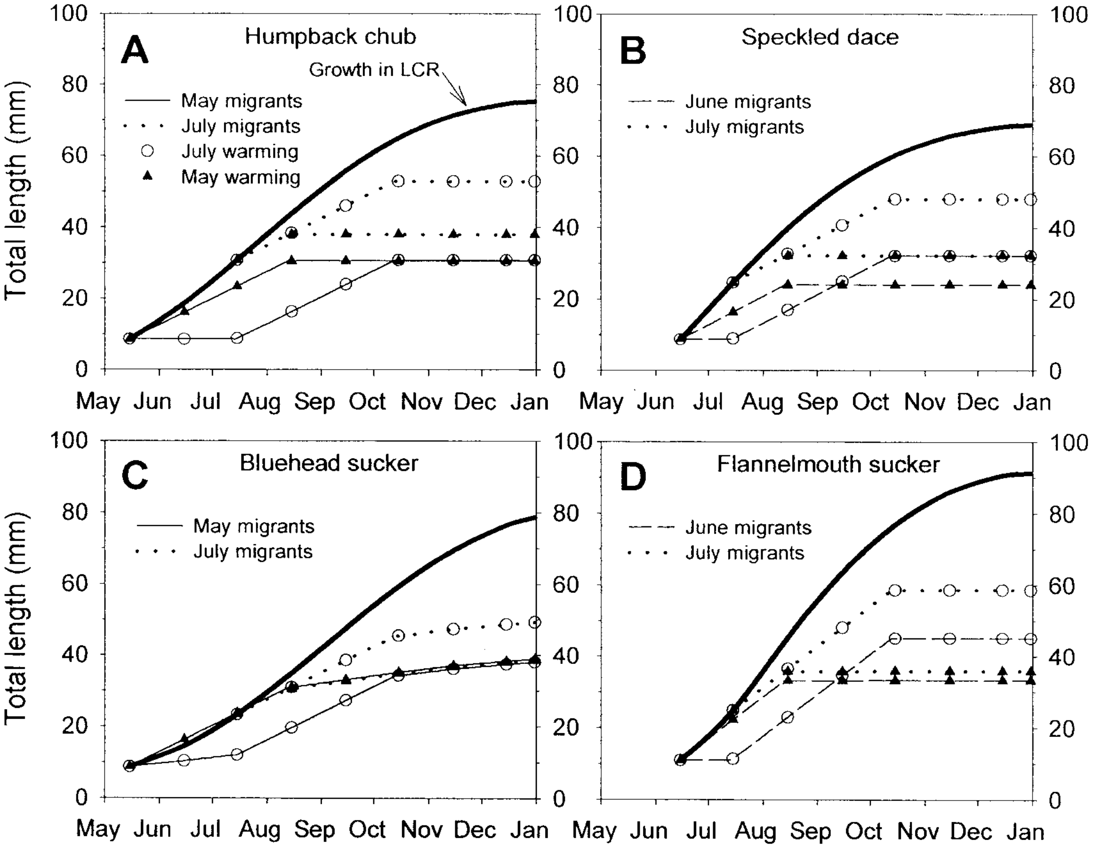

FIGURE 2.—Modeled juvenile growth of (**A**) humpback chub, (**B**) speckled dace, (**C**) bluehead suckers, and (**D**) flannelmouth suckers in the Little Colorado River (LCR; thick black line), Arizona, and for fish that immigrate into the Colorado River warmed to 17.5°C for 90 d. Lines with black triangles show growth with a warming period initiated in May, and those with open circles show growth with a warming period initiated in July. Line type indicates growth of fish that immigrate on different dates (the 15th of May and July for humpback chub and bluehead suckers and the 15th of June and July for speckled dace and flannelmouth suckers).

perience a shorter warm period than the earlier immigrants (if the warming began in an earlier month). Increasing the warming period from 90 to 120 d resulted in a gain (by the end of age 0) in length of approximately 11 mm for flannelmouth sucker, 7 mm for humpback chub, 8 mm for speckled dace, and 5 mm for bluehead suckers. The difference between maximum and minimum lengths attained at the end of age 0 (Figure 2) was greatest for flannelmouth suckers (25 mm), followed by speckled dace (24 mm), humpback chub (22 mm), and bluehead suckers (12 mm). For a given date of initiation of warming, the longer the fish remained in the Little Colorado River, the greater their size at the end of age 0.

Discussion

All four native fish species experienced rapid juvenile growth in the Little Colorado River, and growth rates were highly correlated with temperature. Although our study was not experimental, the positive relationship between water temperature and fish growth is well established. As estimated from our regressions, the effects of temperature on growth rates of humpback chub and flannelmouth suckers corroborate those determined in laboratory tests (Clarkson and Childs 2000).

Our models indicated that age-0 fish migrating into a cold Colorado River would cease to grow (speckled dace and humpback chub) or have near-zero growth rates (bluehead suckers and flannelmouth suckers). Thus, these fish will probably be subject to more prolonged predation risks (Rice et al. 1987; Luecke et al. 1990), size-dependent competition (Fausch and White 1986; Elliott 1994; Post et al. 1999; Taniguchi and Nakano 2000), and other stresses (e.g., cold coma; Clarkson and Childs 2000) associated with cold water temperatures. Therefore, with regard to temperature effects, fish that immigrate into the Colorado River as larvae are likely to experience greater mortality than those that disperse at later stages. Other factors, such as predation and food availability, may differentially affect juvenile survival in the two rivers, but those are beyond the scope of this paper.

Warming the Colorado River during spring through summer would allow immigrant fish larvae to grow to larger sizes than they do now and might thus increase their survival. However, these results will be species-specific, because growth rates, the relationship between temperature and growth rates, and the timing of larval drift (Robinson et al. 1998) differ among species. Bluehead suckers may benefit least from warming; the correlation between growth and water temperature was weakest for this species, and modeling indicated positive growth in the cold Colorado River. In addition, having a long rather than a short period of warming would be more beneficial, because the longer the duration, the greater the size fish will attain by the end of age 0, and presumably the greater will be their survival. Benefits to age-0 fish may be maximized if initiation of warming slightly precedes peak larval drift. Initiation of warming in May could benefit humpback chub and bluehead suckers more than flannelmouth suckers and speckled dace because the former tend to hatch (based on growth models) and drift (Robinson et al. 1998) earlier in spring than the latter two. Nevertheless, because temperatures in a warmed Colorado River would not be as great as those in the Little Colorado River, or even the predam Colorado River, fish that remain in the Little Colorado River would probably attain greater lengths than those that emigrate, regardless of the duration or timing of warming.

Finally, we recommend adaptive management of dam operations with regard to thermal modifications, because warming the Colorado River might also adversely affect native fishes by enhancing growth and reproduction of nonnative fish species (Kaeding and Osmundson 1988; Minckley 1991; Clarkson and Childs 2000). For instance, growth peaks occur at approximately 15°C for rainbow trout *Oncorhynchus mykiss* (Railsback and Rose 1999) and brown trout *Salmo trutta* (Preall and Ringler 1989), both of which are known to prey on Colorado River native fish species (Marsh and Douglas 1997). Warming the river may thus increase nonnative fish predation on and competition with native fishes.

Alternatively, warming the Colorado River spring through autumn may have the additional benefit of stimulating native fishes to spawn in the main stem. Warming the river during this period would better simulate (compared with current conditions) predam seasonal water temperatures, and warming water temperatures are believed to be one of the spawning cues for humpback chub (Muth et al. 2000), flannelmouth suckers (Weiss 1993), and speckled dace (Kaya 1991). Temperature-related interactions among native and nonnative fishes should be evaluated before and during the implementation of warm water releases. If warming has an obvious beneficial effect on nonnative fishes, then implementation of a coldwater flood in spring might reduce nonnative fish populations and help minimize the potential impact of these species on native fishes (Clarkson and Childs 2000). If warming has an obvious detrimental effect on native fish populations, then reversion to coldwater releases should be considered.

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