Characterizing Growth and Condition of Endangered Humpback Chub in the Lower Colorado River

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Abstract

This paper is a preface to the two papers that follow in this issue. The two papers (by Pine et al. and Hayes et al.) use long-term fish sampling data from ongoing Humpback Chub monitoring efforts and archival otolith samples (from museums) collected in the lower Colorado and Little Colorado Rivers during periods of both cold- and warm-water conditions to assess whether Humpback Chub growth characteristics may have responded to changes in water temperature. Growth patterns are often of interest to resource managers because growth integrates a large range of environmental and ecological factors, including habitat conditions. Together, these papers contribute information to a large collection of recent studies, developing a line of evidence designed to inform management decisions related to water releases, dam operations, and management actions that could be taken to aid recovery of native fish populations in regulated river systems around the world.

Keywords: Humpback Chub; Colorado River; regulated river; growth

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Introduction

Riverine ecosystems undergo well-documented hydrologic, geomorphic, and ecological responses to dams and flow regulations (Ligon et al. 1995; Stanford and Ward 2001; Nilsson et al. 2005). Understanding the effects of dam construction and operation on riverine ecosystems can help to inform decisions regarding dam removal (Shuman 1995; Poff and Hart 2002), the operation of existing dams for conservation purposes (Richter and Thomas 2007; Olden and Naimen 2010), or policy decisions and conservation actions related to new dam construction

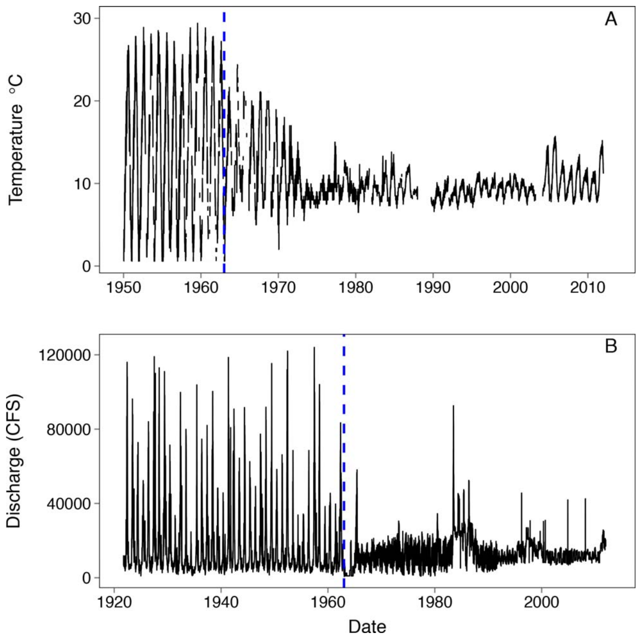

Figure 1. Panel (**A**) is a time series of water temperatures taken at Lee's Ferry, Colorado River, Arizona, with most recent data collected at U.S. Geological Survey Gauge 0938000 and other data provided by S. Wright, U.S. Geological Survey Grand Canyon Monitoring and Research Center (personal communication). Panel (**B**) is a time series of discharges in cubic feet per second (CFS) taken at the same location. The vertical blue line in each panel represents when Glen Canyon Dam was completed in 1963. Breaks in observations are due to missing data. Data are used to assess relationships between growth and condition of Humpback Chub *Gila cypha* in the mainstem Colorado River downstream of Glen Canyon Dam in companion papers by Pine et al. and Hayes et al. in this issue.

(Finer and Jenkins 2012). Defined as the "lower" Colorado River, the ecosystem below Glen Canyon Dam, Arizona, was significantly altered following the closure of Glen Canyon Dam in 1963. Water storage and hydropower demands have reduced the seasonality and magnitude of flows (Topping et al. 2003), resulted in the retention of sand and fine sediments in Lake Powell (Schmidt et al. 2004; Wright et al. 2005), and drastically altered water temperature regimes with colder summer and warmer winter water temperatures (Vernieu et al. 2005; Wright et al. 2008). These changes have altered food web structure and function (Cross et al. 2011, 2013), and nonnative fish and invertebrates have flourished (Coggins et al. 2011; Cross et al. 2011,2013) while the majority of native invertebrate and fish species are in decline or have been extirpated (Minckley and Deacon 1991; Cross et al. 2013).

To promote the recovery and long-term viability of natural resources downstream of Glen Canyon Dam, a preferred alternative for dam operations was selected by the U.S. Department of Interior in 1996 (USDOI 1996). This Record of Decision also authorized the Glen Canyon Dam Adaptive Management Program to carry out large-scale experiments, which would inform dam operation and other management options for conservation of key cultural, physical, and biological resources (USDOI 1996). The adaptive management program work group comprises a diverse group of stakeholders that represent a variety of interests, including conservation of resources in Grand Canyon National Park, cultural values, recreational use of Colorado River resources, native fish conservation in the Colorado River ecosystem, and dam operations that meet the water and power needs of millions of people in the southwestern United States (Gloss et al. 2005; Melis et al. 2015).

Native fish populations in the lower Colorado River basin have been in decline since the 1800s, a trend exacerbated by the construction of Hoover and Glen Canyon dams, the filling of Lakes Mead and Powell, and attendant establishment of nonnative fish communities (Minckley et al. 2003). One high-profile native fish species is still extant in the lower Colorado River basin, the Humpback Chub *Gila cypha*. This large and morphologically distinct minnow is currently classified as endangered under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 1967; ESA 1973, as amended) and has received protected status since the Endangered Species Act was passed in 1973. The largest extant population of Humpback Chub persists around the confluence of the Little Colorado River and the regulated Colorado River in Grand Canyon National Park (Kaeding and Zimmerman 1983; Gorman and Stone 1999). Adult Humpback Chub in this population exhibit a spring spawning migration into the Little Colorado River from the Colorado River, while offspring rear in the Little Colorado River or return actively and passively to the Colorado River at various life stages (Gorman and Stone 1999; Limburg et al. 2013). The timing and factors influencing outmigration of juvenile Humpback Chub are not well understood by researchers, and most life stages (i.e., juveniles, subadults, and adults) can be found in both the mainstem Colorado River and the Little Colorado River throughout the year (Valdez and Ryel 1995; Hayden et al. 2012; Limburg et al. 2013).

Researchers have used Humpback Chub as a focal species in assessments of ecosystem response to management actions in Grand Canyon (USDOI 1996), particularly since the decline of the adult population during the 1990s (Coggins et al. 2006b). Researchers do not know the mechanisms by which Humpback Chub populations declined following dam construction, but their leading hypotheses include 1) habitat changes related to flow modifications and reductions in sediment input (Converse et al 1998), 2) competition with or predation by nonnative fish (Yard et al. 2011; Coggins et al. 2011), 3) nonnative parasites (Hoffnagle et al. 2006), or 4) changes in water temperature (Clarkson and Childs 2000).

The hydrology and temperature of the Colorado River in Grand Canyon is driven by complex interactions between Glen Canyon Dam operations, Lake Powell elevation, and water inputs from the upper Colorado River basin. Key changes in this reach of the Colorado River since the completion of Glen Canyon Dam and the filling of Lake Powell (1963–1980) include the replacement of seasonal low flows with daily minimum water releases, increases in median daily river discharge, retention of sediment above Glen Canyon Dam in Lake Powell, erosion

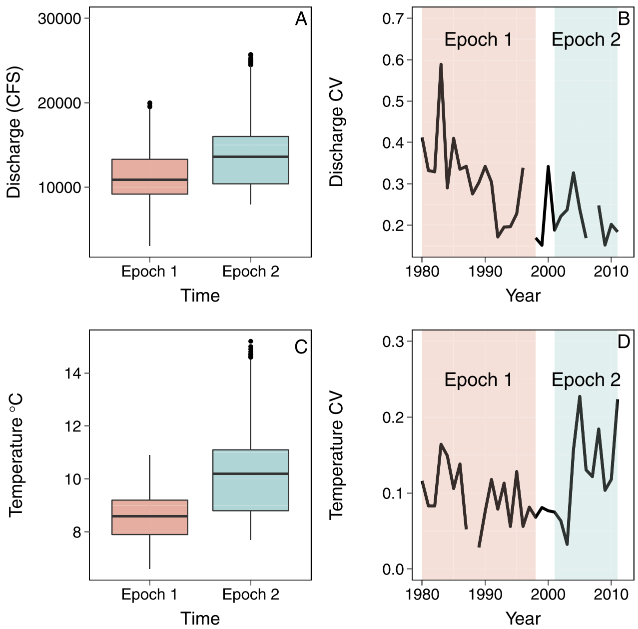

Figure 2. River-discharge and water-temperature (°C) information for the Colorado River, Arizona, measured at Lee's Ferry, Colorado River, Arizona, taken at U.S. Geological Survey Gauge 0938000 for epoch 1 (1980–1998) and epoch 2 (2001–2011). Panel (**A**) is the box plots of annual flow for each epoch, Panel (**B**) is the coefficient of variation (CV) in annual flows for each year. Panel (**C**) is the box plots of annual water temperature for each epoch, Panel (**D**) is the coefficient of variation (CV) in annual water temperature for each year. Breaks in lines are due to missing data for this gaging station. Data are used to assess relationships between growth and condition of Humpback Chub *Gila cypha* in the mainstem Colorado River downstream of Glen Canyon Dam in companion papers by Pine et al. and Hayes et al. in this issue.

of sandbars, and decreased variation in seasonal river temperature (Wright et al. 2005; Melis et al. 2015).

Since about 2001, a combination of factors—including changes in Glen Canyon Dam daily operations (which began in 1996) and drought conditions in the upper Colorado River basin—have led to declining reservoir elevations and variable levels of inflow to Lake Powell (Pulwarty and Melis 2001). This has resulted in warmer epilimnetic water being withdrawn through the penstocks of Glen Canyon Dam (Wright et al. 2008) thus increasing lower Colorado River water temperature since about 2002 (Melis et al. 2015; Figure 1). While the annual water temperature variation is still considerably less than during the pre-dam era, water temperatures in recent years were similar to those expected under possible management actions (i.e., low summer steady flow; Ralston 2011) or as a result of low reservoir levels related to climate change (Christensen et al. 2004). The USFWS, in consultation with the Bureau of Reclamation, has issued a number of Biological Opinions on the operations of Glen Canyon Dam that identified warming the mainstem Colorado River as an essential action to create suitable habitat for Humpback Chub to spawn in the mainstem Colorado River (USDOI 1994; USDOI 2008, Trammell et al. 2002). Several laboratory and modeling studies have further suggested that warm water discharges from Glen Canyon dam may benefit native fish species through improvements in growth rate (Clarkson and Childs 2004; Petersen and Paukert 2005; Coggins and Pine 2010). This hypothesis led to experimental low-discharge water releases during summer (Trammell et al. 2002; Ralston 2011) to test these responses, as well as consideration of a selective water withdrawal device on the upstream face of the dam to allow for water withdrawals above the thermocline (Vermeyen 2008). Both options involve substantial financial cost and uncertainty as to whether the ecosystem will have a positive, negative, or neutral response.

We developed two manuscripts for this issue (Hayes et al. 2017; Pine et al. 2017) using long-term fish sampling data from ongoing Humpback Chub monitoring efforts and archival otolith samples (from museums) collected in the lower Colorado and Little Colorado rivers during periods of both cold- and warm-water conditions to assess whether Humpback Chub growth characteristics may have responded to changes in water temperature. Growth patterns are often of interest to resource managers because growth integrates a large range of environmental and ecological factors, including habitat conditions (Quinn and Peterson 1996; Rosenfeld and Boss 2001), food availability (Aresco and Guyer 1999), and predation risk (Werner and Gilliam 1984). Growth metrics are widely used by researchers to evaluate how fish populations respond to management actions, due in part to the positive correlation of growth and survival (Lorenzen 2000; Charnov et al. 2012). These growth metrics are also used by researchers to characterize spatial variations across different biotic conditions, such as changes in prey availability or gradients in environmental conditions (Nicieza and Metcalfe 1997; King et al. 1999). Any management actions that lead to improvements in Humpback Chub growth rates are therefore of significant interest to resource managers to aid in recovery of this species. Taking advantage of existing samples collected prior to and during the observed river warming period creates a research opportunity that can help inform future management actions at little additional risk to the species or costs to stakeholders.

In the first paper (Pine et al. 2017 [this issue]) we fit growth models to all available Humpback Chub age and growth data to improve on parameter estimates and uncertainties of Humpback Chub growth. This information is of key importance in population assessment models (Coggins et al. 2006a, 2006b; Coggins and Walters 2009). We then take advantage of data on hydrologic conditions in recent decades (since 2001; Melis et al. 2015) to compare growth of juvenile Humpback Chub during an earlier period of cooler, more hydrologically variable riverine conditions (1980–1998; epoch 1; Figure 2) to growth during the more recent period of warmer water and less variable flows (2001–2011; epoch 2; Figure 2). We defined these epochs based on the ages of fish and years of collection so that the growth patterns that we examined were reflective of

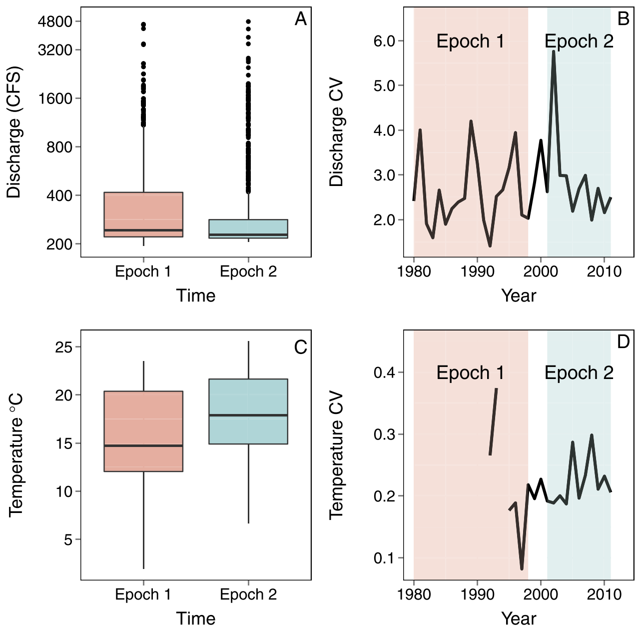

Figure 3. River discharge and water temperature (°C) for the Little Colorado River at Cameron, Arizona, at U.S. Geological Survey Gauge 0940200 for epoch 1 (1980–1998) and epoch 2 (2001–2011). Panel (**A**) is the box plots of annual flow for each epoch, Panel (**B**) is the coefficient of variation (CV) in annual flows for each year. Panel (**C**) is the box plots of annual water temperature for each epoch, Panel (**D**) is the coefficient of variation (CV) in annual water temperature for each year. Breaks in lines are due to missing data for this gaging station. Data are used to assess relationships between growth and condition of humpback chub *Gila cypha* in the Little Colorado River in companion papers by Pine et al. and Hayes et al. in this issue.

environmental conditions observed during the life of the fish. We finally compare growth of juvenile Humpback Chub ($<$ age 2) between the lower Colorado River and Little Colorado River to compare growth in a system where environmental conditions are modified by dam operations (Colorado River) to growth in a system with less-modified environmental conditions (Little Colorado; Figure 3).

In our second paper (Hayes et al. 2017 [this issue]), we describe length–weight relationships for juvenile and subadult ($<$ 200-mm total length) Humpback Chub in the lower Colorado and Little Colorado rivers. For another native species in the Colorado River basin (Colorado pikeminnow *Ptychocheilus lucius*), a positive relationship has been shown between fish condition, size, and survival (Thompson et al. 1991). This relationship has not been been examined for Humpback Chub. As a first step we assess length–weight relationships for juvenile and subadult Humpback Chub in these two systems. We compare length–weight relationships between months in the Colorado River to examine monthly patterns, and we then assess annual variation in length–weight relationships both within the lower Colorado and Little Colorado rivers and then between these rivers. Finally, we relate our estimates of length–weight parameters to environmental conditions in each river, again including periods with contrasting water temperature and river discharge patterns in the mainstem Colorado River and the unregulated Little Colorado River. This information provides a line of evidence to merge with a large collection of recent studies (Coggins et al. 2011; Hayden et al. 2012; Cross et al. 2013; Gerig et al. 2013; Limburg et al. 2013; Van Haverbeke et al. 2013; Finch et al. 2014, 2015; Dodrill et al. 2015 and others) designed to inform management decisions related to water releases, dam operations, and management actions that could be taken to aid recovery of native fish populations in regulated river systems around the world.

Methods

Study site

The Grand Canyon reach of the Colorado River is an approximately 400-km section of river bounded by the two largest reservoirs in the United States: upstream Lake Powell and downstream Lake Mead (Andrews 1991;USDOI 1996; by convention Lee's Ferry is river kilometer [rkm] 0). This river reach is considered an area of cultural, biological, and geologic significance by tribal, state, federal, and nongovernmental interests in the United States, and as a result is safeguarded by the Grand Canyon Protection Act of 1992. Due to hypolimnetic discharge from stratified Lake Powell, the Colorado River within Grand Canyon is generally stenothermic and cool (Voichick and Wright 2007) with average water temperatures ranging from about 8 to 10°C during the initial filling of Lake Powell (1963–1980), warming to about 8 to 15°C during years of lower reservoir levels, and with warmer water releases occurring since about 2001 (Figure 1). Due to the influence of Glen Canyon Dam, river turbidity is generally low, yet can seasonally increase by tributary flooding from the Paria and Little Colorado rivers (Topping et al. 2000).

The Little Colorado River is the largest tributary of the Colorado River between Lakes Powell and Mead. It enters the Colorado River 126 km below Glen Canyon Dam and 100 km below Lee's Ferry. The lower 21 km is spring fed, with perennial base flows of $\sim$ 229 ft^3/s (6.5 m^3/s; Gorman and Stone 1999; Stone 2010). The carbonated spring water forms large travertine dam complexes as it degasses. The largest of these dam complexes is located 14 km upstream from the confluence with the Colorado River and may act as a barrier to upstream fish movement. Headwater reaches of the Little Colorado River are modified by agricultural and groundwater use; Little Colorado River flows are seasonally variable, with peak flows coinciding with spring runoff and late-summer monsoon rains. Turbidity is generally low during periods of base flow, but can reach very high levels ($>$ 10,000 formazin nephelometric units) during periods of flooding (Stone 2010). Water temperatures in the Little Colorado River are also seasonally variable and, compared to the mainstem Colorado River, are warmer during spring, summer, and fall, and cooler in winter.

Fish collections

Researchers have intensively studied Humpback Chub in the Little Colorado River and mainstem Colorado River near the confluence for more than three decades (Valdez and Ryel 1995, Gorman and Stone 1999; Coggins et al. 2006; Voichick and Wright 2007). These two areas are frequently studied by fisheries biologists because most Humpback Chub in this reach of the mainstem Colorado River undertake a potamodromous spawning migration into the Little Colorado River (Gorman and Stone 1999; Limburg et al. 2013), where they are more easily sampled. We compiled different subsets of data from Humpback Chub sampling programs from 1979 to 2011, depending on data availability and the relevant hypotheses. In general, field personnel collected data for Humpback Chub in the Little Colorado River using seines, hoop nets, minnow traps, and trammel nets, and in the mainstem Colorado River using seines, boat-mounted electrofishing, hoop nets, minnow traps, and trammel nets (see additional details in 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, with the majority of sampling taking place directly downstream of the Little Colorado River confluence (km 126.1–128.6 for samples collected 2009–2011). Researchers measured total length of each fish to the nearest millimeter and 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 accuracy of all measurements and minimize injury to fish.

River conditions

We obtained all river discharge and water temperature data for the mainstem Colorado River from the U.S. Geological Survey (USGS) gauge 0938000 at Lee's Ferry or records from other USGS sources (S. Wright, USGS Grand Canyon Monitoring and Research Center, personal communication). This is the only mainstem river gauge in this river reach with temperature records covering the same time period as our fish samples. This gauge is located 100 km upstream of our study site. While water warming does occur as water flows downstream to our study site, we assumed that this warming rate was similar across years and that water temperature was mostly driven by reservoir elevation and hydrology (Wright et al. 2009). We assessed Little Colorado River flow patterns from USGS gauge 0940200 (the gauge station with the most complete records, near Cameron, Arizona) and temperature data from USGS gauge 09402300, the only gauge with water temperature records in the Little Colorado River beginning in 1992. We could not use the same gauge for both discharge and temperature information because the Little Colorado River gauge near Cameron, Arizona (0940200) has a long record of discharge information (but no temperature data) while the gauge farther downstream near the confluence (09402300) is the only Little Colorado River gauge with temperature data (but limited discharge information). We visually compared river discharge and seasonal temperature regimes before and after dam closure in 1963 to examine annual patterns and variability. We constructed discharge and temperature duration curves for two epochs that encompassed residency of sampled fish (1980–1993, 2001–2011). Because individual years within these two time periods have different data available, we identify in our two manuscripts the specific years for which data are available to test our hypotheses about how growth patterns may have changed in response to planned and unplanned changes in Colorado River discharge and water temperature (Melis et al. 2015).

Supplemental Material

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Reference S1. Andrews ED. 1991. Sediment transport in the Colorado River basin. Pages 54–74 in Colorado River ecology and dam management. Proceedings of a Symposium, May 24–25, 1990, Santa Fe, New Mexico. Washington, D.C.: National Academy Press.

Found at DOI: http://dx.doi:10.3996/042016-JFWM-036.S1; also available at: http://www.nap.edu/read/1832/chapter/6.

Reference S2. 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:10.3996/042016-JFWM-036.S2; also available at: http://pubs.usgs.gov/of/2009/1075/of2009-1075.pdf.

Reference S3. Gloss SP, Lovich JE, Melis TS, editors. 2005. The state of the Colorado River ecosystem in Grand Canyon. Reston, Virginia: U.S. Geological Survey Circular 1282.

Found at DOI: http://dx.doi:10.3996/042016-JFWM-036.S3; also available at: http://pubs.usgs.gov/circ/1282/.

Reference S4. Ralston BE. 2011. Summary report of responses of key resources to the 2000 low summer steady flow experiment, along the Colorado River downstream from Glen Canyon Dam, Arizona. Reston, Virginia: U.S. Geological Survey Open-File Report 2011-1220.

Found at DOI: http://dx.doi:10.3996/042016-JFWM-036.S4; also available at: http://pubs.usgs.gov/of/2011/1220/of2011-1220.pdf.

Reference S5. Schmidt JC, Topping DJ, Grams PE, Hazel JE. 2004. System-wide changes in the distribution of fine sediment in the Colorado River corridor between Glen Canyon Dam and Bright Angel Creek, Arizona. Utah

State University, Logan, Utah: Department of Aquatic, Watershed, and Earth Resources report.

Found at DOI: http://dx.doi:10.3996/042016-JFWM-036.S5; also available at: http://www.usbr.gov/uc/rm/amp/amwg/mtgs/05mar02/Attach_05a.pdf.

Reference S6. Topping DJ, Rubin DM, Vierra LE Jr. 2000. Colorado River sediment transport: 1. natural sediment supply limitation and the influence of the Glen Canyon Dam. Water Resources Research 36:515–542.

Found at DOI: http://dx.doi:10.3996/042016-JFWM-036.S6; also available at: http://pubs.er.usgs.gov/publication/70023155.

Reference S7. Topping DJ, Schmidt JC, Vierra LE Jr. 2003. Computation and analysis of the instantaneous-discharge record at Lee's Ferry, Arizona—May 8, 1921, through September 30, 2000. Reston, Virginia: U.S. Geological Survey professional paper 1677.

Found at DOI: http://dx.doi:10.3996/042016-JFWM-036.S7; also available at: http://pubs.usgs.gov/pp/pp1677/.

Reference S8. Trammell M, Valdez RA, Carothers SW, Ryel, R. 2002. Effects of a low steady summer flow experiment on native fishes of the Colorado River in Grand Canyon—final report. Flagstaff, Arizona: SWCA, Inc. Environmental Consultants, submitted to U.S. Geological Survey, Grand Canyon Monitoring and Research Center, cooperative agreement no. 99–FC–40–2260.

Found at DOI: http://dx.doi:10.3996/042016-JFWM-036.S8; also available at: http://www.gcmrc.gov/library/reports/biological/fish_studies/SWCA/99-FC-40-2260%20LSSF/LSSF-FinalRepNov2002.doc.

Reference S9. [USDOI] U.S. Department of Interior. 1994. Endangered and threatened wildlife and determination of critical habitat for the Colorado River endangered fishes: razorback sucker, Colorado squawfish, humpback chub, and bonytail sucker. 50 CFR Part 17. Final Rule. March 17. Federal Register 59:13374–13400.

Found at DOI: http://dx.doi:10.3996/042016-JFWM-036.S9; also available at: http://www.fws.gov/carlsbad/SpeciesStatusList/CH/19940321_fCH_BOCH.pdf .

Reference S10. [USDOI] U.S. Department of Interior. 1996. Record of Decision Operation of Glen Canyon Dam Final Environmental Impact Statement. Washington, D.C.: U.S. Department of the Interior.

Found at DOI: http://dx.doi:10.3996/042016-JFWM-036.S10; also available at: http://www.usbr.gov/uc/rm/amp/pdfs/sp_appndxG_ROD.pdf.

Reference S11. [USDOI] U.S. Department of Interior. 2008. Final Biological Opinion for the Operation of Glen Canyon Dam. Phoenix, Arizona: U.S. Fish and Wildlife Service, AESO/SE 22410-1993-F-167R1.

Found at DOI: http://dx.doi:10.3996/042016-JFWM-036.S11; also available at: http://www.usbr.gov/uc/envdocs/bo/FinalGCDBO2-26-08.pdf.

Reference S12. Valdez RA, Ryel RJ. 1995. Life history and ecology of humpback chub (*Gila cypha*) in the Colorado River, Grand Canyon, Arizona. Final report. Logan, UT: BIO/WEST, Inc. to the Bureau of Reclamation, Salt Lake City, Utah, contract no. 0-CS-40-09110.

Found at DOI: http://dx.doi:10.3996/042016-JFWM-036.S12; also available at: http://www.gcmrc.gov/library/reports/biological/Fish_studies/Biowest/Valdez1995f.pdf.

Reference S13. 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:10.3996/042016-JFWM-036.S13; also available at: http://pubs.usgs.gov/ds/2007/251/.

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References

Andrews ED. 1991. Sediment transport in the Colorado River Basin. Pages 54–74 in Colorado River ecology and dam management. Proceedings of a Symposium, May 24–25, 1990, Santa Fe, NM. Washington, D.C.: National Academy Press. (See *Supplemental Material*, Reference S1, http://dx.doi:10.3996/042016-JFWM-036.S1); also available: http://www.nap.edu/read/1832/chapter/6 (April 2016).

Aresco MJ, Guyer C. 1999. Growth of the tortoise *Gopherus polyphemus* in slash pine plantations of south-central Alabama. Herpetologica 55:499–506.

Christensen NS, Wood AW, Voisin N, Lettenmaier DP, Palmer RN. 2004. The effects of climate change on the hydrology and water resources of the Colorado River basin. Climatic Change 62:337–363.

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

Coggins LG Jr, Pine WE III. 2010. Development of a temperature-dependent growth model for the endangered humpback chub using capture–recapture data. Open Fish Science Journal 3:122–131.

Coggins LG Jr, Pine WE III, Walters CJ, Martell SJD. 2006a. Age-structured mark–recapture analysis: a virtual-population-analysis-based model for analyzing age-structured capture–recapture data. North American Journal of Fisheries Management 26:201–205.

Coggins LG Jr, Pine WE III, Walters CJ, Van Haverbeke DR, Ward D, Johnstone HC. 2006b. Abundance trends and status of the Little Colorado River population of humpback chub. North American Journal of Fisheries Management 26:233–245.

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 S2, http://dx.doi:10.3996/042016-JFWM-036.S2); also available: http://pubs.usgs.gov/of/2009/1075/of2009-1075.pdf (April 2016).

Coggins LG, Yard MD, Pine WE III. 2011. Nonnative fish control in the Colorado River in Grand Canyon, Arizona: an effective program or serendipitous timing? Transactions of the American Fisheries Society 140:456–470.

Converse YK, Hawkins CP, Valdez RA. 1998. Habitat relationships of subadult humpback chub in the Colorado River through Grand Canyon: spatial variability and implications of flow regulation. Regulated Rivers: Research and Management 14:267–284.

Cross WF, Baxter CV, Donner KC, Rosi-Marshall EJ, Kennedy TA, Hall RO, Wellard-Kelly HA, Rogers RS. 2011. Ecosystem ecology meets adaptive management: food web response to a controlled flood on the Colorado River, Glen Canyon. Ecological Applications 21:2016–2033.

Cross WF, Baxter CV, Rosi-Marshall EJ, Hall RO Jr, Kennedy TA, Donner KC, Wellard-Kelly HA, Seegert SEZ, Behn KE, Yard MD. 2013. Food web dynamics in a large river discontinuum. Ecological Monographs 83:311–337.

Dodrill MJ, Yackulic CB, Gerig B, Pine WE III, Korman J, Finch C. 2015. Do management actions to restore rare habitat benefit native fish conservation? Distribution of juvenile native fish among shoreline habitats of the Colorado River. River Research and Applications 31:1203–1217.

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, Yackulic CB, Dodrill MJ, Yard M, Gerig BS, Coggins LG, 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.

Finer M, Jenkins CN. 2012. Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes–Amazon connectivity. PLoS ONE 7(4):e35126.

Gloss SP, Lovich JE, Melis TS, editors. 2005. The state of the Colorado River ecosystem in Grand Canyon. Reston, Virginia: U.S. Geological Survey Circular 1282. (See *Supplemental Material*, Reference S3, http://dx.doi:10.3996/042016-JFWM-036.S3); also available: http://pubs.usgs.gov/circ/1282/ (April 2016).

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.

Hayden TA, Limburg KE, Pine WE III. 2012. Using otolith chemistry tags and growth patterns to distinguish movements and provenance of native fish in Grand Canyon. River Research and Application 29:1318–1329.

Hayes FP, Dodrill MJ, Gerig BS, Finch C, Pine WE III. 2017. Body condition of endangered humpback chub in relation to temperature and discharge in the lower Colorado River. Journal of Fish and Wildlife Management 8:333–342.

Hoffnagle TL, Choudhury A, Cole RA. 2006. Parasitism and body condition in humpback chub from the Colorado and Little Colorado rivers, Grand Canyon, Arizona. Journal of Aquatic Animal Health 18:184–193.

Kaeding LR, Zimmerman MA. 1983. Life-history and ecology of the humpback chub in the Little Colorado and Colorado rivers of the Grand Canyon. Transactions of the American Fisheries Society 112:577–594.

King JR, Shuter BJ, Zimmerman AP. 1999. Empirical links between thermal habitat, fish growth, and climate change. Transactions of the American Fisheries Society 128:656–665.

Ligon FK, Dietrich WE, Trush WJ. 1995. Downstream ecological effects of dams. BioScience 45:183–192.

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(12):e84235.

Melis TS, Walters CJ, Korman J. 2015. Surprise and opportunity for learning in Grand Canyon: the Glen Canyon Dam Adaptive Management Program. Ecology and Society 20(3):22.

Minckley WL, Deacon JE, editors. 1991. Battle against extinction: native fish management in the American West. Tucson, Arizona: University of Arizona Press.

Minckley WL, Marsh PC, Deacon JE, Dowling TE, Hedrick PW, Matthews WJ, Mueller G. 2003. A conservation plan for native fishes of the lower Colorado River. BioScience 53:219–234.

Nicieza AG, Metcalfe NB. 1997. Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability. Ecology 78:2385–2400.

Olden JD, Naiman RJ. 2010. Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. Freshwater Biology 55:86–107.

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

Poff NL, Hart DD. 2002. How dams vary and why it matters for the emerging science of dam removal. BioScience 52:659–668.

Pulwarty R, Melis T. 2001. Climate extremes and adaptive management on the Colorado River: lessons from the 1997–1998 ENSO Event. Journal of Environmental Management 63:307–324.

Quinn TP, Peterson NP. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences 53:1555–1564.

Ralston BE. 2011. Summary report of responses of key resources to the 2000 low summer steady flow experiment, along the Colorado River downstream from Glen Canyon Dam, Arizona. Reston, Virginia: U.S. Geological Survey Open-File Report 2011-1220. (See *Supplemental Material*, Reference S4, http://dx.doi:10.3996/042016-JFWM-036.S4); also available: http://pubs.usgs.gov/of/2011/1220/of2011-1220.pdf (April 2016).

Richter BD, Thomas GA. 2007. Restoring environmental flows by modifying dam operations. Ecology and Society 12(1):12.

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.

Schmidt JC, Topping DJ, Grams PE, Hazel JE. 2004. System-wide changes in the distribution of fine sediment in the Colorado River corridor between Glen Canyon Dam and Bright Angel Creek, Arizona. Utah State University, Logan, Utah: Department of Aquatic, Watershed, and Earth Resources. (See *Supplemental Material*, Reference S5, http://dx.doi:10.3996/042016-JFWM-036.S5); also available: http://www.usbr.gov/uc/rm/amp/amwg/mtgs/05mar02/Attach_05a.pdf (April 2016).

Shuman JR. 1995. Environmental considerations for assessing dam removal alternatives for river restoration. Regulated Rivers: Research and Management 11:249–261.

Stanford JA, Ward JV. 2001. Revisiting the serial discontinuity concept. Regulated Rivers: Research and Management 17:303–310.

Stone DM. 2010. Overriding effects of species-specific turbidity thresholds on hoop-net catch rates of native fishes in the Little Colorado River, Arizona. Transactions of the American Fisheries Society 139:1150–1170.

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.

Topping DJ, Rubin DM, Vierra LE Jr. 2000. Colorado River sediment transport: 1. natural sediment supply limitation and the influence of the Glen Canyon Dam. Water Resources Research 36:515–542. (See *Supplemental Material*, Reference S6, http://dx.doi:10.3996/042016-JFWM-036.S6); also available: http://pubs.er.usgs.gov/publication/70023155 (April 2016).

Topping DJ, Schmidt JC, Vierra LE Jr. 2003. Computation and analysis of the instantaneous-discharge record at Lee's Ferry, Arizona—May 8, 1921, through September 30, 2000. Reston, Virginia: U.S. Geological Survey professional paper 1677. (See *Supplemental Material*, Reference S7, http://dx.doi:10.3996/042016-JFWM-036.S7); also available: http://pubs.usgs.gov/pp/pp1677/ (April 2016).

Trammell M, Valdez RA, Carothers SW, Ryel, R. 2002. Effects of a low steady summer flow experiment on native fishes of the Colorado River in Grand Canyon—final report. Flagstaff, Arizona: SWCA, Inc. Environmental Consultants, submitted to U.S. Geological Survey, Grand Canyon Monitoring and Research Center, cooperative agreement no. 99–FC–40–2260. (See *Supplemental Material*, Reference S8, http://dx.doi:10.3996/042016-JFWM-036.S8); also available: http://www.gcmrc.gov/library/reports/biological/fish_studies/SWCA/99-FC-40-2260%20LSSF/LSSF-FinalRepNov2002.doc

[USDOI] U.S. Department of Interior. 1994. Endangered and threatened wildlife and determination of critical habitat for the Colorado River endangered fishes:

razorback sucker, Colorado squawfish, humpback chub, and bonytail sucker. 50 CFR Part 17. Final Rule. March 17. Federal Register 59:13374–13400. (See *Supplemental Material*, Reference S9, http://dx.doi:10.3996/042016-JFWM-036.S9); also available: http://www.fws.gov/carlsbad/SpeciesStatusList/CH/19940321_fCH_BOCH.pdf (April 2016).

[USDOI] U.S. Department of Interior. 1996. Record of Decision Operation of Glen Canyon Dam Final Environmental Impact Statement. Washington, D.C.: U.S. Department of Interior. (See *Supplemental Material*, Reference S10, http://dx.doi:10.3996/042016-JFWM-036.S10); also available: http://www.usbr.gov/uc/rm/amp/pdfs/sp_appndxG_ROD.pdf (April 2016).

[USDOI] U.S. Department of Interior. 2008. Final Biological Opinion for the Operation of Glen Canyon Dam. Phoenix, Arizona: U.S. Fish and Wildlife Service, AESO/SE 22410-1993-F-167R1. (See *Supplemental Material*, Reference S11, http://dx.doi:10.3996/042016-JFWM-036.S11); also available: http://www.usbr.gov/uc/envdocs/bo/FinalGCDBO2-26-08.pdf (April 2016).

[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.

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 S12, http://dx.doi:10.3996/042016-JFWM-036.S12); also available: http://www.gcmrc.gov/library/reports/biological/Fish_studies/Biowest/Valdez1995f.pdf (April 2016).

Van Haverbeke DR, Stone DM, Coggins LG, 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.

Vermeyen T. 2008. The Glen Canyon Dam temperature control device: restoring downstream habitat for endangered fish recovery. Pages 1–9 in World Environmental and Water Resources Congress 2008. Honolulu, Hawaii: American Society of Civil Engineers.

Vernieu WS, Hueftle SJ, Gloss SP. 2005. Water quality in Lake Powell and the Colorado River. in Gloss SP, Lovich JE, Melis TS. State of the Colorado River ecosystem in Grand Canyon. Reston, Virginia: U.S. Geological Survey Circular 1282.

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 S13, http://dx.doi:10.3996/042016-JFWM-036.S13); 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.

Wright SA, Anderson CR, Voichick N. 2009. A simplified water temperature model for the Colorado River below Glen Canyon Dam. River Research and Applications 25:675–686.

Wright SA, Melis TS, Topping DJ, Rubin DM. 2005. Influence of Glen Canyon Dam operations on downstream sand resources of the Colorado River in Grand Canyon, Pages 17–31 in Gloss SP, Lovich JE, Melis TS, editors. The state of the Colorado River ecosystem in Grand Canyon. Reston, Virginia: U.S. Geological Survey Circular 1282.

Wright SA, Schmidt JC, Melis TS, Topping DJ, Rubin DM. 2008. Is there enough sand? Evaluating the fate of Grand Canyon sandbars. GSA Today 18(8):4–10.

Yard MD, Coggins LG Jr, Baxter CV, Bennett GE, Korman J. 2011. Trout piscivory in the Colorado River, Grand Canyon: effects of turbidity, temperature, and fish prey availability. Transactions of the American Fisheries Society 140:471–486.