Western North American Naturalist 78(1), © 2018, pp. 26–38

Humpback Chub (*Gila cypha*) range expansion in the western Grand Canyon

David L. Rogowski[1], Robin J. Osterhoudt[1], Harrison E. Mohn[2], and Jan K. Boyer[1,*]

[1]*Arizona Game and Fish Department, 5000 West Carefree Drive, Phoenix, AZ 88086*
[2]*BIO-WEST, Inc., 1063 West 1400 North, Logan, UT 84321-2291*

Abstract.—The Colorado River in the Grand Canyon holds the largest remaining population of Humpback Chub *Gila cypha,* an endangered fish endemic to the Colorado River basin. Early surveys in the 1990s found that most Humpback Chub occupied the Little Colorado River and nearby areas in the mainstem Colorado River and were uncommon in the western Grand Canyon (below Kanab Creek, at river kilometer [rkm] 257.2). From 1939 to 2002, the Colorado River was typically inundated by Lake Mead to rkm 407 (at full pool). Since 2000, Lake Mead water levels have declined, and the current inflow is located almost 100 km downstream at rkm 503.1. Thus, the Arizona Game and Fish Department (AGFD) extended its system-wide monitoring downstream to Pearce Ferry rapid (rkm 478.6) in 2011. Electrofishing is relatively inefficient at capturing Humpback Chub, but a small number of captures from 2011 to 2015 in the western Grand Canyon suggested that the Humpback Chub may have expanded its range downstream. Subsequently, hoop nets were added to AGFD system-wide monitoring in 2016 to better describe Humpback Chub distribution. The distribution of Humpback Chub observed in 2016 and 2017 differed from previous descriptions; we documented relatively large numbers of Humpback Chub, including age-0 fish, in the western Grand Canyon and observed the highest catches downstream of Diamond Creek (rkm 389.1). This suggests that a recent range expansion has occurred and that Humpback Chub in the western Grand Canyon do not utilize the Little Colorado River for reproduction and might therefore constitute a new subpopulation.

Resumen.—El río Colorado en el área del Gran Cañón alberga la más grande población remanente de *Gila cypha,* un pez amenazado endémico de la cuenca del río Colorado. Muestreos en la década de los 1990 encontraron que la mayor cantidad de *G. cypha* ocupaban el río Little Colorado y áreas cercanas a éste sobre el río Colorado, pero que la especie era poco común en la parte oeste del Gran Cañón, río abajo de Kanab Creek, en el kilómetro de río (rkm) 257.2. Entre 1939–2002, el río Colorado estaba típicamente inundado por el lago Mead hasta el rkm 407 (a máxima capacidad de llenado del lago). Desde el año 2000 los niveles del lago Mead han caído, y hoy la entrada de agua al lago se encuentra casi 100 km río abajo de su nivel máximo, en el rkm 503.1. Por ello, el Arizona Game and Fish Department (AGFD) extendió su programa de monitoreo aguas abajo, al rápido Pearce Ferry (rkm 478.6) en el año 2011. La electropesca es poco eficiente para la captura de *G. cypha,* pero un pequeño número de capturas en 2011–2015 en la parte oeste del Gran Cañón sugirió que la especie puede haber expandido su rango de distribución aguas abajo. Después, en el año 2016, redes de aro fueron añadidas al sistema de monitoreo del AGFD para lograr una mejor descripción de la distribución de *G. cypha.* La distribución de *G. cypha* observada en 2016 y 2017 difirió de descripciones previas; se documentó un relativamente alto número de *G. cypha,* incluyendo peces de edad cero, en la parte oeste del Gran Cañón, con las capturas más abundantes río abajo de Diamond Creek (rkm 389.1). Esto sugiere que ha ocurrido una relativamente reciente expansión del rango de la especie y que los *G. cypha* en la parte oeste del Gran Cañón no están utilizando el río Little Colorado para reproducción, pudiendo constituir una nueva subpoblación.

Humpback Chub *Gila cypha* is an endangered cyprinid fish endemic to the Colorado River basin (Miller 1946). It once was widely distributed and fairly common in canyon-bound reaches of the Colorado River and tributaries (Holden and Stalnaker 1975). With the development of the western United States and the regulation of the Colorado River and tributaries, the abundance and distribution of the Humpback Chub have declined. Currently there are 6 extant populations, with only one of those populations—the Grand Canyon population—considered healthy and viable (USFWS 2002, Badame 2008, Jackson 2010, Francis et al. 2016). Since the completion of Glen Canyon and Hoover Dams, the Colorado

*Corresponding author: jboyer@azgfd.gov

DLR orcid.org/0000-0003-0264-0223 JKB orcid.org/0000-0002-6746-0824

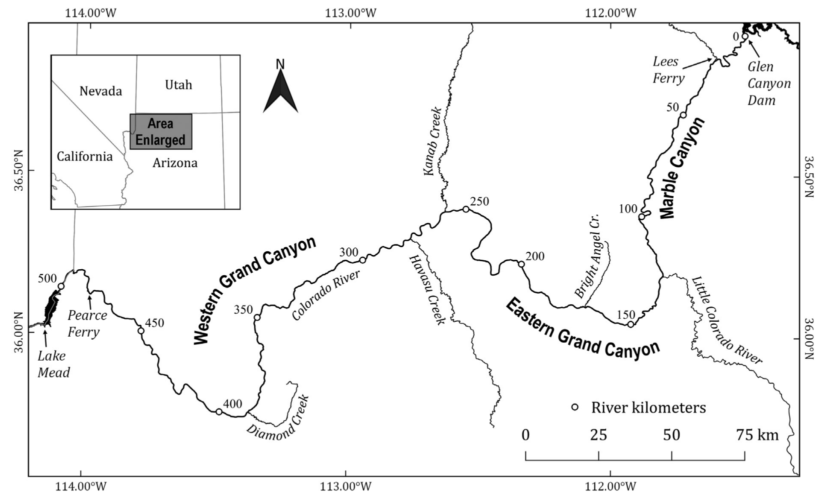

Fig. 1. Map of the study area. River kilometers (rkm) starting at the Glen Canyon Dam (rkm 0.0) are shown in 50-km segments. The western Grand Canyon is defined as the confluence of Kanab Creek with the Colorado River (rkm 231.7) to the Lake Mead inlet (varies with lake elevation; rkm 503.1 in 2017).

River has been significantly altered in this reach (Fig. 1). The Colorado River below the Glen Canyon dam has become colder and clearer, with higher daily fluctuations in flow but less variability in seasonal and annual flow (Topping et al. 2003). In recent years, periodic high-flow events have been conducted primarily to redistribute sand and build beaches, but these flows (approximately 1050–1220 m^3/s; Melis 2011) have been much lower than historical spring floods (>2850 m^3/s; Schmidt et al. 2001).

In spite of the changes to the Colorado River, numbers of Humpback Chub near the Little Colorado River Confluence (Fig. 1), the only area in the Grand Canyon where quantitative population estimates are available, have fluctuated over time but have maintained a population higher than anywhere else in the Colorado River Basin (Coggins et al. 2006, Van Haverbeke et al. 2013). The most recent study available estimates that 10,000 Humpback Chub are present near the Little Colorado River Confluence (Yackulic et al. 2014). One goal of the Glen Canyon Dam Adaptive Management Program (GCDAMP), instituted in 1997 in response to the 1995 Environmental Impact Statement on the Operations of Glen Canyon Dam (USDOI 1995), is to ensure that the management and operation of the Glen Canyon Dam does not have undue negative impacts on the Humpback Chub (USDOI 2016). Through the GCDAMP and preceding programs, a variety of research, monitoring, conservation, and recovery projects have focused on Humpback Chub. Initial efforts in the early 1990s (Valdez and Ryel 1995) determined capture methods and described Humpback Chub distribution, and more recent efforts involved translocation of Humpback Chub from the Little Colorado River to other tributaries in the system (e.g., Havasu Creek, Shinumo Creek; Spurgeon et al. 2015).

Since the initial investigations into the distribution of Humpback Chub in the 1980s and 1990s, little work has been explicitly directed at determining the distribution of Humpback Chub. Since Valdez and Ryel (1995), monitoring for Humpback Chub has concentrated on locations the authors called aggregations (updated by Persons et al. 2016), with most of the research and monitoring centered on the Little Colorado River aggregation and occasional sampling outside the aggregations in recent years (Persons et al. 2016). Valdez and Ryel (1995) defined aggregations as "consistent and disjunct groups of fish with no significant exchange of individuals with other aggregations, as indicated by recapture of PIT-tagged juveniles and adults and movement of radio-tagged adults." The Little Colorado River is an unregulated tributary that is the home and spawning grounds to a large proportion of the Humpback Chub population in the Grand Canyon (Valdez and

Ryel 1995, Van Haverbeke et al. 2013). One shortfall of these monitoring programs is that they tell us little about the distribution of Humpback Chub throughout the system (e.g., from Glen Canyon Dam to the Lake Mead inflow).

Currently, the Arizona Game and Fish Department's (AGFD) long-term monitoring is the only fisheries project employing random, system-wide (Lees Ferry to Lake Mead) sampling to obtain information on the distribution of fishes in the mainstem Colorado River. However, there has been little success in capturing Humpback Chub because electrofishing has been the primary system-wide sampling method. Humpback Chub are not commonly vulnerable to electrofishing (Coggins 2008), and electrofishing is size-selective for small Humpback Chub (Paukert 2004). For example, in 2014, sixteen Humpback Chub from 547 sites were captured via electrofishing (0.029 fish/sample), and our catch was skewed toward small fish (median = 86 mm total length, minimum = 55 mm, maximum = 285 mm; Rogowski et al. 2015). Thus, electrofishing alone is unlikely to provide accurate estimates of distribution or relative abundance for all age classes of Humpback Chub.

In recent years (2011–2015), a small number of Humpback Chub captures below Diamond Creek (river kilometer [rkm] 389.1; rkm 0.0 = Glen Canyon Dam) have suggested that the Humpback Chub may have extended its range within the Colorado River, particularly in the western Grand Canyon (Fig. 1, Table 1; Kegerries et al. 2016, Persons et al. 2016, Rogowski et al. 2016). Previous sampling (1992–1993, 2004–2005) in the western Grand Canyon found Humpback Chub primarily near Havasu Creek (rkm 278.6) and Pumpkin Spring (rkm 368.1) and detected few or no Humpback Chub downstream of Diamond Creek (Valdez 1994, Valdez and Carothers 1998, Van Haverbeke et al. 2007). For example, extensive sampling in 2004–2005 from Diamond Creek to Pearce Ferry (rkm 478.6) using a variety of gear (electrofishing, seines, trammel nets, angling, and baited hoop nets) captured only 4 Humpback Chub (at rkm 411; Van Haverbeke et al. 2007). Hoop nets are an efficient method to capture Humpback Chub that are between approximately 100 mm and 300 mm total length at aggregation sites (Valdez and Ryel 1995, Stone 2005, Van Haverbeke et al. 2013). Thus, in 2016 we added baited hoop nets to our Grand Canyon long-term monitoring to more effectively investigate distribution and relative abundance of Humpback Chub. Our objective was to determine relative abundance and spatial distribution of Humpback Chub through the entire length of the Colorado River in the Grand Canyon.

METHODS

Our study site covered the Colorado River from Lees Ferry (rkm 25.4) to the inlet of Lake Mead (about rkm 503 in 2017). The Colorado River from Glen Canyon Dam (rkm 0) to Lees Ferry was not included in this study, as other AGFD and U.S. Geological Survey fisheries projects sample this reach extensively and no Humpback Chub have been captured upstream of Lees Ferry since 1970 (Minckley 1996). This region is divided into 3 geographic areas: Marble Canyon (Lees Ferry to Little Colorado River confluence, rkm 25.4–124.4), Eastern Grand Canyon (Little Colorado River confluence to Kanab Creek confluence, rkm 124.4–257.2), and western Grand Canyon (downstream of Kanab Creek, rkm > 257.2; Schmidt and Graf 1990).

Monitoring in 2016–2017 followed standardized methods which have been employed since 2000, but differences in sample size and methods occurred among years due to logistical constraints, changes in the extent of Lake Mead (Fig. 2), and efforts to improve sampling methods. AGFD has typically conducted 2 spring fish-monitoring trips in the mainstem Colorado River each year since 2000, primarily using electrofishing. In 2012, AGFD initiated an annual autumn electrofishing trip. In 2016, baited hoop nets were added to the monitoring program. Historical monitoring is described below followed by detailed methods and sample sizes for our 2016–2017 trips.

Historical Monitoring

Two spring monitoring trips occurred each year between March and June with a few exceptions (e.g., one trip in 2001, 2007, 2011, and 2012), with the spatial distribution of samples and the area sampled changing over time (Table 1). Autumn monitoring trips have occurred annually since 2012 but were sporadic prior to that year (e.g., 2004). Sample site selection from 2000 to 2012 was based on

TABLE 1. Historical Humpback Chub catch from the Arizona Game and Fish Department's electrofishing monitoring of the Colorado River in the Grand Canyon. All electrofishing data (spring and autumn trips, including data that was removed from other analyses because of high turbidity or equipment malfunctions) are included in this table. n/a = no sampling occurred.

Year	Spatial extent of sampling (rkm)	Number of samples	Number of Humpback Chub captured	Little Colorado aggregation (rkm 117.2–149.7)	Western Grand Canyon[a] (rkm > 257.2)	Downstream of Diamond Creek (rkm > 389.1)
2000	55.0–381.1	269	15	15	0	n/a
2001	88.6–342.3	160	1	1	0	n/a
2002	48.7–377.2	818	8	8	0	n/a
2003	39.4–386.1	799	3	2	0	n/a
2004	28.0–469.1	1105	9	6	0	0
2005	32.6–449.4	1107	17	16	0	0
2006	29.1–386.7	811	15	9	0	n/a
2007	39.2–452.5	1252	24	24	0	0
2008	53.4–386.9	652	6	5	0	n/a
2009	53.5–451.4	966	11	0	1	0
2010	45.0–383.4	536	14	10	0	n/a
2011	28.3–445.7	648	12	10	2	1
2012	31.6–443.2	479	18	12	3	0
2013	39.8–453.4	486	12	8	1	0
2014	29.5–459.8	547	16	9	4	3
2015	27.5–476.7	593	30	1	26	12
2016	26.1–477.6	639	26	9	15	4
2017	38.5–478.1	469	15	2	12	9

[a]Western Grand Canyon (rkm > 257.2) is inclusive of the waters downstream of Diamond Creek (rkm > 389.1).

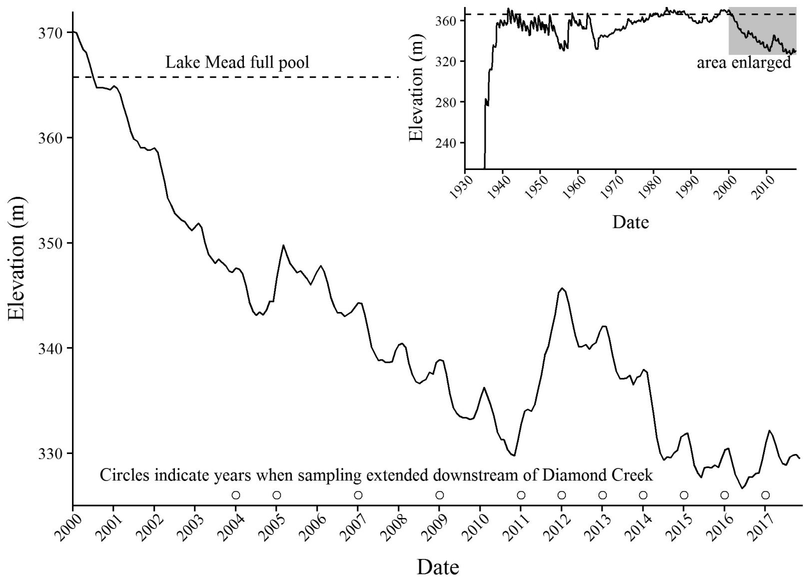

Fig. 2. Lake Mead elevation (meters above sea level, monthly means). At full pool (dashed line, 366 m), the inlet is located near river kilometer (rkm) 407. At the current elevation (330 m), the Lake Mead Inlet is located approximately 100 km downstream near rkm 503. Circles indicate years when system-wide monitoring extended downstream of Diamond Creek (rkm 389.1).

random stratified sampling among 11 reaches and varying numbers of subreaches (depending on rapids and campsite availability). Within each selected subreach, contiguous sampling sites, each consisting of 300 s of electrofishing, were sampled starting from a randomly selected start point on each bank and moving downstream. Prior to 2013, turbidity was recorded as high or low; subsequently, a turbidity meter (Hach 2100P) was used to obtain quantitative turbidity measurements (Nephelometric Turbidity Units = NTU) each evening.

Current Sample-Site Selection

The Colorado River was divided into 250-m sample sites along the left and right banks of the river from Lees Ferry (rkm 25.4) to Pearce Ferry Rapid (rkm 478.6). Reaches of the river were divided into 8-km segments or shorter segments due to rapids, resulting in 84 reaches with 3507 available sample sites. The available sampling area included approximately 86% of the river length; areas not included were reaches that were logistically impossible to sample due to dangerous rapids. Each reach was weighted according to the percentage of available sample sites within that reach relative to the sampling area (spring: rkm 25.4–478.6; autumn: rkm 389.1–478.6), and reaches to sample were randomly selected (spring: n = 30; autumn: n = 4). The number of reaches corresponded to the sampling nights available in our system-wide monitoring trips. After a reach was selected, 12–24 electrofishing sample sites and 4–20 hoop net sample sites were selected within the reach. Numbers of sample sites per reach varied because in shorter reaches (due to rapids), the number of sample sites was decreased proportionate to the length of the reach. In autumn, 4–24 electrofishing sites and 16–24 hoop nets sites were sampled per reach.

Sampling

All sites (start and end) were identified via the use of a GPS unit (Garmin 62s) and navigated to with the guide of orthophoto maps. Every evening before electrofishing, 2 turbidity measurements in NTU were taken (Hach 2100P turbidity meter). A mean turbidity value (NTU) for the night was calculated from these 2 measurements.

Electrofishing occurred at night (commencing with the appearance of 2 stars or planets) with two 16-ft. (4.9-m) Achilles inflatable or Osprey aluminum sport boats outfitted for electrofishing with an ETS Complex Pulse System unit (MBS-1DPQ-CR-AZ; ETS Electrofishing Systems, LLC, Madison, WI) powered by a 6500-W generator (Honda EG6500). Boats were equipped with a spherical steel anode (25.4 cm diameter) partially submerged (~5 cm exposed) off the bow of the boat. The cathode was either a spherical steel cathode totally immersed off the stern of the Achilles boats or the hull of the Osprey boats. An evaluation of both boats demonstrated that the electrofishing capabilities of the Achilles and Osprey boats were similar (D. Foster and A. Temple, personal communication, 2015). During spring trips, 260–580 V and 13–22 A were applied, with voltage decreasing and amperage increasing in a downstream direction in response to increasing water conductivity. Each sample across all trips consisted of a single electrofishing pass along a 250-m shoreline transect. We recorded date, start time, and time (seconds) spent actively electrofishing a site. Each boat included 2 biologists (netters) and 1 boatman. Beginning with our second spring trip in 2017, only 1 netter was utilized per boat because of safety concerns.

Hoop nets were baited with approximately 117 g (volume of measuring cup) of Aquamax fish food and set overnight within a 250-m sample site exclusive of our electrofishing sites. Net set locations within the sample site were based on the ability to effectively secure the net depending on water depth, tie-off structures, and river currents. Hoop nets measured 1.3 m long and 0.6 m in diameter with 6.35-mm mesh and consisted of 3 hoops and a single 0.1-m throat. For hoop nets, we recorded set date and time, pull date and time, and latitude and longitude. Most nets were deployed between 11:30 and 17:00 and fished for a mean of 17.9 h/day (SD = 1.5 h).

In 2017 monitoring was extended downstream of Pearce Ferry, where rapids and sandbars make access difficult from upstream. On 21–23 February 2017, AGFD and BIO-WEST, Inc., sampled approximately 14 km of river (between an unnamed rapid at rkm 488.9 and the Lake Mead Inlet rkm 503.1; Fig. 1). We used the random sampling methods described above and selected 10 sites each in 2 reaches over 2 nights to sample with baited (Aquamax) hoop nets (20 total). Hoop nets fished for a mean of 19.7 h (SD = 2.6 h). These hoop nets were slightly longer (1.45 m) with the same diameter and mesh size as those used upstream. From 23 March to 3 May 2017, BIO-WEST, Inc., continued sampling between rkm 483.9 and the Lake Mead Inlet one day per week during 6 of the 7 available weeks. Hoop nets were 1.3 m in length, consisted of 4 hoops and 2 throats, and had the same diameter and mesh size as those used elsewhere. Net set locations were spread out over this section of river, where specific sets were based on the ability to effectively secure the net depending on water depth, tie-off structures, and river currents. Hoop nets (n = 34) were baited with dry dog food and fished for a mean of 14.5 h (SD = 5.2 h).

All fish captured were processed according to standard fish-handling protocols for the Grand Canyon (Persons et al. 2015). Species and total length (TL) were recorded for all fish. All Humpback Chub were scanned with a portable passive integrated transponder (PIT) tag reader (Biomark: HPRplus or 2001F-ISO), and Humpback Chub ≥80 mm TL were implanted with a 134.2-kHz PIT tag if no tag was detected. Other fisheries projects within the Grand Canyon use the same fish processing and PIT tag protocols; thus we were able to identify recaptured fish regardless of whether initial capture occurred during our sampling or another project.

Analysis

Catch per unit effort (CPUE, fish/h) for each species was calculated for each sampling site. Historical data were used to summarize numbers of Humpback Chub captured with electrofishing in different areas of the Grand Canyon from 2000 to 2017 (Table 1).We compared electrofishing and hoop-netting effectiveness using the number of Humpback Chub captured per site in our 2016 and 2017 sampling. Electrofishing sites were excluded from analyses if the water was too turbid (>160 mean NTU) to effectively net fish or if the equipment malfunctioned. Length frequency histograms of all Humpback Chub captured in 2016 and 2017 were used to examine the size structure of Humpback Chub. Hoop-net catch data from winter, spring, and autumn were used to describe the spatial distribution of Humpback Chub throughout the Grand Canyon. We calculated the percentage of fish that were recaptures (had a PIT tag) in each area of the canyon. We pooled

TABLE 2. Comparison of Humpback Chub catch from electrofishing and baited hoop nets at randomly selected sites in the Colorado River from Lees Ferry to Pearce Ferry, Arizona, 2016 and 2017 (spring and autumn data included).

Year	Sampling gear	Sites sampled	Total catch	Mean effort (h/site)	CPUE, fish/h [95% CI]	Fish/site [95% CI]
2016	Electrofishing	639	26	0.121	0.369 [0.168, 0.569]	0.041 [0.016, 0.065]
	Baited hoop nets	319	179	17.9	0.031 [0.023, 0.039]	0.561 [0.414, 0.708]
2017	Electrofishing	537	13	0.123	0.181 [0.068, 0.294]	0.024 [0.009, 0.039]
	Baited hoop nets	459	588	17.6	0.070 [0.054, 0.086]	1.281 [0.989, 1.573]

2016 and 2017 data because the sample size of recaptures was small, and we only counted unique individuals (i.e., if a fish was captured multiple times during our 2016–2017 sampling, only the earliest capture record was used). To investigate whether Humpback Chub were resident below Diamond Creek or were from upstream areas, we looked up previous capture locations (RM) for all Humpback Chub recaptured, including fish which were initially tagged and recaptured during our 2016–2017 sampling.

Mean Humpback Chub CPUE was calculated for 3 areas: Marble Canyon, eastern Grand Canyon, and western Grand Canyon. Most nets (496 of 636) captured no Humpback Chub, so we used zero-inflated Poisson models with an offset for effort (h) (Zeileis et al. 2008, Zuur et al. 2009) to compare catch of Humpback Chub between aggregation sites (Valdez and Ryel 1995) and nonaggregation sites from spring sampling. We attempted the same comparison of catch between the updated aggregation sites (Persons et al. 2016) and nonaggregation sites, but a small sample size (28 nets) in aggregations outside of the Little Colorado River limited our ability to make meaningful comparisons to nonaggregation sites (562 nets). We excluded data taken below Pearce Ferry Rapid and data taken during autumn sampling from the CPUE comparison because these were not systemwide sampling efforts (no aggregation sites were sampled).

RESULTS

For 2016, mean electrofishing time for a site (n = 639 sites) was 435 s (SD = 137 s) in spring; for 2017 (n = 469 sites) it was 423 s (SD = 142 s). Due to a few days of high turbidity in 2017, a number of sites (86) were classified as supplemental data and not included in the analyses. Only 26 Humpback Chub in 2016 (0.04 fish/sample) and 8 in 2017 (0.017 fish/sample) were captured via electrofishing (Table 1). Low Humpback Chub catch is consistent with previous years' electrofishing results; from 2000 to 2017, numbers of Humpback Chub captured ranged from 1 to 30 (Table 1). Hoop nets set in spring of 2016 and 2017 captured greater numbers of Humpback Chub per sample than electrofishing, by an order of magnitude (Table 2). Relative abundance of Humpback Chub in the Colorado River between Lees Ferry (rkm 25.4) and Lake Mead (rkm 503.1) generally increased in a downstream direction (Fig. 3). Humpback Chub hoop-net CPUE was low in Marble Canyon (rkm 25.4–124.4; mean CPUE = 0.010 fish/h) and in the eastern Grand Canyon (rkm 124.4–257.2; 0.014 fish/h), where Humpback Chub were rarely captured except near the Little Colorado River Confluence (rkm 124.4). Higher hoop-net CPUE for Humpback Chub was observed in the western Grand Canyon (rkm 257.2–478.6; 0.075 fish/h), with the highest CPUE (0.128 fish/h) observed between Diamond Creek (rkm 389.1) and Pearce Ferry Rapid (rkm 478.6). Humpback Chub CPUE was lower (0.0195 fish/h) from Pearce Ferry Rapid to the Lake Mead inlet (rkm 503.1).

Below Diamond Creek, we observed all age and size classes in our catch (Fig. 4), including age-0 fish (<100 mm). Recaptures were investigated by pooling 2016 and 2017 catch data and limiting analysis to unique fish (only the first capture record was used for a fish recaptured multiple times in 2016 and 2017). Upstream of Diamond Creek, 30% of unique Humpback Chub (≥80 mm) were recaptures with PIT tags (47 of 159 fish), and near the Little Colorado River confluence 62% of fish (≥80 mm) were recaptures. Conversely, only 4% of Humpback Chub (≥80 mm) captured downstream of Diamond Creek (20 of 536 fish) were recaptures. In 2016 and 2017, we captured 536 unique individuals ≥80 mm (taggable size) downstream of Diamond Creek;

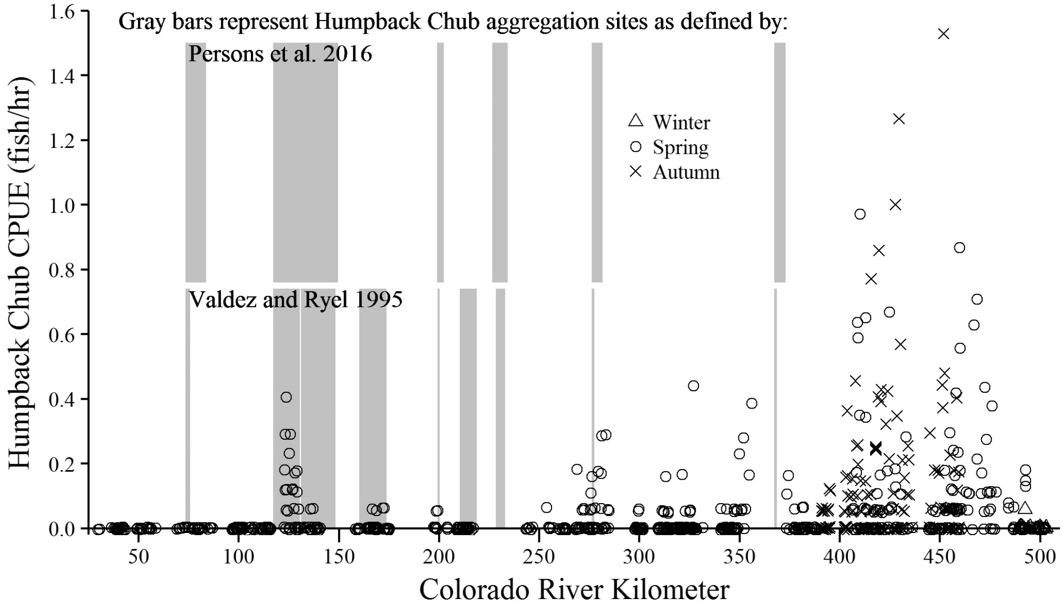

Fig. 3. Humpback Chub catch per unit effort (CPUE; fish/h) for baited hoop nets (n = 775) by river kilometer (rkm) in 2016 and 2017. Points are jittered to show overlapping points. Gray bars show aggregation sites defined by Valdez and Ryel (1995) as modified by Persons et al. (2016). Sample-site points are classified by season: spring (rkm 25.4–503.1), autumn (rkm 389.1–478.3) and winter (rkm 488.9–503.1).

255 of these individuals were ≥200 mm (size cutoff for Humpback Chub population estimates; e.g., Badame 2008, Jackson 2010, Francis et al. 2016). We did not see any evidence that recaptured fish downstream of Diamond Creek originated from upstream areas; all recaptured Humpback Chub (n = 29) in this area were originally tagged below Diamond Creek since 2016 by us on one of our previous trips (fish that were tagged in 2016 and 2017 and recaptured on a later trip are counted as recaptures) or by the U.S. Fish and Wildlife Service (D.R. Van Haverbeke, personal communication, 2017).

In spring 2016 and 2017, within the Little Colorado River aggregation, we captured Humpback Chub in 57% of our nets (16 of 28 nets). Within other aggregations (defined by Valdez and Ryel 1995), Humpback Chub were captured in 12% of nets (8 of 68 nets). Due to our random selection of sample sites, we did not sample all aggregations (Fig. 3). Outside of aggregations, Humpback Chub were captured in 21% of nets (116 of 540 nets). Means and 95% confidence intervals of Humpback Chub hoop-net CPUE were 0.0918 fish/h (0.0667, 0.1233) in the Little Colorado River aggregation, 0.0083 fish/h (0.0040, 0.0155) in all other aggregations, and 0.0356 fish/h (0.03178, 0.0395) in nonaggregation sites. We did not detect any differences in the probability of capturing Humpback Chub (zero-inflated Poisson model with offset for effort in hours: $Z = -1.124$, df = 4, $P = 0.261$) or catch of Humpback Chub ($Z = -1.792$, df = 5, $P = 0.073$) between aggregation sites and nonaggregation sites. Most Humpback Chub captured at aggregation sites were captured in the Little Colorado River aggregation; when the Little Colorado River aggregation was excluded, catch of Humpback Chub was lower at aggregation sites ($Z = -2.549$, df = 4, $P = 0.0108$) than at nonaggregation sites, although there was no difference in the probability of capturing Humpback Chub ($Z = -0.461$, df = 4, $P = 0.645$) between aggregation sites and nonaggregation sites.

DISCUSSION

The Humpback Chub is widely distributed through the Colorado River within Grand Canyon, particularly in western reaches of the canyon. The distribution of Humpback Chub in the Colorado River that we documented in 2016–2017 is broader than that described by

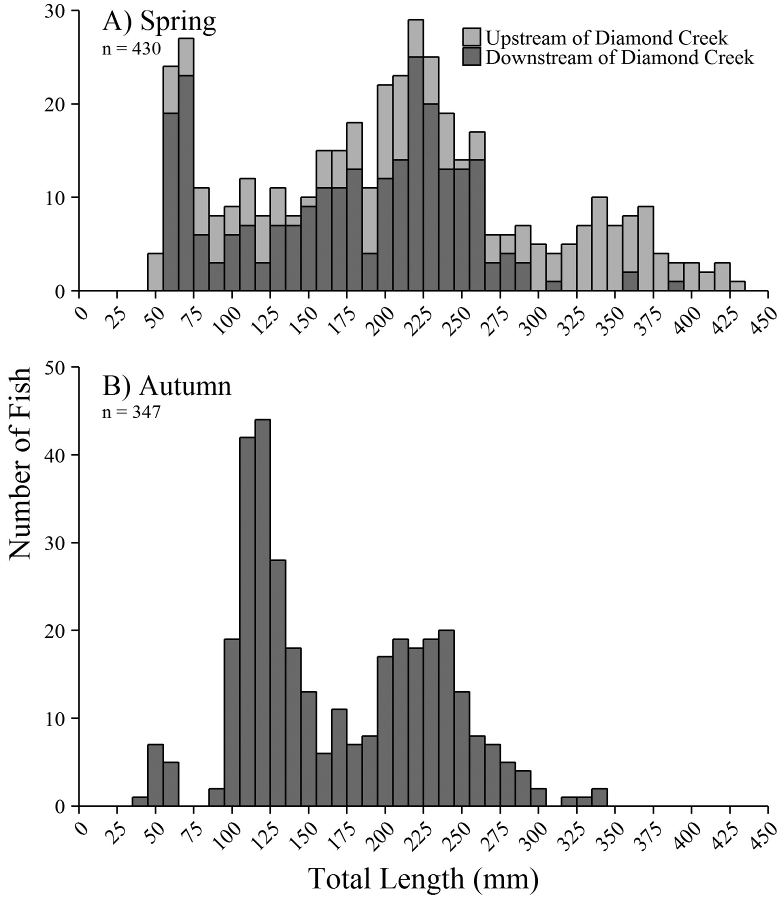

Fig. 4. Length-frequency distribution of all Humpback Chub captured during (A) spring (April and May 2016–2017) and (B) autumn (October 2016–2017) electrofishing and hoop-net surveys on the Colorado River between Lees Ferry and Lake Mead. n = number of fish. Spring surveys covered rkm 0 to 503.1 and autumn surveys covered rkm 389.1 to 478.3.

Valdez and Ryel (1995) and Valdez (1994), suggesting that the Humpback Chub has expanded its range since the early 1990s. We found little concordance between our results and the aggregations that Valdez and Ryel described in 1995, except near the Little Colorado River, where relative abundance of Humpback Chub remains high. No aggregation sites were identified below Diamond Creek (rkm 389.1), as only one Humpback Chub was captured below Diamond Creek at rkm 434 (Valdez 1994). The hydrology in the western Grand Canyon was different in the 1990s compared to current conditions; Lake Mead elevations were higher, and the Colorado River inlet was located at approximately rkm 407 (currently the inlet is at about rkm 503). The distribution of Humpback Chub we observed also did not match the recently updated aggregation areas described by Persons et al. (2016), but those descriptions were based on sampling concentrated on the Little Colorado River and other aggregation areas, with very few samples located between Diamond Creek and the Lake Mead inlet (Persons et al. 2016). We recommend that representative monitoring (i.e., broad spatial coverage and random site selection) from Lees Ferry to Lake Mead is necessary to accurately describe the distribution of Humpback Chub in this area of the Colorado River.

Our hoop-net sampling below Diamond Creek yielded a Humpback Chub CPUE higher than that observed in all other areas of the river. The relatively high density of Humpback Chub below Diamond Creek is likely due to a recent range expansion. Much of the Grand Canyon downstream of Diamond Creek was inundated by Lake Mead (to rkm 407) when the reservoir was at or near full pool, and Humpback Chub typically do not use lentic habitat (Holden and Stalnaker 1975). However, as the elevation of Lake Mead has decreased due to drought in recent years (Udall and Overpeck 2017), the once-buried riverine channel has now been uncovered, resulting in more lotic habitat for Humpback Chub. Concurrently, sampling in this area also increased. Based on our electrofishing catch data and limited data from other studies (Valdez 1994, Valdez and Carothers 1998, Van Haverbeke et al. 2007), it would appear that Humpback Chub use of the Colorado River below Diamond Creek is a fairly recent occurrence. The number of small Humpback Chub captured below Diamond Creek, compared to upstream areas, also suggests a recent range expansion; if fish had occupied this area for a long time, we would have expected more large fish as we find in upstream areas.

The western Grand Canyon appears to provide habitat for all Humpback Chub life stages, including spawning and nursery habitat, particularly below Diamond Creek (rkm 389.1). We captured Humpback Chub of all size classes, including age-0 fish (<100 mm), downstream of Diamond Creek. Furthermore, very few fish captured below Diamond Creek were recaptures, and all recaptured fish in this area were initially captured below Diamond Creek. Humpback Chub in the western Grand Canyon likely remain below Diamond Creek for spawning, and recruitment is occurring in this area. Distances from historical aggregation sites provide additional evidence that Humpback Chub in the western Grand Canyon do not utilize the Little Colorado River or other aggregation sites. Adult Humpback Chub typically have restricted movements (Paukert et al. 2006, Gerig et al. 2014) with larval drift estimated at <9 km (Robinson et al. 1998). This does not negate the fact that some Humpback Chub can and do move large distances (Gorman and Stone 1999, Coggins et al. 2006), and Humpback Chub in the western Grand Canyon may have originated from the Little Colorado River or other upstream areas. Humpback Chub larvae from the Little Colorado River would have to drift 265 km to reach Diamond Creek; thus, Humpback Chub abundance in the western Grand Canyon is likely driven by local spawning and recruitment, not by frequent emigration from upstream populations.

Most of the substrate and channel morphologies below Diamond Creek are not characteristic of typical Humpback Chub habitat, but the relatively higher temperature (compared to upstream reaches) and turbidity in this reach may improve spawning success and juvenile survival. Humpback Chub are more commonly associated with highly constrained canyon-bound reaches (Miller 1946, Holden and Stalnaker 1975). Below Diamond Creek, where the river cuts through sediment deposited in Lake Mead, a wider channel, silt substrate, and cutbank shore habitat are common. Cold water temperatures limit hatching rates and juvenile survival and are thought to be a limiting factor for Humpback Chub in much of the mainstem Colorado River (Yackulic et al. 2014). Water temperatures below Spencer Creek (rkm 450.3; mean 14.4 °C; USGS gauge 09404220) averaged 3.30 °C warmer than at Lees Ferry (rkm 25.4; USGS gauge 09380000) for 2016, and from May through September averaged 5.50 °C warmer (mean at Spencer Creek, 17.0 °C). These warmer water temperatures below Diamond Creek may facilitate successful hatching and rearing of Humpback Chub.

Studies and recovery proposals related to the effects of dam operations on Humpback Chub in the Grand Canyon have focused exclusively on Glen Canyon Dam (e.g., USDOI 1995, 2016), which is upstream of the Grand Canyon population. Our findings demonstrate that downstream water management at Hoover Dam and Lake Mead also influences habitat availability and Humpback Chub distribution. Continued water use in the Lower Colorado River basin coupled with drought lowered the elevation of Lake Mead, thereby increasing the amount of river habitat available in the Grand Canyon and facilitating a range expansion of Humpback Chub.

The presence of a new and potentially large subpopulation of Humpback Chub in the western Grand Canyon is a hopeful development for the recovery of this endangered species. The Grand Canyon population of Humpback Chub is considered healthy and viable, but until recently most individuals in the population occupied a relatively small area (~32 km) of the Colorado River (~475 km available) near the Little Colorado River (Kaeding and Zimmerman 1983, Douglas and

Marsh 1996, Gorman and Stone 1999, Coggins et al. 2006). Geographically restricted populations are vulnerable to localized disturbances (MacArthur and Wilson 1967); the expansion of Humpback Chub into the western Grand Canyon reduces the likelihood that disturbances (e.g., predator invasions, disease, water quality changes) in the Little Colorado River would threaten the persistence of this population. To increase population redundancy and resiliency, the U.S. Fish and Wildlife Service in conjunction with the National Park Service has been translocating Humpback Chub to other tributaries of the Colorado River within the Grand Canyon (Spurgeon et al. 2015). The apparent natural range expansion of Humpback Chub into the western Grand Canyon accomplishes the same recovery plan goal of establishing an additional spawning aggregation (USFWS 2002), thereby improving the resilience of the Humpback Chub population in the Grand Canyon.

Monitoring and population assessments to address progress toward recovery goals (USFWS 2002) have historically focused on the Little Colorado River (e.g., Yackulic et al. 2014) and the aggregation sites (Valdez and Ryel 1995, Persons et al. 2016). Our work, along with others' work (e.g., Persons et al. 2016), indicates that Humpback Chub are utilizing areas of the Colorado River where they have not historically been observed, in numbers equivalent to the aggregation sites. Additionally, we have captured 536 unique Humpback Chub (≥80 mm total length) in hoop nets downstream of Diamond Creek, including 255 Humpback Chub ≥200 mm total length; this number equals or exceeds population estimates for several Upper Colorado River basin areas (Yampa River—Finney 2006; Cataract Canyon—Badame 2008) that are considered critical habitat (USFWS 1994). We recommend continued monitoring of the Colorado River in the western Grand Canyon, including newly exposed riverine areas such as the area below Pearce Ferry Rapid. Future species status assessments and recovery goals should include the western Grand Canyon in order to accurately characterize the Grand Canyon population of Humpback Chub. In addition, the western Grand Canyon of the Colorado River to the inflow at Lake Mead should be considered critical habitat for the Humpback Chub if the population there remains viable.

ACKNOWLEDGMENTS

The Grand Canyon Monitoring and Research Center provided funding for the Arizona Game and Fish Department via the Bureau of Reclamation's Glen Canyon Dam Adaptive Management Program, while the Bureau of Reclamation under the technical representation of Dr. Mark McKinstry provided funding for BIO-WEST, Inc. This material is based on work supported by the U.S. Geological Survey under Cooperative Agreement No. G15AC00166 and Bureau of Reclamation contract number GS-10F-0331S. We thank Ron Kegerries and St. Judes LLC personnel Erica Byerley, Kirk Burnett, Colin Evans, Laura Fallon, Dennis Harris, Nate Jordan, Don Massman, Jason Moore, Mark Perkins, Katie Proctor, Bryan Smith, and Jeremy Swindlehurst. We also thank Carol Fritzinger, Dave Foster, and Seth Felder for coordinating trip schedules and maintaining equipment. Numerous Arizona Game and Fish Department personnel and others volunteered their time to collect these data, and to them our thanks are due. Thanks to Norman Mercado-Silva for translating the abstract into Spanish.

LITERATURE CITED

BADAME, P.V. 2008. Population estimates for Humpback Chub (*Gila cypha*) in Cataract Canyon, Colorado River, Utah, 2003–2005. Utah Division of Wildlife Resources—Moab Field Station, Moab, UT.

COGGINS, L.G., JR. 2008. Active adaptive management for native fish conservation in the Grand Canyon—implementation and evaluation. Doctoral dissertation, University of Florida, Gainesville, FL.

COGGINS, L.G., JR., W.E. PINE III, C.J. WALTERS, D.R. VAN HAVERBEKE, D.L. WARD, AND L. JOHNSTONE. 2006. Abundance and status of the Little Colorado River population of Humpback Chub *Gila cypha.* North American Journal of Fisheries Management 26:233–245.

DOUGLAS, M.E., AND P.C. MARSH. 1996. Population estimates/population movements of *Gila cypha,* an endangered cyprinid fish in the Grand Canyon region of Arizona. Copeia 1996:15.

FINNEY, S. 2006. Adult and juvenile Humpback Chub monitoring for the Yampa River population, 2003–2004. Final Report Project No. 133, U.S. Fish and Wildlife Service, Vernal, UT.

FRANCIS, T.A., K.R. BESTGEN, AND G.C. WHITE. 2016. Population status of Humpback Chub, *Gila cypha,* and catch indices and population structure of sympatric Roundtail Chub, *Gila robusta,* in Black Rocks, Colorado River, Colorado, 1998–2012. Larval Fish Laboratory Contribution 199. Final Report from the U.S. Fish and Wildlife Service to the Upper

Colorado River Endangered Fish Recovery Program, Project Number 131. Grand Junction, CO.

GERIG, B., M.J. DODRILL, AND W.E. PINE. 2014. Habitat selection and movement of adult Humpback Chub in the Colorado River in Grand Canyon, Arizona, during an experimental steady flow release. North American Journal of Fisheries Management 34:39–48.

GORMAN, O.T., AND D.M. STONE. 1999. Ecology of spawning Humpback Chub, *Gila cypha*, in the Little Colorado River, near Grand Canyon, Arizona. Environmental Biology of Fishes 55:115–133.

HOLDEN, P.B., AND C.B. STALNAKER. 1975. Distribution of fishes in the Dolores and Yampa river systems of the Upper Colorado Basin. Southwestern Naturalist 19:403.

JACKSON, J. 2010. Population estimate for Humpback Chub (*Gila cypha*) and Roundtail Chub (*Gila robusta*) in Westwater Canyon, Colorado River, Utah 2003–2005. Utah Division of Wildlife Resources, Final Report, Moab, UT.

KAEDING, L.R., AND M.A. ZIMMERMAN. 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.

KEGERRIES, R., B. ALBRECHT, E.I. GILBERT, W.H. BRANDENBURG, A.L. BARKALOW, H. MOHN, R. ROGERS, M. MCKINSTRY, B. HEALY, J. STOLBERG, ET AL. 2016. Razorback Sucker *Xyrauchen texanus* research and monitoring in the Colorado River inflow area of Lake Mead and the lower Grand Canyon, Arizona and Nevada. Final report prepared by BIO-WEST, Inc., for the U.S. Bureau of Reclamation, Upper Colorado Region, Salt Lake City, UT.

MACARTHUR, R.H., AND E.O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

MELIS, T.S., EDITOR. 2011. Effects of three high-flow experiments on the Colorado River ecosystem downstream from Glen Canyon Dam, Arizona. Circular 1336, U.S. Geological Survey, Reston, VA.

MILLER, R.R. 1946. *Gila cypha*, a remarkable new species of cyprinid fish from the Colorado River in Grand Canyon, Arizona. Journal of the Washington Academy of Sciences 36:409–415.

MINCKLEY, C.O. 1996. Observations on the biology of Humpback Chub in the Colorado River Basin 1980–1990. Doctoral dissertation, Northern Arizona University, Flagstaff, AZ.

PAUKERT, C.P. 2004. Comparison of electrofishing and trammel netting variability for sampling native fishes. Journal of Fish Biology 65:1643–1652.

PAUKERT, C.P., L.G. COGGINS JR, AND C.E. FLACCUS. 2006. Distribution and movement of Humpback Chub in the Colorado River, Grand Canyon, based on recaptures. Transactions of the American Fisheries Society 135:539–544.

PERSONS, W.R., D.R. VAN HAVERBEKE, AND M.J. DODRILL. 2016. Colorado River fish monitoring in Grand Canyon, Arizona; 2002–14 Humpback Chub aggregations. USGS Numbered Series 2016–1177, U.S. Geological Survey, Reston, VA.

PERSONS, W.R., D.L. WARD, AND L.A. AVERY. 2015. Standardized methods for Grand Canyon fisheries research 2015 [ver. 1.1, January 2015]. U.S. Geological Survey, Techniques and Methods, Book 2, Chapter A12.

ROBINSON, A.T., R.W. CLARKSON, AND R.E. FORREST. 1998. Dispersal of larval fishes in a regulated river tributary. Transactions of the American Fisheries Society 127:772–786.

ROGOWSKI, D.L., R.J. OSTERHOUDT, L.K. WINTERS, AND P.N. WOLTERS. 2016. Colorado River fish monitoring in the Grand Canyon, Arizona—2015. Arizona Game and Fish Department, Annual Report to the Grand Canyon Monitoring and Research Center, Flagstaff, AZ.

ROGOWSKI, D.L., P.N. WOLTERS, AND L.K. WINTERS. 2015. Colorado River fish monitoring in the Grand Canyon, Arizona—2014. Annual Report to the Grand Canyon Monitoring and Research Center, Flagstaff, AZ.

SCHMIDT, J.C., AND J.B. GRAF. 1990. Aggradation and degradation of alluvial sand deposits, 1965–1986, Colorado River, Grand Canyon National Park, Arizona. U.S. Geological Survey Professional Paper 1493, U.S. Geological Survey, Denver, CO.

SCHMIDT, J.C., R.A. PARNELL, P.E. GRAMS, J.E. HAZEL, M.A. KAPLINSKI, L.E. STEVENS, AND T.L. HOFFNAGLE. 2001. The 1996 controlled flood in Grand Canyon: flow, sediment transport, and geomorphic change. Ecological Applications 11:657–671.

SPURGEON, J.J., C.P. PAUKERT, B.D. HEALY, M. TRAMMELL, D. SPEAS, AND E. OMANA-SMITH. 2015. Translocation of Humpback Chub into tributary streams of the Colorado River: implications for conservation of large-river fishes. Transactions of the American Fisheries Society 144:502–514.

STONE, D.M. 2005. Effect of baiting on hoop net catch rates of endangered Humpback Chub. North American Journal of Fisheries Management 25:640–645.

TOPPING, D.J., J.C. SCHMIDT, AND L.E. VIERRA. 2003. Computation and analysis of the instantaneous-discharge record for the Colorado River at Lees Ferry, Arizona—May 8, 1921, through September 30, 2000. Professional Paper 1677, U.S. Geological Survey, Reston, VA.

UDALL, B., AND J. OVERPECK. 2017. The twenty-first century Colorado River hot drought and implications for the future. Water Resources Research 53:2404–2418.

[USDOI] UNITED STATES DEPARTMENT OF THE INTERIOR, BUREAU OF RECLAMATION. 1995. Operation of Glen Canyon Dam, Colorado River Storage Project, Arizona: Final Environmental Impact Statement. U.S. Department of the Interior, Bureau of Reclamation, Salt Lake City, UT.

[USDOI] UNITED STATES DEPARTMENT OF THE INTERIOR. 2016. Glen Canyon Dam Long-Term Experimental and Management Plan Final Environmental Impact Statement: U.S. Department of the Interior, Bureau of Reclamation, Salt Lake City, Utah, and National Park Service, Lakewood, Colorado.

[USFWS] UNITED STATES FISH AND WILDLIFE SERVICE. 1994. Determination of critical habitat for the Colorado River endangered fishes: Razorback Sucker, Colorado Squawfish, Humpback Chub, and Bonytail Chub. Federal Register 59:13374–13400.

[USFWS] UNITED STATES FISH AND WILDLIFE SERVICE. 2002. Humpback Chub (*Gila cypha*) recovery goals: amendment and supplement to the Humpback Chub Recovery Plan. U.S. Fish and Wildlife Service, Mountain-Prairie Region (6), Denver, CO.

VALDEZ, R.A. 1994. Effects of interim flows from Glen Canyon Dam on the aquatic resources of the lower

Colorado River from Diamond Creek to Lake Mead. Phase I Report to Hualapai Natural Resources Department by BIO-WEST, Inc., Logan, UT.

VALDEZ, R.A., AND S.W. CAROTHERS. 1998. The aquatic ecosystem of the Colorado River in Grand Canyon: Grand Canyon data integration project synthesis report. Final Report to U.S. Bureau of Reclamation, Upper Colorado Region, Salt Lake City, Utah, by SWCA, Inc., Environmental Consultants, Flagstaff, AZ.

VALDEZ, R.A., AND R.J. RYEL. 1995. Life history and ecology of the Humpback Chub (*Gila cypha*) in the Colorado River, Grand Canyon, Arizona. Bureau of Reclamation, Final Report to Bureau of Reclamation, BIO-WEST Report No. TR-250-08. Salt Lake City, UT.

VAN HAVERBEKE, D.R., R.S. ROGERS, M.V. LAURETTA, AND K. CHRISTENSEN. 2007. 2005 Grand Canyon long-term fish monitoring. Colorado River, Diamond Creek to Lake Mead. Final Report to U.S. Geological Survey Grand Canyon Monitoring and Research Center.

VAN HAVERBEKE, D.R., D.M. STONE, L.G. COGGINS, AND M.J. PILLOW. 2013. Long-term monitoring of an endangered desert fish and factors influencing population dynamics. Journal of Fish and Wildlife Management 4:163–177.

YACKULIC, C.B., M.D. YARD, J. KORMAN, AND D.R. VAN HAVERBEKE. 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.

ZEILEIS, A., C. KLEIBER, AND S. JACKMAN. 2008. Regression models for count data in R. Journal of Statistical Software 27(8):1–25.

ZUUR, A., E.N. IENO, N. WALKER, A.A. SAVELIEV, AND G.M. SMITH. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY.

Received 29 June 2017
Revised 20 December 2017
Accepted 12 January 2018
Published online 27 March 2018