Articles

Body Condition of Endangered Humpback Chub in Relation to Temperature and Discharge in the Lower Colorado River

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Abstract

Determining the population status of endangered Humpback Chub *Gila cypha* is a major component of the adaptive management program designed to inform operation of Glen Canyon Dam upstream from Grand Canyon, Arizona. In recent decades, resource managers have identified a portfolio of management actions (with intermittent implementation) to promote population recovery of Humpback Chub, including nonnative fish removal, changes in water release volumes and discharge ramping schedules, and reductions in hydropower peaking operations. The Humpback Chub population in Grand Canyon has increased over this same period, causal factors for which are unclear. We took advantage of unusual hydrology in the Colorado River basin in 2011 to assess trends in juvenile Humpback Chub length–weight relationships and condition in the Colorado River below Glen Canyon Dam as well as in the unregulated Little Colorado River. Within each river, we observed higher length–weight *b*-parameter estimates (exponent of the standard power equation) at higher water temperatures. We also found higher slope estimates for the length–weight relationship at higher temperatures in the Little Colorado River. Slope estimates were more variable in the Colorado River, where mean water temperatures were more uniform. The next step is to examine whether Humpback Chub length–weight relationships influence population metrics such as abundance or survival. If these relationships exist, then monitoring condition in juvenile Humpback Chub would provide a quick and low-cost technique for assessing population response to planned management experiments or changing environmental conditions.

Keywords: regulated river, endangered species, fish condition, monitoring, dams

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Introduction

Ecologists and natural resources managers are often interested in assessments of fish growth since growth integrates a large range of environmental and ecological factors (Werner and Gilliam 1984; Rosenfeld and Boss 2001; Pine et al. 2017b). For species of conservation concern, such as the endangered Humpback Chub *Gila cypha* (U.S. Fish and Wildlife Service [USFWS] 1967; U.S. Endangered Species Act [ESA 1973, as amended]), information on growth can provide information on how the species responds to management actions designed to promote population recovery. Because growth and condition data are simple and inexpensive to collect, they can provide more rapid interpretation of environmental conditions and insight into how a species responds to management actions designed to promote population recovery.

Humpback Chub are large, morphologically distinct minnows (family Cyprinidae) endemic to turbulent canyons of the Colorado River. The largest population of Humpback Chub persists around the confluence of the Colorado and Little Colorado rivers in Grand Canyon, Arizona (Coggins et al. 2006; Coggins and Walters 2009). Humpback Chub conservation is a major component of the Glen Canyon Dam Adaptive Management Program (Coggins and Walters 2009), which directs operation of the multimillion dollar hydropower facility at the upper end of Grand Canyon. The inability to determine causative environmental factors for Humpback Chub population fluctuations remains among the most persistent limitations of ecosystem management in Grand Canyon.

In this paper we make spatial and temporal comparisons of juvenile Humpback Chub length–weight relationships between the Colorado River and Little Colorado River and examine whether physical conditions within each river system affect the length–weight relationship. Our objectives were to 1) compare length–weight relationships between months in the Colorado River, 2) examine annual variation in length–weight relationships both within each river and between river systems, and 3) describe the relationship between temperature, variation in discharge, and parameters describing the length–weight relationship. These comparisons can help with understanding how key physicochemical variables such as temperature and discharge affect condition of Humpback Chub. This type of incremental improvement in understanding can help inform management decisions related to water releases, dam operations, and management actions, all of which can aid recovery of Humpback Chub and other fish populations in regulated river systems.

Methods

Fish biologists have intensively studied Humpback Chub in the Little Colorado River and mainstem Colorado River for more than three decades (Valdez and Ryel 1995; Gorman and Stone 1999; Coggins et al. 2006). In order to make temporal and spatial comparisons, we compiled available data from Humpback Chub sampling programs during the 1990s and augmented this dataset with measurements collected in 2011 (Table 1). We restricted our analyses of Humpback Chub length–weight relationships to samples collected in the same season (late summer or early fall) to eliminate bias from seasonal variation in growth or condition (Anderson and Neumann 1996; Froese 2006). Humpback Chub were collected by field personnel in the Little Colorado River using seines, hoop nets, minnow traps, and trammel nets; in the mainstem Colorado River they used the same gear plus boat electrofishing (see additional details in Douglas and Marsh 1996 and Valdez and Ryel 1995). Sampling occurred in the lower 13.5 km of the Little Colorado River, and in the mainstem Colorado River between km 96 and 200 (below the Glen Canyon Dam), with the majority of sampling taking place directly downstream of the Little Colorado River confluence. During 2011, field personnel collected all fish with hoop nets from the lower 3 km of the Little Colorado River and from km 102 to 106 in the Colorado River. They measured total length (TL) of each fish to the nearest millimeter and also recorded weight in grams. In all cases, they took care to measure and weigh fish out of the wind and on a stable surface to maximize measurement accuracy. We obtained length–weight data from before 2011 from the U.S. Geological Survey Grand Canyon Monitoring and Research Center database (USGS 2011). We assumed that catchability was equal across all fish condition levels.

We examined the length–weight relationship for juvenile Humpback Chub ($<$ 200 mm TL and generally $<$ age 3) using several different approaches. We used the standard length–weight model, $W = aL^b$ (equation 1), where W is fish weight in grams, L is total length in millimeters, and a and b are model parameters (Safran 1992). We then fit equation (1) to the respective data for each analysis (Table 1) and estimated a and b parameters using a nonlinear optimization routine in program R (Text S1, *Supplemental Material*; Data S1, *Supplemental Material*; Data S3, *Supplemental Material*; R Development Core Team 2012). We approximated standard errors as the square root of the diagonal elements of the covariance matrix. We then calculated approximate 95% confidence intervals by multiplying the approximate standard errors by two, then adding or subtracting these values from the parameter estimate. We used model parameters to fit curves that describe the relationship between length and weight across the range of sizes for each month, year, or year $+$ river combination assessed.

In addition to fitting the standard length–weight model, we used a generalized linear modelling approach to conduct an analysis of covariance (ANCOVA; Text S2, *Supplemental Material*; Data S2, *Supplemental Material*) on the natural-log-transformed length and weight data following standard fisheries methodology (Pope and Kruse 2007). Using ANCOVA, we tested for differences in the intercepts and slopes of the length–weight relationship by month, year, or year $+$ river. We examined residual plots to ensure that the assumptions of the ANCOVA were met. We ranked models using the Akaike

Table 1. Summary of length–weight analysis parameters for Humpback Chub *Gila cypha* collected in the mainstem Colorado River (CO) in the Grand Canyon and Little Colorado River (LCR), Arizona, during August (A), September (S), and October (O) 1991–2011. We discuss comparisons C1, C2, C3, and C4 in the Methods section; an X designates the use of a dataset in a given comparison. We give the total number of fish sampled (*N*) and estimates of *a* and *b* parameters, including the approximate 95% confidence intervals (Cis), for each comparison.

Comparison[a]					Months										
CI	C2	C3	C4	Year	A	S	O	River	*a*	Approx. 95% lower CI for *a*	Approx. 9 5% upper CI for *a*	*b*	Approx. 95% upper CI for *b*	Approx. 95% lower CI for *b*	*N*
—	—	X	X	1991	X	—	—	LCR	7.53E-06	8.41E-06	6.65E-06	2.97	3.00	2.95	616
—	—	X	X	1992	X	—	—	LCR	5.50E-06	6.41E-06	4.59E-06	3.05	3.08	3.01	242
—	—	X	X	1993	X	—	—	LCR	7.67E-06	8.59E-06	6.75E-06	2.96	2.98	2.94	809
—	—	X	X	1994	X	—	—	LCR	5.67E-06	6.42E-06	4.93E-06	3.00	3.03	2.98	738
—	—	X	X	2011	X	—	—	LCR	3.60E-07	4.97E-07	2.23E-07	3.59	3.66	3.52	100
—	X	—	—	1991		X	—	CO	1.18E-06	1.54E-06	8.12E-07	3.41	3.47	3.35	78
—	X	—	—	1992	X	X	X	CO	3.82E-06	4.59E-06	3.05E-06	3.18	3.22	3.14	124
—	—	—	X	1992	X	—	—	CO	4.12E-05	5.45E-05	2.79E-05	2.70	2.76	2.63	42
—	X	—	—	1993	X	X	X	CO	3.50E-06	4.01E-06	3.00E-06	3.17	3.20	3.14	363
—	—	—	X	1993	X	—	—	CO	3.31E-06	4.49E-06	2.14E-06	3.19	3.26	3.12	56
—	X	—	—	1998	X	X	—	CO	2.12E-06	2.49E-06	1.74E-06	3.29	3.33	3.26	152
—	—	—	X	1998	X	—	—	CO	2.25E-06	2.77E-06	1.73E-06	3.28	3.33	3.23	98
—	X	—	—	1999		X	—	CO	6.55E-07	7.96E-07	5.14E-07	3.53	3.57	3.49	113
—	X	—	—	2011	X	X	X	CO	4.30E-06	4.62E-06	3.99E-06	3.13	3.14	3.11	1082
X	—	—	X	2011	X	—	—	CO	2.89E-06	3.21E-06	2.56E-06	3.21	3.24	3.19	406
X	—	—	—	2011		X	—	CO	4.84E-06	5.42E-06	4.26E-06	3.10	3.13	3.08	410
X	—	—	—	2011		—	X	CO	7.46E-06	8.57E-06	6.35E-06	3.01	3.04	2.98	266

[a] C1 = comparison 1, differences in the length–weight relationship in the mainstem Colorado River between August, September, and October 2011; C2 = comparison 2, 6 y of data collected during August, September, or October to compare changes between years within the mainstem Colorado River; C3 = comparison 3, 8 y of data collected during August, September, or October to compare changes between years for the Little Colorado River; C4 = comparison 4, between rivers and sampling years using a single common month (August).

information criterion (AIC) and selected the most parsimonious model within each scenario for interpretation. We report parameter values for the best model (lowest AIC).

Using the nonlinear and linear approaches, we analyzed four different scenarios to detect any relationship between time, location, and condition of juvenile Humpback Chub. For our first comparison, we tested for differences in the length–weight relationship in the mainstem Colorado River between 3 mo during 2011 (August, September, and October; Table 1, comparison 1). Second, we used 6 y of data collected during August, September, or October to compare changes between years within the mainstem Colorado River (Table 1, comparison 2). Third, we repeated the annual comparisons for the Little Colorado River using 8 y of data (Table 1, comparison 3). Fourth, we made comparisons between rivers and sampling years using a single common month (August; Table 1, comparison 4).

We also used parameter estimates from the nonlinear and linear model fitting of comparison 4 (August data) to explore the relationship between physical river conditions such as temperature and discharge and changes in the length–weight relationship for juvenile Humpback Chub. To explore these relationships, we plotted the length–weight *b* parameter and slope estimates against mean temperature and coefficient of variation in discharge as a description of river condition for the 6 mo immediately preceding fish capture (March–August). Temperature data were only available for 3 y in the Little Colorado River (1992, 1993, 2011; Pine et al. 2017a [this issue]).

Results

Humpback Chub body condition declined from August to October 2011 in the mainstem Colorado River

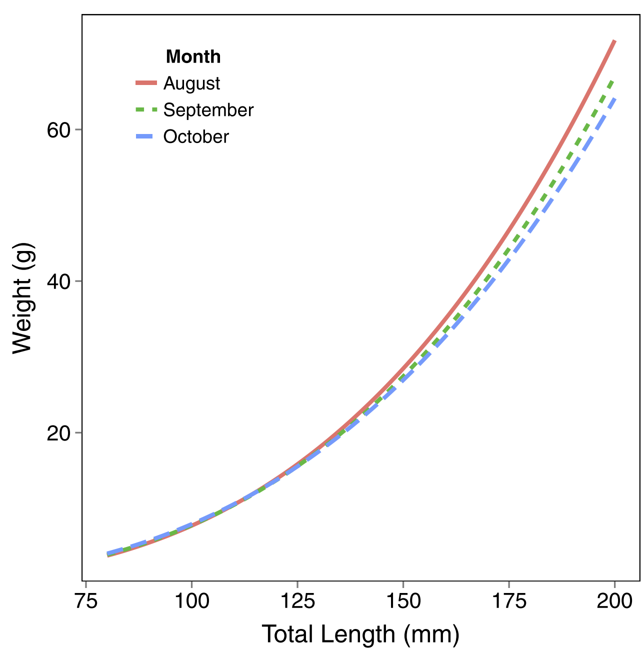

Figure 1. Monthly predicted weights of Humpback Chub *Gila cypha* in the Grand Canyon reach of the Colorado River during August, September, and October of 2011. See Table 1, comparison 1, for parameter estimates.

Table 2. Akaike information criterion (AIC) comparison table for analysis of covariance ANCOVA models fit to each of the comparisons (Table 1) describing the length–weight relationships of Humpback Chub *Gila cypha* in the Grand Canyon reach of the mainstem Colorado River and the Little Colorado River, Arizona. RY is a factor that codes for each river-and-year combination.

Comparison[a]	Model	AIC	ΔAIC	K
C1	log(length) + month	−1949.3	0.0	4
C1	log(length) · month	−1948.9	0.5	6
C1	log(length)	−1907.2	42.1	2
C2	log(length) · year	−1512.2	0.0	12
C2	log(length) + year	−1508.8	3.4	7
C2	log(length)	−1344.3	167.9	2
C3	log(length) · year	−1381.8	0.0	10
C3	log(length) + year	−1343.1	38.7	6
C3	log(length)	−1046.6	335.2	2
C4	log(length) · ry	−2081.4	0.0	18
C4	log(length) · river + year	−2027.7	53.7	9
C4	log(length) · year	−1843.4	238.0	12
C4	log(length) + river	−1677.1	404.3	3
C4	log(length) · river	−1675.2	406.2	4
C4	log(length) + year	−1674.4	407.0	7
C4	log(length)	−500.5	1580.9	2

[a] C1 = comparison 1, differences in the length–weight relationship in the mainstem Colorado River between August, September, and October 2011; C2 = comparison 2, 6 y of data collected during August, September, or October to compare changes between years within the mainstem Colorado River; C3 = comparison 3, 8 y of data collected during August, September, or October to compare changes between years for the Little Colorado River; C4 = comparison 4, between rivers and sampling years using a single common month (August).

(Figure 1), despite increasing temperatures throughout the period (see Pine et al. 2017a [this issue]: figure 1). Both the *a* and *b* parameters indicated that length–weight relationships were significantly different among months (Table 1, comparison 1). Interestingly, the best-fitting linear model contained a common slope parameter, but different intercepts for each month (Tables 2 and 3, comparison 1). The fitted curves show that juvenile Humpback Chub longer than approximately 160 mm are progressively lighter for a given length from August ($n = 406$) to September ($n = 410$) and October ($n = 266$) in the mainstem Colorado River (Figure 1).

The relationship between length and weight in Humpback Chub differed between years in the mainstem Colorado River (Table 1, comparison 2). Both the nonlinear length–weight model and the most supported linear model (lowest AIC) estimated different slope and intercept terms for each year (Tables 2 and 3, comparison 2). As an example, small juvenile Humpback Chub (< 150 mm TL) were estimated to be heavier for a given length in 1992 than other years, but in this same year larger juveniles were estimated to be lighter (Figure 2, left panel). In the most recent year (2011) in the mainstem Colorado River, juvenile Humpback Chub appear to be of average weight for a given length (Figure 2, left panel).

The length–weight relationship in the Little Colorado River differed between years based on both the length–weight regression and the linear model fitting (Table 1, comparison 3). Both approaches estimated unique slope and intercept values for each year (Tables 2 and 3, comparison 3), and several of the slope and intercept coefficients for this model were significant. In general, larger juvenile Humpback Chub (about 150–200 mm TL) weighed more for a given length in 2011 compared to the early and mid-1990s. Length–weight relationships for smaller juvenile Humpback Chub (about 75–150 mm TL) were similar across years.

When comparing the length–weight relationship among years and rivers for Humpback Chub, we found that a unique slope and intercept for each river and year was supported by the ANCOVA (Table 2, comparison 4). Again, several of the slope and intercept coefficients for this model are significant (e.g., 2011) suggesting that the change in weight with respect to length is different between the two rivers and across years (Table 3). The fitted length–weight curves show that weight for a given length is higher in the mainstem Colorado River compared to the Little Colorado River (Figure 3), despite the modified flow regime.

Within the Little Colorado River, we generally observed higher length–weight *b* parameter estimates at higher temperatures (Figure 4). We also observed higher slope estimates (Table 3) at higher temperatures in the Little Colorado River (Figure 4). Slope estimates for the Colorado River had a wider range (2.85–3.22; Table 3) showing no strong relationship (Figure 4) across the relatively small range of mean temperature values observed (8.3–10.3°C; Pine et al. 2017a [this issue]). Neither the length–weight *b* parameter nor the slope estimate showed a strong relationship with the coefficient of variation in Colorado River discharge. In the Little Colorado River, we found slope estimates were higher at higher coefficients of variation (Figure 4).

Discussion

We observed variation in length–weight relationships for juvenile Humpback Chub across 3 mo in the Colorado River, as well as annual variation in this relationship within both the Little Colorado and Colorado rivers. During 2009–2011, water temperatures in the mainstem Colorado were among the highest observed since Glen Canyon Dam was completed (see Pine et al. 2017a [this issue]: figure 1). Provided there is sufficient food, elevated water temperatures should increase juvenile Humpback Chub growth (Robinson and Childs 2001). We found that the juvenile Humpback Chub length–weight relationship during this warm-water period in 2011 did not differ from the relationship seen in the 1990s. In fact, at the larger fish sizes (> 150mm TL), the predicted weight for a given length was lower in 2011 compared with several years in the early 1990s. These results are corroborated by Finch et al. (2014), who documented that Humpback Chub grew more slowly in 2011, despite the warmer water temperatures. This counterintuitive response indicates that Humpback Chub in Grand Canyon may be food-limited, even if optimal temperatures and more natural flow regimes are experimentally provided.

Table 3. Coefficient estimates (log scale) for the top Akaike information criterion (AIC)–ranked analysis of covariance models for each comparison of Humpback Chub *Gila cypha* length–weight parameters (see Table 1) for fish collected from the Grand Canyon reach of the mainstem Colorado River (CO) and the Little Colorado River (LCR), Arizona. Parameter estimates are shown in bold if significant at an alpha of 0.05.

Comparison[a]	Parameter	Estimate	SE	Comparison	Parameter	Estimate	SE
C1	*b*	**3.14**	0.01	C4	*b*1991 LCR	**2.96**	0.04
C1	*a*August	−**12.40**	0.05	C4	*b*1992 LCR	3.02	0.07
C1	*a*September	−**12.43**	0.01	C4	*b*1993 LCR	**2.86**	0.06
C1	*a*October	−**12.45**	0.01	C4	*b*1994 LCR	**3.22**	0.05
C2	*b*1991	**3.27**	0.07	C4	*b*2011 LCR	**3.11**	0.06
C2	*b*1992	**3.05**	0.08	C4	*b*1992 CO	2.85	0.11
C2	*b*1993	**3.11**	0.08	C4	*b*1993 CO	3.1	0.14
C2	*b*1998	3.23	0.09	C4	*b*1998 CO	**3.22**	0.08
C2	*b*1999	3.28	0.10	C4	*b*2011 CO	**3.16**	0.05
C2	*b*2011	3.14	0.07	C4	*a*1991 LCR	−**11.75**	0.20
C2	*a*1991	−**12.97**	0.33	C4	*a*1992 LCR	−11.98	0.34
C2	*a*1992	−**11.83**	0.40	C4	*a*1993 LCR	−11.29	0.28
C2	*a*1993	−**12.26**	0.37	C4	*a*1994 LCR	−**13.14**	0.26
C2	*a*1998	−12.74	0.41	C4	*a*2011 LCR	−**12.46**	0.27
C2	*a*1999	−13.01	0.50	C4	*a*1992 CO	−10.88	0.55
C2	*a*2011	−12.42	0.34	C4	*a*1993 CO	−12.19	0.62
C3	*b*1991	**2.96**	0.04	C4	*a*1998 CO	−**12.73**	0.40
C3	*b*1992	3.02	0.07	C4	*a*2011 CO	−**12.50**	0.26
C3	*b*1993	2.86	0.06	—	—	—	—
C3	*b*1994	**3.22**	0.06	—	—	—	—
C3	*b*2011	**3.11**	0.06	—	—	—	—
C3	*a*1991	−**11.75**	0.21	—	—	—	—
C3	*a*1992	−11.98	0.36	—	—	—	—
C3	*a*1993	−11.29	0.30	—	—	—	—
C3	*a*1994	−**13.14**	0.28	—	—	—	—
C3	*a*2011	−**12.46**	0.29	—	—	—	—

[a] C1 = comparison 1, differences in the length–weight relationship in the mainstem Colorado River between August, September, and October 2011; C2 = comparison 2, 6 y of data collected during August, September, or October to compare changes between years within the mainstem Colorado River; C3 = comparison 3, 8 y of data collected during August, September, or October to compare changes between years for the Little Colorado River; C4 = comparison 4, between rivers and sampling years using a single common month (August).

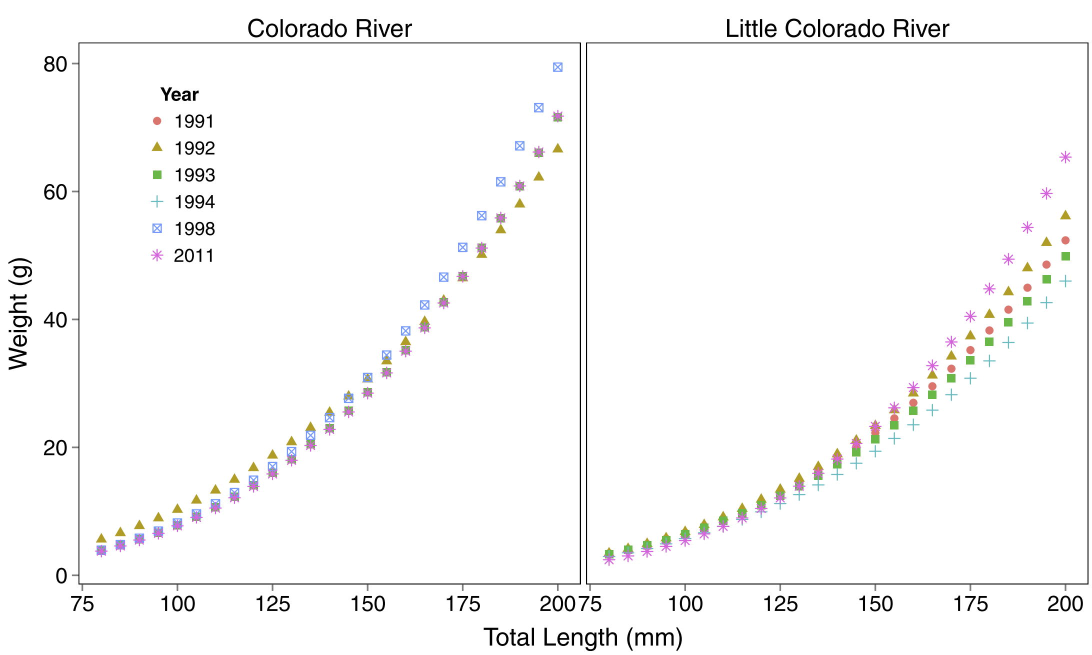

Figure 2. Annual predicted weights of Humpback Chub *Gila cypha* in the Grand Canyon reach of the Colorado River (1991, 1992, 1993, 1998, 1999, 2011) and Little Colorado River (1991, 1992, 1993, 1994, 2011), including data collected during August, September, and October. See Table 1, comparison 2 (Colorado River) and comparison 3 (Little Colorado River), for parameter estimates.

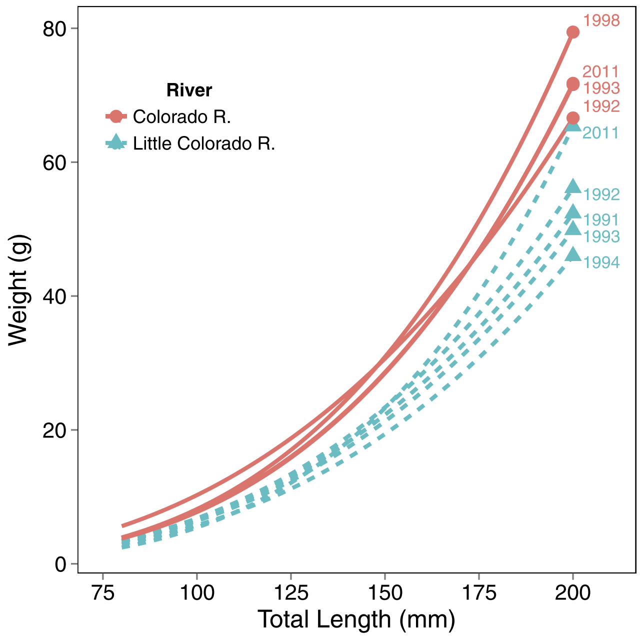

Figure 3. Predicted weights of Humpback Chub *Gila cypha* in the Grand Canyon reach of the Colorado River and Little Colorado River using data collected only in August each year. See Table 1, comparison 4, for parameter estimates. The Colorado River curves for 1993 and 2011 are very similar, resulting in overplotting of these curves.

Between 1991 and 2011, we also observed that juvenile Humpback Chub condition in the Little Colorado River increased, while juvenile Humpback Chub condition in the mainstem Colorado remained generally stable. It is unknown why Little Colorado River condition increased over this interval, but Van Haverbeke et al. (2013) found increasing trends in abundance since 2000 of Humpback Chub, Flannelmouth Sucker *Catostomus latipinnis*, and Bluehead Sucker *Catostomus discobolus* in the Little Colorado River, with some of the highest abundance estimates occurring in 2009–2011. These increases in condition and abundance may be the result of improved growing conditions.

Similarly, within the Colorado River near the confluence with the Little Colorado River, Finch et al. (2015) estimated juvenile Humpback Chub abundance during 2009–2011 and found the highest abundance in 2011, despite finding no changes in condition. Cross et al. (2011) documented that prey consumption rates by fishes in the Colorado River nearly equaled or exceeded invertebrate production, which may cause food limitation that could lead to lower condition. We were only able to estimate length–weight relationships for 1 y (2011) during the time period Van Haverbeke et al. (2013) noted increasing abundance for Humpback Chub; but in this one year Humpback Chub showed the most robust size for a given length of all the years we examined (Figures 2 and 3). Despite the increasing temporal trend in Humpback Chub length–weight relationships in the Little Colorado River, condition in this important tributary is still below that of juvenile Humpback Chub occupying the mainstem Colorado River. Researchers have reported relationships between energy reserves and overwinter survival for a variety of other fish species (Thompson et al. 1991; Ludsin and DeVries 1997), and the unexpected relationship between mainstem Colorado River occupancy and higher condition we observed merits further study given other similar surprises in Humpback Chub life history that were described by Limburg et al. (2013) and Yackulic et al. (2014).

A previous study of adult Humpback Chub found higher condition in Grand Canyon compared with other Humpback Chub populations in the upper Colorado River basin (Meretsky et al. 2000), attributing this result to dam-mediated changes in production and a seasonally stable food base (Stevens et al. 1997). Since 2003, mainstem Colorado River temperatures in this reach have increased from an annual range of about 8–10°C to about 8–14°C, because of lower reservoir levels in Lake Powell (Voichick and Wright 2007). For congener *Gila* species, such as Bonytail *Gila elegans,* temperatures of less than 14°C depressed the growth of juveniles in laboratory conditions (Kappenman et al. 2012). In laboratory experiments with larval and small juvenile Humpback Chub (< 50 mm TL), Clarkson and Childs (2000) found that water temperatures of 10°C led to very little growth for juvenile Humpback Chub, but at 14°C growth substantially increased. From 1988 to 1994 mainstem Colorado River temperatures exceeded 10°C less than 10% of the time and never exceeded 14°C. From 2009 to 2011 the Colorado River exceeded 10°C around 60% of the time and exceeded 14°C up to 10% of the time (Pine et al. 2017a [this issue]). Important future research might examine how wild Humpback Chub respond when water temperatures reach and surpass the 14°C threshold, especially because growth (Finch et al. 2014) and survival (Finch et al. 2015) of juvenile Humpback Chub can have counterintuitive responses to more natural flow regimes. For juvenile Colorado Pike Minnow *Ptychocheilus lucius*, Thompson et al. (1991) found that lipid levels were related to survival and condition. If a similar relationship exists for Humpback Chub, tracking condition by routinely weighing juvenile fish could create a framework for a relatively low-cost additional line of inference on juvenile Humpback Chub population response to changing environmental conditions or management actions. Bioenergetics-based approaches that explicitly consider temperature, coupled with predictions of how food resources may respond to increased temperatures, would provide additional insights into how Humpback Chub may respond to shifting temperature regimes.

We did observe higher length–weight *b* parameter estimates and higher slope estimates with higher temperatures in the Little Colorado River, which aligns with bioenergetics predictions for this species, assuming consumption is not limited (Petersen and Paukert 2005). Additional years of data could elucidate these relationships (at minimal cost), especially when compared with environmental conditions in the regulated Colorado River. Conversely, temperature or flow variation may

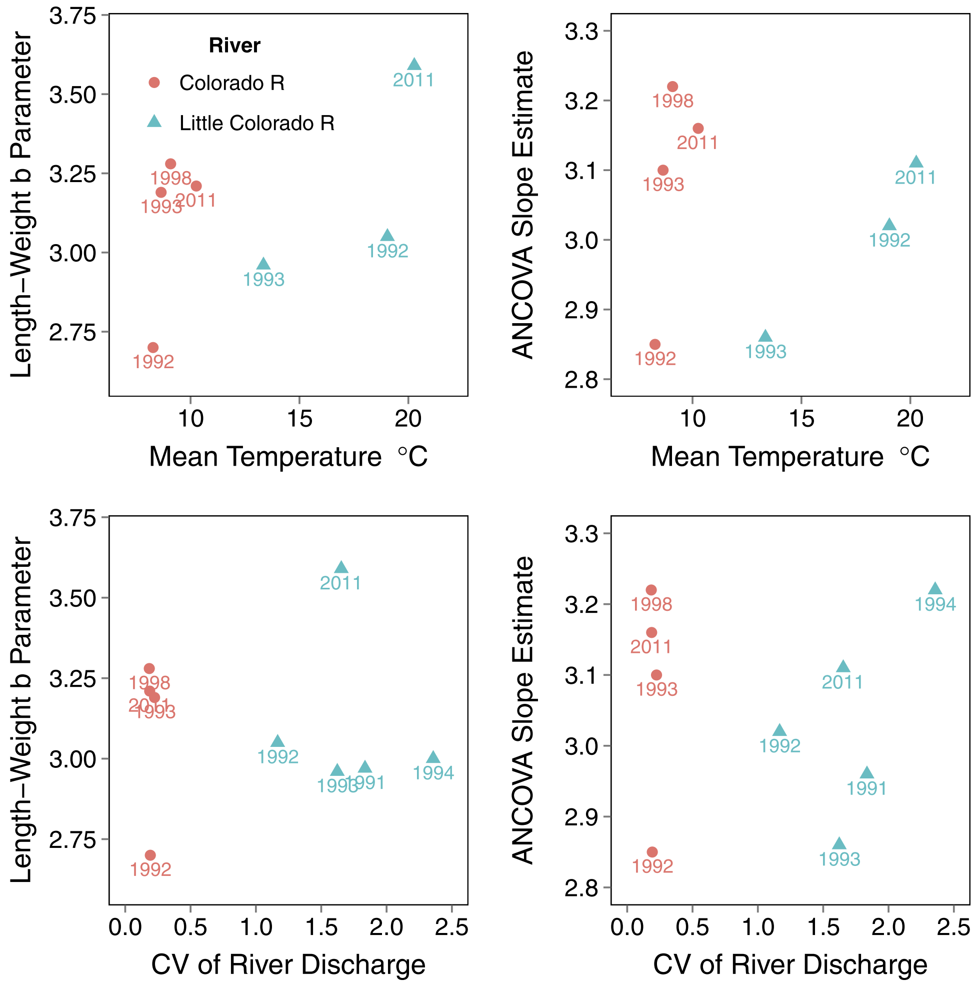

Figure 4. Comparison of parameters describing the length–weight relationship for juvenile Humpback Chub *Gila cypha* from the nonlinear (length–weight *b* parameter) and linear (analysis of covariance [ANCOVA] slope parameter) model fitting and the mean river temperate and coefficient of variation (CV) in discharge. Both the mean temperatures and CVs in discharge are calculated for a 6-mo period (March–August) in the Colorado (red circles) and Little Colorado (blue triangles) rivers, representing conditions prior to fish capture in August. See Table 1 or Table 3 for parameter estimates.

not be the most important environmental factors to growth and condition of juvenile Humpback Chub. Characterizing elements of flow regimes using various hydrologic indices is a rapidly growing area of research (Gao et al. 2009; Kennard et al. 2010) that may provide alternative metrics for capturing environmental variation and relating this variation to condition or growth of fish.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding authors for the article.

Data S1. The file "Data S1.csv" contains all data used for Text S1 analyses, (*Supplemental Material*). This data file contains the following headers: TRIP_ID = textual description of each individual fish collected based on information in the U.S. Geological Survey Grand Canyon Monitoring and Research Center database; RIVER = river sampling occurred; DATE = date of collection in a MM/DD/YYYY format; MONTH = month of collection; YEAR = year of collection; TOTAL_LENGTH = total length of Humpback Chub collected; WEIGHT = weight of fish in grams.

Found at DOI: http://dx.doi:10.3996/062014-JFWM-047.S1. (64KB CSV)

Data S2. The file "Data S2.csv" contains data used for the ANCOVA analyses in Text S2, *Supplemental Material*. This data file contains the following headers: TRIP_ID = textual description of each individual fish collected based on information in the U.S. Geological Survey Grand Canyon Monitoring and Research Center database; RIVER = river sampling occurred; DATE = date of collection in a MM/DD/YYYY format; MONTH = month of collection; YEAR = year of collection; TOTAL_LENGTH = total length of Humpback Chub collected; WEIGHT = weight of fish in grams.

Found at DOI: http://dx.doi:10.3996/062014-JFWM-047.S2. (165KB CSV)

Data S3. The file "Data S3.csv" contains data used for the second part of the analyses in Text S1, *Supplemental Material*. This data file contains the following headers: TRIP_ID = textual description of each individual fish collected based on information in the U.S. Geological Survey Grand Canyon Monitoring and Research Center database; RIVER = river sampling occurred; DATE = date of collection in a MM/DD/YYYY format; MONTH = month of collection; YEAR = year of collection; TOTAL_LENGTH = total length of Humpback Chub collected; WEIGHT = weight of fish in grams.

Found at DOI: http://dx.doi:10.3996/062014-JFWM-047.S3. (151KB CSV)

Text S1. Computer code (R data code) to fit the mainstem Colorado River length–weight data to monthly comparisons is contained in the file "Hayes JFWM Supplemental file 1.R." This file also contains the computer code used to fit the length–weight data and comparisons between the mainstem Colorado River and Little Colorado River. The code is annotated step by step. (The associated data are found in Data S1 and Data S3, *Supplemental Material*.)

Found at DOI: http://dx.doi:10.3996/062014-JFWM-047.S4. (19KB R)

Text S2. Computer code (R data code) for the ANCOVA model fitting of length–weight relationships for Humpback Chub is contained in the file "Hayes JFWM Supplemental file 2.R." The code is annotated line by line. (The associated data are found in Data S2, *Supplemental Material*.)

Found at DOI: http://dx.doi:10.3996/062014-JFWM-047.S5. (5KB R)

Reference S1. Coggins LG Jr, Walters CJ. 2009. Abundance trends and status of the Little Colorado River population of Humpback Chub: an update considering data from 1989–2008. Reston, Virginia: U.S. Geological Survey Open-File Report 2009-1075.

Found at DOI: http://dx.doi:10.3996/062014-JFWM-047.S6; also available at: http://pubs.usgs.gov/of/2009/1075/of2009-1075.pdf. (793KB PDF)

Reference S2. Valdez RA, Ryel RJ. 1995. Life history and ecology of Humpback Chub (*Gila cypha*) in the Colorado River, Grand Canyon, Arizona. Final report to the Bureau of Reclamation, Salt Lake City, Utah, contract no. 0-CS-40-09110. Logan, Utah: BIO/WEST Report, Inc.

Found at DOI: http://dx.doi:10.3996/062014-JFWM-047.S7; also available at: http://www.gcmrc.gov/library/reports/biological/Fish_studies/Biowest/Valdez1995f.pdf. (18507KB PDF)

Reference S3. Voichick N, Wright SA. 2007. Water-temperature data for the Colorado River and tributaries between Glen Canyon Dam and Spencer Canyon, northern Arizona, 1988–2005. Reston, Virginia: U.S. Geological Survey Data Series 251.

Found at DOI: http://dx.doi:10.3996/062014-JFWM-047.S8. (877KB PDF)

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References

Anderson RO, Neumann RM. 1996. Length, weight, and associated structural indices. Pages 447–481 in Murphy BR, Willis DW, editors. Fisheries techniques. 2nd edition. Bethesda, Maryland: American Fisheries Society.

Clarkson RW, Childs MR. 2000. Temperature effects of hypolimnial-release dams on early life stages of Colorado River basin big-river fishes. Copeia 2000:402–412.

Coggins LG Jr, Pine WE III, Walters CJ, Van Haverbeke DR, Ward D, Johnstone HC. 2006. Abundance trends and status of the Little Colorado River population of humpback chub. North American Journal of Fisheries Management 26:201–205.

Coggins LG Jr, Walters CJ. 2009. Abundance trends and status of the Little Colorado River population of humpback chub: an update considering data from 1989–2008. Reston, Virginia: U.S. Geological Survey Open-File Report 2009-1075. (See *Supplemental Material*, Reference S1, http://dx.doi:10.3996/062014-JFWM-047.S6); also available: http://pubs.usgs.gov/of/2009/1075/of2009-1075.pdf (April 2016).

Cross WF, Baxter CV, Donner KC, Rosi-Marshall EJ, Hall RO, Kennedy TA, Donner KC, Wellard-Kelly HA, Seegert SEZ, Behn KE, Yard MD. 2011. Food web dynamics in a large river discontinuum. Ecological Monographs 83:311–337.

Douglas ME, Marsh PC. 1996. Population estimates population movements of *Gila cypha*, an endangered cyprinid fish in the Grand Canyon region of Arizona. Copeia 1996:15–28.

Finch C, Pine WE III, Limburg KE. 2014. Do hydropeaking flows alter juvenile fish growth rates? A test with juvenile humpback chub in the Colorado River. River Research and Applications 31:156–164.

Finch C, Pine WE III, Yackulic CB, Dodrill MJ, Yard M, Gerig BS, Coggins LG Jr, Korman J. 2015. Assessing juvenile native fish demographic responses to a steady flow experiment in a large regulated river. River Research and Applications 32:763–775.

Froese R. 2006. Cube law, condition factor, and weight–length relationships: history, meta-analysis and recommendations. Journal of Applied Ichthyology 22:241–253.

Gao Y, Vogel RM, Kroll CN, Poff NL, Olden J. 2009. Development of representative indicators of hydrologic alteration. Journal of Hydrology 374:136–147.

Gorman OT, Stone DM. 1999. Ecology of spawning humpback chub, *Gila cypha*, in the Little Colorado River near Grand Canyon, Arizona. Environmental Biology of Fishes 55:115–133.

Kappenman KM, Cureton ES, Ilgen J, Toner M, Fraser WC, Kindschi GA. 2012. Thermal requirements of the bonytail (*Gila elegans*): application to propagation and thermal-regime management of rivers of the Colorado River basin. The Southwestern Naturalist 57:421–429.

Kennard MJ, Mackay SJ, Pusey BJ, Olden JD, Marsh N. 2010. Quantifying uncertainty in estimation of hydrologic metrics for ecohydrological studies. River Research and Applications 26:137–156.

Limburg KE, Hayden TA, Pine WE III, Yard MD, Kozdon R, Valley JW. 2013. Of travertine and time: otolith chemistry and microstructure detect provenance and demography of endangered humpback chub in Grand Canyon, USA. PLoS ONE 8:e84235.

Ludsin SA, DeVries DR. 1997. First-year recruitment of largemouth bass: the interdependency of early life stages. Ecological Applications 7:1024–1038.

Meretsky VJ, Valdez RA, Douglas ME, Brouder MJ, Gorman OT, Marsh PC. 2000. Spatiotemporal variation in length-weight relationships of endangered humpback chub: implications for conservation and management. Transactions of the American Fisheries Society 129:613–637.

Petersen JH, Paukert CP. 2005. Development of a bioenergetics model for humpback chub and evaluation of water temperature changes in the Grand Canyon, Colorado River. Transactions of the American Fisheries Society 134:960–974.

Pine WE III, BS Gerig, C Finch. 2017a. Characterizing growth and condition of the endangered humpback chub in the lower Colorado River. Journal of Fish and Wildlife Management 8:313–321.

Pine WE III, Limburg K, Dodrill MJ, Chagaris D, Coggins LG, Gerig BS, Finch C, Speas D, Yard MD, Persons W, Hendrickson DA. 2017b. Growth of endangered humpback chub in relation to temperature and discharge in the lower Colorado River. Journal of Fish and Wildlife Management 8:322–332.

Pope KL, Kruse CG. 2007. Condition. Pages 423–471 in Brown M, Guy C, editors. Analysis and interpretation of freshwater fisheries data. Bethesda, Maryland: American Fisheries Society.

R Development Core Team. 2012. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available: http://www.R-project.org/ (April 2016).

Robinson AT, Childs MR. 2001. Juvenile growth of native fishes in the Little Colorado River and in a thermally modified portion of the Colorado River. North American Journal of Fisheries Management 21:809–815.

Rosenfeld JS, Boss S. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Canadian Journal of Fisheries and Aquatic Sciences 58:585–593.

Safran P. 1992. Theoretical analysis of the weight–length relationship in fish juveniles. Marine Biology 112:545–551.

Stevens LE, Shannon JP, Blinn DW. 1997. Colorado River benthic ecology in Grand Canyon, Arizona, USA: dam, tributary and geomorphological influences. River Research and Applications 13:129–149.

Thompson JM, Bergersen EP, Carlson CA, Kaeding LR. 1991. Role of size, condition, and lipid content in the overwinter survival of age-0 Colorado squawfish. Transactions of the American Fisheries Society 120:346–353.

[ESA] U.S. Endangered Species Act of 1973, as amended, Pub. L. No. 93-205, 87 Stat. 884 (Dec. 28, 1973). Available; http://www.fws.gov/endangered/esa-library/pdf/ESAall.pdf

[USFWS] U.S. Fish and Wildlife Service. 1967. Native Fish and wildlife endangered species. Federal Register 32:4001.

[USGS] U.S. Geological Survey. 2011. Grand Canyon Monitoring and Research Center database. Flagstaff, Arizona: U.S. Geological Survey. Available: http://www.gcmrc.gov/publications/library.aspx (April 2016).

Valdez RA, Ryel RJ. 1995. Life history and ecology of humpback chub (*Gila cypha*) in the Colorado River, Grand Canyon, Arizona. Final report to the Bureau of Reclamation, Salt Lake City, Utah, contract no. 0-CS-40-09110. Logan, Utah: BIO/WEST Report, Inc. (See *Supplemental Material*, Reference S2, http://dx.doi:10.3996/062014-JFWM-047.S7); also available: http://www.gcmrc.gov/library/reports/biological/Fish_studies/Biowest/ Valdez1995f.pdf (April 2016).

Van Haverbeke DR, Stone DM, Coggins LG Jr, Pillow MJ. 2013. Long-term monitoring of an endangered desert fish and factors influencing population dynamics. Journal of Fish and Wildlife Management 4:163–177.

Voichick N, Wright SA. 2007. Water-temperature data for the Colorado River and tributaries between Glen Canyon Dam and Spencer Canyon, northern Arizona, 1988–2005. Reston, Virginia: U.S. Geological Survey Data Series 251. (See *Supplemental Material*, Reference S8, http://dx.doi:10.3996/062014-JFWM-047.S3); also available: http://pubs.usgs.gov/ds/2007/251/ (April 2016).

Werner EE, Gilliam JF. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393–425.

Yackulic CB, Yard MD, Korman J, Van Haverbeke DR. 2014. A quantitative life history of endangered humpback chub that spawn in the Little Colorado River: variation in movement, growth and survival. Ecology and Evolution 4:1006–1018.