Western North American Naturalist 80(2), © 2020, pp. 146–156

Small-bodied fish surveys demonstrate native fish dominance over 300 kilometers of the Colorado River through Grand Canyon, Arizona

Ron B. Kegerries[1,*], Brandon Albrecht[1], Mark C. McKinstry[2], Ron J. Rogers[1], Richard A. Valdez[3], Adam L. Barkalow[4], Eliza I. Gilbert[5], Harrison E. Mohn[1], Brian Healy[6], and Emily Omana Smith[2]

[1]*BIO-WEST, Inc., Logan, UT 84321*
[2]*U.S. Bureau of Reclamation, Upper Colorado Region, Salt Lake City, UT 84138*
[3]*SWCA Environmental Consultants, Logan, UT 84321*
[4]*American Southwest Ichthyological Researchers, LLC, Albuquerque, NM 87102*
[5]*U.S. Fish and Wildlife Service, New Mexico Ecological Services Field Office, Albuquerque, NM 87113*
[6]*National Park Service, Grand Canyon National Park, Flagstaff, AZ 86001*

Abstract.—The Colorado River in Grand Canyon is highly regulated, with hypolimnetic releases that are generally unfavorable for endemic native fishes. However, both long-term drought and changes in dam operations have led to changes in river conditions, including the addition of approximately 125 km of riverine environment due to the contraction of Lake Mead. Through sampling of small-bodied fish, we were able to describe the Grand Canyon fish community and define the current native fish distribution from near Bright Angel Creek downstream to Pearce Ferry. Beginning in 2014 and continuing through 2018, we sampled the fish community via seining and documented a fish community that was dominated (>95%) by native fish through approximately 300 km of river. Nonnative species that were once commonly captured, such as Red Shiner *Cyprinella lutrensis,* Common Carp *Cyprinus carpio*, and Channel Catfish *Ictalurus punctatus*, were rarely encountered in Grand Canyon during this more recent sampling, which makes the Colorado River in Grand Canyon National Park a rare contemporary example of native fish populations regaining dominance over invasive fishes in the desert southwest.

Resumen.—El Río Colorado en el Gran Cañón es un río altamente regulado con liberaciones hipolimnéticas que generalmente no son favorables para los peces nativos endémicos. Sin embargo, la sequía a largo plazo y los cambios en las operaciones de las represas han provocado cambios en las condiciones de los ríos, que incluyen la adición de aproximadamente 125 km de ambiente ribereños debido a la contracción del Lago Mead. Mediante una muestra de peces de cuerpo pequeño, pudimos describir la comunidad de peces del Gran Cañón y definir la distribución actual de peces nativos desde cerca de Bright Angel Creek río abajo hasta Pearce Ferry. A partir de 2014 y hasta 2018, tomamos muestras de la comunidad de peces a través de un cerco y documentamos una comunidad de peces (>95%) dominada por peces nativos a través de aproximadamente 300 kilómetros de río. Las especies no nativas como Red Shiner *Cyprinella lutrensis*, Common Carp *Cyprinus carpio* y Channel Catfish *Ictalurus punctatus*, que una vez se capturaron comúnmente, rara vez se encontraron en el Gran Cañón durante este muestreo más reciente, lo que convirtió al Río Colorado en el Parque Nacional del Gran Cañón sea un raro y contemporáneo ejemplo en el que las poblaciones de peces nativos han recuperado el dominio sobre los peces invasores no nativos en el desierto del suroeste.

Historically, the Colorado River basin included 35 fish species within 22 genera and 11 families (Miller 1959), and 23 of those species could be found within the mainstem Colorado River (Jordan 1891, Evermann and Rutter 1894, Woodbury 1959, McDonald and Dotson 1960, Stone and Rathbun 1968, Holden and Stalnaker 1975, Suttkus et al. 1976, Minckley and Blinn 1976, Carothers and Minckley 1981, Kaeding and Zimmerman 1983, Miller and Smith 1984, Maddux et al. 1988). More specifically, 8 species from 5 genera and 2 families were found within the Grand Canyon reach of the Colorado River

*Corresponding author: rkegerries@bio-west.com

RBK orcid.org/0000-0001-6166-3906 RAV orcid.org/0000-0002-2067-8500 ALB orcid.org/0000-0002-0444-0463
EIG orcid.org/0000-0003-0426-4065 BH orcid.org/0000-0002-4402-638X

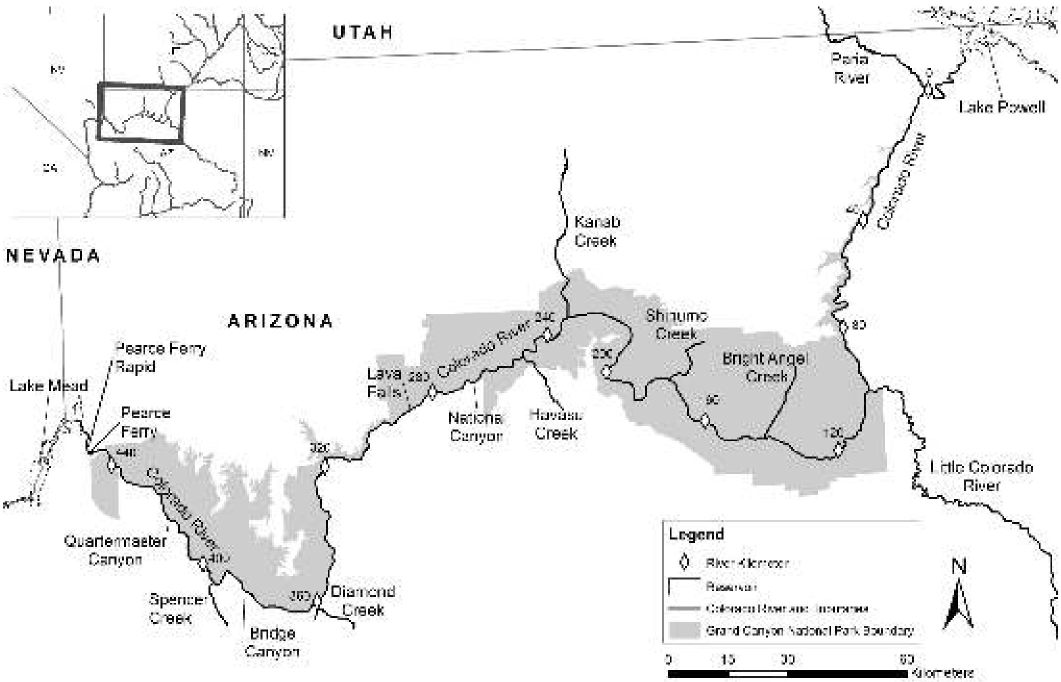

Fig. 1. Colorado River and notable tributaries, as well as reference points from Glen Canyon Dam to Lake Mead (Grand Canyon).

(Valdez and Carothers 1998). Valdez and Carothers (1998) provided a detailed review of fish surveys and data collected from the early 1800s through the mid-1990s; it described the Grand Canyon fish assemblage before 1850 as consisting of Humpback Chub *Gila cypha*, Bonytail *Gila elegans*, Roundtail Chub *Gila robusta*, Colorado Pikeminnow *Ptychocheilus lucius*, Speckled Dace, *Rhinichthys osculus*, Flannelmouth Sucker *Catostomus latipinnis*, Bluehead Sucker *Catostomus discobolus*, and Razorback Sucker *Xyrauchen texanus*.

Shifts in the Colorado River fish assemblage began in the early 1900s, following introductions of nonnative fishes and alterations of the riverine environments due to water development (Gloss et al. 2005). In the early 1900s, Rainbow Trout *Oncorhynchus mykiss* and Brown Trout *Salmo trutta* were introduced into spring-fed Colorado River tributaries within Grand Canyon National Park as sportfish (Williamson and Tyler 1932). After the creation of Lake Mead by Hoover Dam in 1935, other nonnative fishes were stocked in the reservoir for sport, bait, and forage (Hubbs 1954, Valdez and Carothers 1998). Upstream travel of nonnative fishes from the reservoir led to drastic changes in the Grand Canyon fish community. Fish surveys within Glen Canyon and Grand Canyon following the closure of Glen Canyon Dam (1963) reported a total of 36 species, of which 8 were native. By the 1990s, 18 nonnative species were present in Grand Canyon, mostly because of federally and state-sponsored nonnative fish stockings (Miller 1961, Carothers and Brown 1991, Minckley et al. 1991, Quartarone 1993, Valdez and Carothers 1998). During this time, the most notable fish community change was the increase of salmonid species in the colder Glen Canyon Dam tailwaters and in Grand Canyon spring-fed tributaries (Valdez and Carothers 1998).

Fish sampling in Grand Canyon has been disjunct, nonrandom, and primarily tied to specific research projects, especially those for Humpback Chub. Fish community sampling efforts from 1990 to 1993 focused on describing the Humpback Chub population within Grand Canyon from Lees Ferry (RKM 0.0) to Diamond Creek (RKM 364.0) (Valdez and Ryel 1997) (Fig. 1). Sampling from 1992 to 1995 occurred from Diamond Creek (RKM 364.0) to below Pearce Ferry (RKM 460.3) to

TABLE 1. Colorado River native and nonnative fish species present in studies from 1990 to 2018 throughout the Colorado River in Grand Canyon.

Species	Scientific name	1990–1993[a]	1992–1995[b]	2004–2006[c]	2006[d]	2014–2018
Bluehead Sucker	*Catostomus discobolus*	X	X	X	X	X
Flannelmouth Sucker	*Catostomus latipinnis*	X	X	X	X	X
Humpback Chub	*Gila cypha*	X	X	X	X	X
Speckled Dace	*Rhinichthys osculus*	X	X	X	X	X
NATIVE SPECIES COUNT		4	4	4	4	4
Black Bullhead	*Ameiurus melas*	X	X		X	
Black Crappie	*Pomoxis nigromaculatus*		X			
Bluegill	*Lepomis macrochirus*		X	X		
Brook Trout	*Salvelinus fontinalis*	X				
Brown Trout	*Salmo trutta*	X			X	X
Channel Catfish	*Ictalurus punctatus*	X	X	X	X	
Common Carp	*Cyprinus carpio*	X	X	X	X	X
Fathead Minnow	*Pimephales promelas*	X	X	X	X	X
Golden Shiner	*Notemigonus crysoleucas*		X			
Green Sunfish	*Lepomis cyanellus*	X	X	X	X	X
Largemouth Bass	*Micropterus salmoides*		X			
Plains Killifish	*Fundulus zebrinus*	X	X	X	X	X
Rainbow Trout	*Oncorhynchus mykiss*	X	X	X	X	X
Red Shiner	*Cyprinella lutrensis*		X	X	X	X
Smallmouth Bass	*Micropterus dolomieu*			X		
Striped Bass	*Morone saxatilis*	X	X	X		
Threadfin Shad	*Dorosoma petenense*		X	X		
Walleye	*Sander vitreus*	X	X			
Western Mosquitofish	*Gambusia affinis*		X	X		X
NONNATIVE SPECIES COUNT		11	16	12	9	8

[a]Valdez and Ryel (1997)
[b]Valdez et al. (1995)
[c]Ackerman et al. (2006)
[d]Ackerman (2008)

assess the effects of interim flows on aquatic resources from the operation of Glen Canyon Dam (Valdez et al. 1995). As part of long-term fish monitoring efforts in 2004–2006, Ackerman et al. (2006) sampled between Diamond Creek (RKM 363.7) and the Grand Canyon National Park boundary (RKM 445.0). Sampling in 2006 from Lees Ferry (RKM 0) to Diamond Creek (RKM 354.0) occurred during native fish monitoring activities in Grand Canyon (Ackerman 2008). All of these studies noted the presence of the same 4 native fish species as well as 9–12 nonnative species (Table 1). Although other fish community monitoring studies have occurred or are ongoing in the Grand Canyon (e.g., Persons et al. 2017, Rogowski and Boyer 2019), we limited our comparisons to those that used at least some seining in a variety of habitat types to target small-bodied fish.

Hypolimnetic releases from Glen Canyon Dam have stabilized water temperatures in the Colorado River and lowered maximum water temperatures. Cooler water temperatures likely hinder native fish reproduction, growth, and survival (Clarkson and Childs 2000). Flow regulation has reduced annual peak flows, raised minimum flows, and increased the daily flow fluctuation through hydropower operations (Topping et al. 2003, Voichick and Wright 2007); all of these things may be detrimental to the Grand Canyon fish community, especially in the early life stages of the fishes (Clarkson and Childs 2000, Bunn and Arthington 2002, Bestgen 2008). Mainstem water temperatures that once ranged from 0 °C to more than 30 °C are now dictated by hypolimnetic water that is released through Glen Canyon Dam and which is limited to a temperature range of 7.2 °C to 12.2 °C when Lake Powell is at full pool. During low reservoir elevations in 2005, the maximum daily mean release temperature increased to 16.1 °C (Ross and Vernieu 2013). The release of hypolimnetic water has also reduced turbidity within the river, which likely favors nonnative sight predators like trout over native fishes, which are adapted to turbid river conditions (Valdez and Ryel 1997, Gloss et al. 2005, Yard et al. 2011, Ward and Vaage 2019). Anthropomorphic changes can impact native species reproduction, growth, and survival; however, Bluehead Sucker, Flannelmouth Sucker, Humpback Chub, and Speckled Dace have all persisted within the Colorado River in the Grand Canyon (Kegerries et al. 2017) despite significant alterations in hydrograph (Schmidt et al. 2001), temperature regime (Ross and Vernieu 2013), food resources (Kennedy et al. 2016), and turbidity (Ward et al. 2016).

In our study, we sampled small-bodied fish from 2014 through 2018 with the primary goal of investigating the presence, reproduction, and subsequent recruitment of the fish community within Grand Canyon from RKM 142.4 (near Bright Angel Creek) downstream to RKM 449.0 (just above Pearce Ferry). Herein, we describe the current Grand Canyon fish community and define present-day native fish distribution through this reach of the Colorado River, based on our seining data. We used these results to infer temporal changes that appear to have occurred within the fish community under varying river conditions.

METHODS

In 2014 and 2015, we sampled small-bodied (age-0+) fishes via seining in Grand Canyon from RKM 288.0, just upstream of Lava Falls, downstream to Pearce Ferry near RKM 449.0 (Fig. 1). Larval fish (protolarvae, mesolarvae, or metalarvae) capture results from the first 2 years of the study indicated that native fish spawn upstream of the study area. Thus, we extended the study area 146 km upstream to near the Bright Angel Creek confluence (RKM 142.4) beginning in 2016.

We selected fish sampling segments using a generalized random tessellation stratified (GRTS) design to maintain an unbiased probability of sampling in rivers that support diverse habitats (Stevens and Olsen 1999, 2003, 2004). We established forty 800-m segments in 2014 and 2015 and fifty-six 800-m segments for the extended study area in 2016–2018, with specific sites within segments that were sampled (seined) during each trip. Results from 2014 and 2015 were included in our analyses despite the truncated study area because it is our opinion that there is sufficient overlap in the 2 study areas, and the GRTS design promotes unbiased sampling.

For sampling, we used a double-weighted seine with dimensions of either 4.6 m × 1.2 m × 3.0 mm or 3.0 m × 1.2 m × 3.0 mm, depending on habitat type and river conditions. At each of the sampling segments, we selected a sampling site where up to 10 seine hauls were conducted within various habitat types. The length of each seine haul was measured with a goal of 10 m per haul. We sampled various habitat types that characterized the diversity of habitats available at each site. The gear type typically limited sampling to habitats shallower than 2.0 m and habitats with 0 or relatively low water velocity.

At each seining location, habitat type and area sampled (length [m] × width [m]) were recorded. All fish collected were identified to species and counted. To keep within trip constraints, yet to allow for an understanding of length distribution, at least 5 randomly selected individuals of each species captured per seine haul were measured for total length (TL) in millimeters (with the exception of Humpback Chub), all of which were measured when captured.

The number of fish collected by species was divided by the area of each seine haul to generate catch per unit effort (CPUE), expressed as the number of fish per meter squared (fish/m^2). Those data were examined by total catch (all fishes) or by species, as well as spatially (segment) and temporally (trip). Catch-rate data were used to track proportional changes in native and nonnative fishes throughout the study area through time. To allow for comparisons to previous studies, the data were also analyzed by river reach above and below Diamond Creek. Similar analyses were conducted for reaches above and below Lava Falls Rapid (RKM 289.4) and Havasu Creek (RKM 253.1).

Since nonnormality is common with data sets related to low-density species, catch-rate data were analyzed using the Shapiro–Wilk test for normality. If residuals were found to be nonnormally distributed ($P \leq 0.05$), the data were transformed ($\ln[1 + \text{CPUE}]$). An analysis of variance (ANOVA) was then used to test for differences in mean $\ln(1 + \text{CPUE})$, following recommendations of Hubert and Fabrizio (2007). When significant differences were found, a Tukey's HSD analysis was performed for all

TABLE 2. The number of fish by species captured in the Colorado River, Grand Canyon, 2014–2018. Parentheses denote percent abundance.

Common name	Scientific name	2014	2015	2016	2017	2018
Native						
Bluehead Sucker	*Catostomus discobolus*	1085 (9.16)	340 (4.99)	1688 (19.9)	2750 (7.16)	1862 (9.32)
Flannelmouth Sucker	*Catostomus latipinnis*	4353 (36.8)	2382 (34.9)	2899 (69.2)	26,598 (69.2)	12,128 (60.7)
Humpback Chub	*Gila cypha*	79 (0.67)	219 (3.21)	62 (0.73)	791 (2.06)	257 (1.29)
Speckled Dace	*Rhinichthys osculus*	5062 (42.7)	2549 (37.4)	2989 (19.8)	7592 (19.8)	5249 (26.3)
TOTAL		10,579 (89.3)	5490 (80.5)	7638 (90.2)	37,731 (98.2)	19,496 (97.6)
Nonnative						
Brown Trout	*Salmo trutta*				1 (<0.01)	9 (0.05)
Common Carp	*Cyprinus carpio*	4 (0.03)	10 (0.15)		2 (0.01)	4 (0.02)
Fathead Minnow	*Pimephales promelas*	1190 (10.0)	1133 (16.6)	146 (1.72)	349 (0.91)	238 (1.19)
Plains Killifish	*Fundulus zebrinus*	13 (0.11)	14 (0.21)	9 (0.11)	54 (0.14)	74 (0.37)
Green Sunfish	*Lepomis cyanellus*	—	—	—	—	1 (0.01)
Western Mosquitofish	*Gambusia affinis*	7 (0.06)	97(1.42)	570 (6.73)	144 (0.37)	53 (0.27)
Red Shiner	*Cyprinella lutrensis*	49 (0.41)	75 (1.10)	104 (1.23)	128 (0.33)	74 (0.37)
Rainbow Trout	*Oncorhynchus mykiss*	3 (0.03)		3 (0.04)	9 (0.02)	23 (0.12)
TOTAL		1266 (10.7)	1329 (19.5)	832 (9.82)	687 (1.79)	476 (2.38)

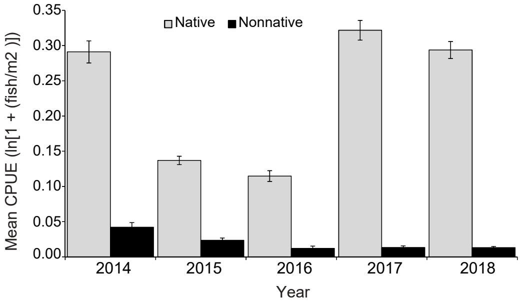

Fig. 2. Mean native and nonnative fish catch per unit effort (CPUE) (ln[1 + (fish/m²)]) by sampling year, Colorado River, Grand Canyon, 2014–2018. Error bars represent ±1 SE.

TABLE 3. Mean catch per unit effort (CPUE) (ln[1 + (fish/m²)]) for native and nonnative fish, Colorado River, Grand Canyon, 2014–2018; results of ANOVA testing ($\alpha \leq 0.05$).

Year	Mean CPUE (ln[1 + (fish/m²)]) Native	Nonnative	F	P
2014	0.291	0.042	215	<0.0001
2015	0.137	0.024	279	<0.0001
2016	0.115	0.012	152	<0.0001
2017	0.322	0.013	476	<0.0001
2018	0.294	0.013	538	<0.0001
COMBINED	0.231	0.019	1562	<0.0001

pairwise comparisons to differentiate homogeneous groups. For all tests, we used an alpha level of 0.05 to test for significance.

RESULTS

Our small-bodied fish sampling between 2014 and 2015, from near Lava Falls downstream to Pearce Ferry, and sampling between 2016 and 2018, from near Bright Angel Creek downstream to Pearce Ferry, yielded 12 total fish species, including 4 native species (Table 2). We captured Bluehead Sucker, Flannelmouth Sucker, Humpback Chub, and Speckled Dace in each year. Nonnative species richness ranged from 5 to 8 species (Table 1). Annual proportional abundance of native species ranged from 80.5% to 98.2% and contrasted with a nonnative proportional abundance that never exceeded 19.5% for any sampling year. Speckled Dace and Flannelmouth Sucker dominated our native fish catch in each year, whereas Fathead Minnow was the most proportionally

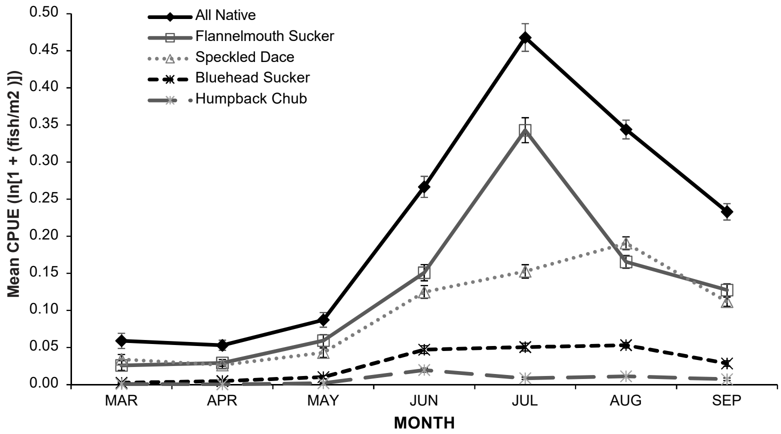

Fig. 3. Mean native fish catch per unit effort (CPUE = ln[1 + (fish/m^2)]) (combined and separated by species) by sampling trip for all years, Colorado River, Grand Canyon, 2014–2018. Error bars represent ±1 SE.

abundant nonnative species. In the reach above Diamond Creek, native fish represented 69.6% of the total catch, whereas native fish increased to 80.3% of the total catch below Diamond Creek for the 5-year study period.

Mean native fish catch rates were significantly higher than nonnative catch rates for all years sampled (Fig. 2, Table 3). For the 5-year period 2014–2018, mean native fish catch rates for 2015 and 2016 were significantly lower than for the other 3 years (ANOVA: $F_{4,8171}$ = 758, P < 0.0001, Tukey's HSD). During the same 5-year period, mean nonnative catch rates were different and higher only in 2014 (ANOVA: $F_{4,8169}$ = 11.9, P < 0.0001, Tukey's HSD).

We performed an analysis of mean catch rates by native species and by sampling trip to identify temporal differences in the native fish captured (Fig. 3). We found native species at significantly higher capture rates in June, July, August, and September (ANOVA: $F_{6,8167}$ = 140, P < 0.0001, Tukey's HSD). Mean catch rates in March, April, and May showed no significant differences among the number of native species captured (Fig. 3). Flannelmouth Sucker and Speckled Dace dominated the native fish species captured; however, we captured Bluehead Sucker and Humpback Chub during all sampling months in lower relative abundance.

Although our native fish catch rates differed among sampling segments in 2014–2018 (ANOVA: $F_{97,8076}$ = 9.68, P < 0.0001; Fig. 4), a pairwise comparison showed no clear pattern or indication that catch rates differed significantly from upstream to downstream. To better assess mean catch rates longitudinally and relate the current data to previous studies, we compared mean catch rates in 2014–2018 above and below Diamond Creek, above and below Lava Falls, and above and below Havasu Creek (Fig. 1). We found mean native fish catch rates below Diamond Creek to be significantly higher than those above (ANOVA: $F_{1,8172}$ = 150, P < 0.0001). We also compared mean catch rates in segments from above Lava Falls and Havasu Creek versus below, using the 2014–2018 data set. We found that mean catch rates for native fish were significantly higher in the mainstem Colorado River below Lava Falls (ANOVA: $F_{1,8172}$ = 265, P < 0.0001) and below Havasu Creek (ANOVA: $F_{1,8172}$ = 256, P < 0.0001) than above either.

Discussion

Our sampling showed significant dominance by native fish throughout our study area. Proportional dominances of 80% to 98% for native fish are unheard of in the rest of the mainstem Colorado River (Minckley and Deacon 1991) and are unexpected in Grand Canyon given the influence of hydropower generation on flows and temperatures. Furthermore, dominance by native fish increased downstream in our study, even with the presence of Lake Mead, a large reservoir known

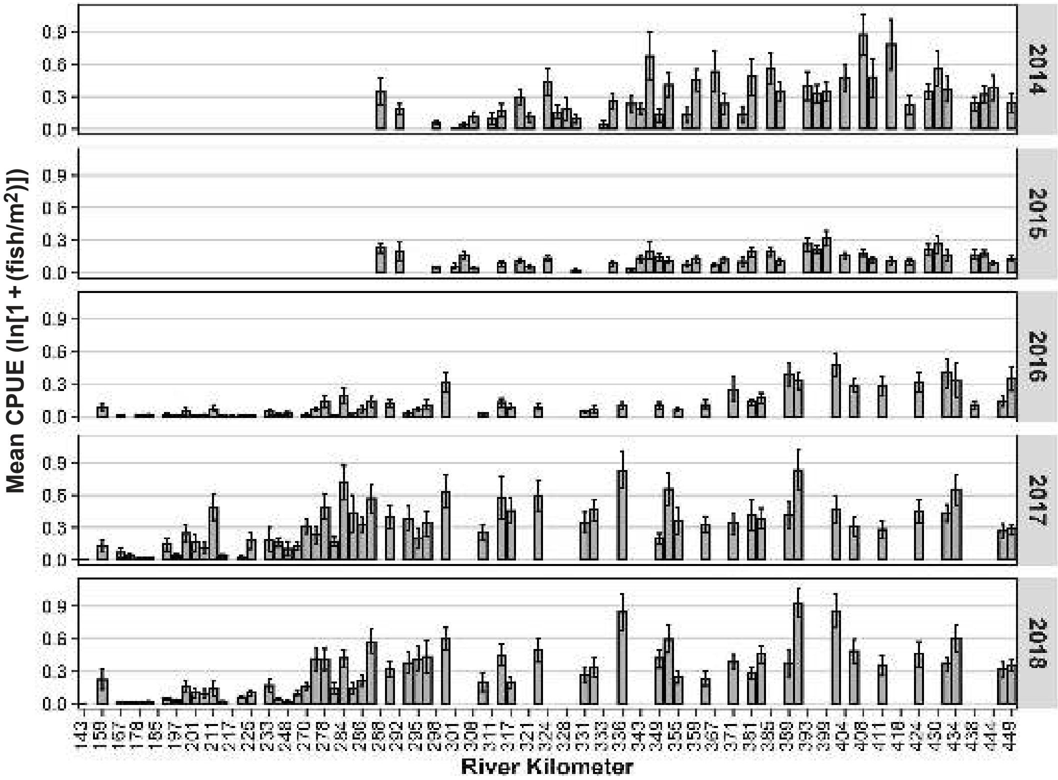

Fig. 4. Mean native fish catch per unit effort (CPUE) (ln[1 + (fish/m^2)]) by sampling year and river kilometer (RKM), Colorado River, Grand Canyon, 2014–2018. Error bars represent ±1 SE.

to harbor nonnative fish. While the native fish community was dominated by 3 species, we still documented 4 of the original 8 species that were found there in the 1800s, and Kegerries et al. (2017) documented a fifth, Razorback Sucker, through larval fish surveys. Additionally, Humpback Chub appear to be expanding their range, and their population within the Grand Canyon is the largest known in the Colorado River basin (Rogowski et al. 2018).

When we compared data presented by Valdez and Ryel (1997)—which included fishes collected using gill nets, trammel nets, hoop nets, minnow traps, electrofishing, and seining between 1990 and 1993—with our seining data (2014–2018) and restricted comparisons to where our study areas overlapped, the same 4 native species were captured, but we found them in higher proportions. Our seining work was limited to riffles, runs, pools, backwaters, embayments, eddies, slackwaters, and shoals <2 m deep, whereas sampling by others included techniques that sampled deeper habitats. However, we feel our results accurately reflect the composition of the fish community in Grand Canyon since we were sampling younger and smaller fish that prefer these shallower habitats. Most native fish captures reported in Valdez and Ryel (1997) were above Diamond Creek, with Flannelmouth Sucker, Bluehead Sucker, and Humpback Chub captured primarily upstream of Havasu Creek. Native fishes were captured more commonly in our 2014–2018 study downstream of Mohawk Canyon (RKM 275.8) and especially downstream of Spencer Creek (RKM 395.9). In 2014–2018, Humpback Chub were also more common and were captured throughout the study area. Nonnative species were more plentiful in 1990–1991, with Rainbow Trout and Brown Trout captured in the upper reaches of the study area where few trout were captured in 2014–2018. The catch rates of many species such as Brown Trout, Common Carp *Cyprinus carpio*, Largemouth Bass *Micropterus salmoides*, and Red Shiner

Cyprinella lutrensis, increased downstream, especially below Diamond Creek in 1990–1993.

In sampling efforts below Diamond Creek in 1992–1995 (Valdez et al. 1995), native fish were not common throughout the study reach and represented only 13% of the total catch. Species such as centrarchids and Threadfin Shad *Dorosoma petenense* became more prevalent downstream and closer to Lake Mead. It should be noted that the elevation of Lake Mead was approximately 30 m higher in 1992–1995 than it was in 2014–2018, and a lotic rather than lentic environment was sampled for the same areas in our study compared with the earlier studies. Due to the declining surface elevations of Lake Mead, the Colorado River in western Grand Canyon changed from a mostly lentic environment below Bridge Canyon (RKM 378.4) in the late 1990s and early 2000s to a mostly lotic environment, adding approximately 125 km of flowing river. Additionally, Pearce Ferry Rapid has formed through a process of superimposition near the inflow area to Lake Mead (Martin and Whitis 2013) and may form a barrier to upstream movement of both native and nonnative fishes. Regardless, the current riverine conditions below Bright Angel Creek appear beneficial to native fishes in Grand Canyon.

Sampling from Lees Ferry to Diamond Creek in 2002 through 2006 (Ackerman 2008) documented 13 species (Table 1), 4 of which were native. Among the 3 sampling methods used (trammel netting, hoop netting, and seining), native fish abundance ranged from 66.2% to 77.3% of the total catch, the majority being Flannelmouth Sucker. Below Diamond Creek, Ackerman et al. (2006) documented 16 fish species, 4 of which were native (Table 1). Native abundance varied by sampling method, with hoop netting capturing nearly 50% native fish. Electrofishing and trammel netting yielded approximately 25% native fish, and seining yielded only about 4% native fish, most of which consisted of Flannelmouth Sucker. The capture of higher proportions of nonnative fish in seines in previous studies supports our assumption that seining is an effective technique for sampling these species at early life stages, and demonstrates that it is unlikely that we missed any species in our sampling. Furthermore, elsewhere in the river basin, seining has been demonstrated as an effective technique for capturing all species of fish that inhabit a southwestern river (Gido and Propst 2012, Franssen and Durst 2014, Franssen et al. 2015).

Despite the different sampling methods and their limitations, an examination of the species composition in western Grand Canyon through time depicts a shift to a fish community dominated by native species that happened within almost 3 decades. Perhaps most notable is the dominance of native fish below Diamond Creek, where Red Shiner, Common Carp, and Channel Catfish *Ictalurus punctatus* once dominated the fish community through the mid-2000s (Valdez et al. 1995, Valdez and Ryel 1997, Ackerman et al. 2006, Ackerman 2008). Since the conversion of lentic environments to lotic, and during the formation of Pearce Ferry Rapid, native fish have become dominant below Diamond Creek (Albrecht et al. 2017). Differing flow regimes, along with increasing water temperature and the contraction of Lake Mead, are some of the factors that could explain this change. Warming water temperatures within the mainstem is a plausible cause for native fish success, but it may not fully explain the recent decline in nonnative fish abundance because nonnatives too would likely benefit from warmer water temperatures (e.g., Rahel and Olden 2008).

Turbidity, particularly below RKM 381.4 (where the river cuts through the deltaic deposits that resulted from the creation of Lake Mead), may also play a role in creating conditions favorable to native fishes (Albrecht at al. 2010, 2017) by providing cover from nonnative predators that rely heavily on visibility for feeding (Johnson and Hines 1999, Yard et al. 2011, Ward et al. 2016). Based on data collected in Lake Mead and Lake Mohave, Albrecht et al. (2010) hypothesized that increased turbidity creates cover and allows Razorback Sucker survival and recruitment in the presence of nonnative fish. Turbidity has been shown to reduce fish predation on larval, juvenile, and adult fish (Johnson and Hines 1999, Albrecht et al. 2010, 2017, Ward et al. 2016, Rogowski et al. 2018, Ward and Vaage 2019). Ward et al. (2016) concluded that relatively small increases in turbidity could reduce the predation of Humpback Chub by Rainbow Trout. Thus, we hypothesize that increased turbidity in the lower Grand Canyon due to the erosion of old river delta deposits reduces the presence of nonnative fishes and potentially their predation of and competition with native fishes. Additional physicochemical studies could help to test this hypothesis.

Most of the nonnative fish species found within Grand Canyon are warm-water species, and many of these species prefer more lentic environments (Minckley 1973, Minckley and Marsh 2009). If Lake Mead continues to recede, a major source of nonnative fish will be moved farther downstream from Grand Canyon. The increasing river length would likely reduce nonnative fish abundance within Grand Canyon, and the turbid, erosive nature of the new river channel would reduce upstream invasion of nonnative fishes from Lake Mead. The current condition of Pearce Ferry Rapid could also serve as a potential barrier or deterrent to upstream movement, which may help protect native fish from additional nonnative competition and predation. Many of the nonnative species that are present as adults in monitoring efforts (e.g., Rogowski and Boyer 2019) are often absent from our small-bodied sampling and are rarely encountered at earlier life stages (Kegerries et al. 2017). Thus, it appears that reproduction and recruitment of nonnative fish may be limited in the Grand Canyon reach of the Colorado River.

Our work provides a contemporary example of an area where native fishes are dominating a large-river, dam-controlled, desert-southwest fish community, which is unprecedented in the Colorado River basin. All of the native fishes represented in our study are imperiled to varying degrees (i.e., listed under the Endangered Species Act, by states or tribes, or as subjects of conservation agreements), except Speckled Dace, which are ubiquitous throughout the Colorado River basin. Thus, environments within Grand Canyon currently provide an important sanctuary for Colorado River fishes. Continued research and monitoring of this fish community within Grand Canyon could provide information on the mechanisms promoting reproduction and recruitment of native fishes under current conditions and could inform recovery and conservation efforts for these species in other locations. Such efforts in other locations would provide a better understanding of water operations and their overall effects on fish communities within the Colorado River basin.

ACKNOWLEDGMENTS

The U.S. Bureau of Reclamation, Upper Colorado Region, Salt Lake City, Utah, and the Lower Colorado River Multi-Species Conservation Program, Boulder City, Nevada, funded the 2014–2017 project under contract number GS-10F-0331S. Grand Canyon National Park River Rangers and Fisheries Program personnel provided logistical support, which was supplemented by O.A.R.S. and Ceiba Adventures. We conducted fish sampling under U.S. National Park Service Permit GRCA-2014-SCI-0048, U.S. Fish and Wildlife Service Permit TE809232-18, and Arizona Game and Fish Department Permits SP668215 and SP706081. We thank the many biologists, technicians, and volunteers for their many hours in the field collecting these data. We specifically thank R. Newton for her work and assistance in permitting coordination with the U.S. National Park Service. R. Dudley, H. Brandenburg, and S. Platania assisted with study design and GRTS system sample-site selection along with field and lab work. P. Holden commented on drafts of this work and was instrumental in assisting with study design and interpretation. Reference to trade names does not imply endorsement by the U.S. Government.

LITERATURE CITED

ACKERMAN, M.W. 2008. 2006 Native fish monitoring activities in the Colorado River, Grand Canyon. Annual Report. Prepared for the Grand Canyon Monitoring and Research Center, Flagstaff, AZ.

ACKERMAN, M.W., D.L. WARD, T. HUNT, R.S. ROGERS, D.R. VAN HAVERBEKE, AND A. MORGAN. 2006. 2006 Grand Canyon long-term fish monitoring Colorado River, Diamond Creek to Lake Mead. Annual Report. Prepared for the Grand Canyon Monitoring and Research Center, Flagstaff, AZ.

ALBRECHT, B., P.B. HOLDEN, R. KEGERRIES, AND M.E. GOLDEN. 2010. Razorback Sucker recruitment in Lake Mead, Nevada–Arizona, why here? Lake and Reservoir Management 26(4):336–344.

ALBRECHT, B., H.E. MOHN, R. KEGERRIES, M.C. MCKINSTRY, R. ROGERS, T. FRANCIS, B. HINES, J. STOLBERG, D. RYDEN, D. ELVERUD, ET AL. 2017. Use of inflow areas in two Colorado River Basin reservoirs by the endangered Razorback Sucker (*Xyrauchen texanus*). Western North American Naturalist 77: 500–514.

BESTGEN, K.R. 2008. Effects of water temperature on growth of Razorback Sucker larvae. Western North American Naturalist 68:15–20.

BUNN, S.E., AND A.H. ARTHINGTON. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30:492–507.

CAROTHERS, S., AND B. BROWN. 1991. The Colorado River through Grand Canyon: natural history and human change. University of Arizona Press, Tucson, AZ. 235 pp.

CAROTHERS, S.W., AND C.O. MINCKLEY. 1981. A survey of the fishes, aquatic invertebrates and aquatic plants of the Colorado River and selected tributaries from Lees Ferry to Separation Rapids. Museum of Northern Arizona, Flagstaff, AZ. 401 pp.

CLARKSON, R.W., AND M.R. CHILDS. 2000. Temperature effects of hypolimnial-release dams on early life stages of Colorado River Basin big-river fishes. Copeia 2000:402–412.

EVERMANN, B.W., AND C. RUTTER. 1894. The fishes of the Colorado Basin. Fishery Bulletin 14:473–486.

FRANSSEN, N.R., AND S.L. DURST. 2014. Prey and nonnative fish predict the distribution of Colorado Pikeminnow (*Ptychocheilus lucius*) in a south-western river in North America. Ecology of Freshwater Fish 23:395–404.

FRANSSEN, N.R., E.I. GILBERT, AND D.L. PROPST. 2015. Effects of longitudinal and lateral stream channel complexity on native and non-native fishes in an invaded desert stream. Freshwater Biology 60:16–30.

GIDO, K.B., AND D.L. PROPST. 2012. Long-term dynamics of native and nonnative fishes in the San Juan River, New Mexico and Utah, under a partially managed flow regime. Transactions of the American Fisheries Society 141:645–659.

GLOSS, S.P., J.E. LOVICH, AND T.S. MELIS, EDITORS. 2005. The state of the Colorado River ecosystem in Grand Canyon. USGS Circular 1282. U.S. Geological Survey, Reston, VA. 220 pp.

HOLDEN, P.B., AND C.B. STALNAKER. 1975. Distribution and abundance of mainstream fishes of the middle and upper Colorado River basins, 1967–1973. Transactions of the American Fisheries Society 104:217–231.

HUBBS, C.L. 1954. Establishment of a forage fish, the Red Shiner *Notropis lutrensis*, in the Lower Colorado River system. California Fish and Game 40(3): 287–294.

HUBERT, W.A., AND M.C. FABRIZIO. 2007. Relative abundance and catch per unit effort. Pages 294–306 *in* C.S. Guy and M.L. Brown, editors, Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, MD.

JOHNSON, J.E., AND R.T. HINES. 1999. Effect of suspended sediment on vulnerability of young Razorback Sucker to predation. Transactions of the American Fisheries Society 128:648–655.

JORDAN, D.S. 1891. Report of explorations in Utah and Colorado during the summer of 1889 with an account of the fishes found in each of the river basins examined. U.S. Fish Commission Bulletin 9: 1–40.

KAEDING, L.R., AND M.A. ZIMMERMAN. 1983. Life history and ecology of the Humpback Chub in the Little Colorado and Colorado rivers in Grand Canyon. Transactions of the American Fisheries Society 112: 577–594.

KEGERRIES, R.B., B.C. ALBRECHT, E.I. GILBERT, W.H. BRANDENBURG, A.L. BARKALOW, M.C. MCKINSTRY, H.E. MOHN, B.D. HEALY, J.R. STOLBERG, E.C. OMANA SMITH, ET AL. 2017. Occurrence and reproduction by Razorback Sucker *Xyrauchen texanus* in the Grand Canyon, Arizona. Southwestern Naturalist 62:227–232.

KENNEDY, T.A., J.D. MUEHLBAUER, C.B. YACKULIC, D.D. LYTLE, S.A. MILLER, K.L. DIBBLE, E.W. KORTENHOEVEN, A. METCALFE, AND C.V. BAXTER. 2016. Flow management for hydropower extirpates aquatic insects, undermining river food webs. BioScience 66: 561–575.

MADDUX, H.M., D.M. KUBLY, J.C. DEVOS JR., W.R. PERSONS, R. STAEDICKE, AND R.L. WRIGHT. 1988. Effects of varied flow regimes on aquatic resources of Glen and Grand Canyons. Bureau of Reclamation, Salt Lake City, UT.

MARTIN, T., AND D. WHITIS. 2013. Guide to the Colorado River in the Grand Canyon: Lees Ferry to South Cove. Fifth edition. Vishnu Temple Press, Flagstaff, AZ. 120 pp.

MCDONALD, D.B., AND P.A. DOTSON. 1960. Pre-impoundment investigation of the Green River and Colorado River developments. *In*: Federal Aid in Fish Restoration Investigations of Specific Problems in Utah's Fishery. Federal Aid Project No. F-4-R-6, Departmental Information Bulletin No. 60–3. State of Utah, Department of Fish and Game, Salt Lake City, UT. 70 pp.

MILLER, R.R. 1959. Origin and affinities of the freshwater fish fauna of western North America. Pages 187–222 *in* C.L. Hubbs, editor, Zoogeography. Publication 51, American Association for the Advancement of Science, Washington, DC.

MILLER, R.R., 1961. Man and the changing fish fauna of the American Southwest. Michigan Academy of Science, Arts, and Letters 46:365–404.

MILLER, R.R., AND G.R. SMITH. 1984. Fish remains from Stanton's Cave, Grand Canyon of the Colorado, AZ, with notes on the taxonomy of *Gila cypha.* Pages 61–65 *in* R. Euler, editor, Archaeology, Geology, and Paleobiology of Stanton's Cave. Grand Canyon Natural History Association Monograph 6, Grand Canyon, AZ.

MINCKLEY, C.O., AND D.W. BLINN. 1976. Summer distribution and reproductive status of fish of the Colorado River and its tributaries in Grand Canyon National Park and vicinity during 1975. Technical Report No. 14. Grand Canyon National Park, Colorado River Research Program, Contribution Number 42. 17 pp.

MINCKLEY, W.L. 1973. Fishes of Arizona. Arizona Game and Fish Department, Phoenix, AZ. 293 pp.

MINCKLEY, W.L., AND J.E. DEACON. 1991. Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson, AZ. 517 pp.

MINCKLEY, W.L., AND P.C. MARSH. 2009. Inland fishes of the greater Southwest. University of Arizona Press, Tucson, AZ. 426 pp.

MINCKLEY, W.L., P.C. MARSH, J.E. BROOKS, J.E. JOHNSON, AND B.L. JENSEN. 1991. Management toward recovery of the Razorback Sucker. Pages 303–357 *in* W.L. Minckley and J.E. Deacon, editors, Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson, AZ.

PERSONS, W.R., D.R. VAN HAVERBEKE, AND M.J. DODRILL. 2017. Colorado River fish monitoring in Grand Canyon, Arizona; 2002–14 Humpback Chub aggregations. U.S. Geological Survey, Reston, VA. 43 pp.

QUARTARONE, F. 1993. Historical accounts of Upper Colorado River basin endangered fish. U.S. Fish and Wildlife Service, Recovery and Implementation Program for

Endangered Fish of the Upper Colorado River Basin, Denver, CO. 66 pp.

RAHEL, F.J., AND J.D. OLDEN. 2008. Assessing the effects of climate change on aquatic invasive species. Conservation Biology 22:521–533.

ROGOWSKI, D.L., AND J.K. BOYER. 2019. Colorado River fish monitoring in Grand Canyon, Arizona—2018 Annual Report. Arizona Game and Fish Department, Grand Canyon Monitoring and Research Center, Flagstaff, AZ. 45 pp.

ROGOWSKI, D.L., R.J. OSTERHOUDT, H.E. MOHN, AND J.K. BOYER. 2018. Humpback Chub (*Gila cypha*) range expansion in the western Grand Canyon. Western North American Naturalist 78:26–38.

ROSS, R.P., AND W.S. VERNIEU. 2013. Nearshore temperature findings for the Colorado River in Grand Canyon, Arizona: possible implications for native fish. USGS Fact Sheet No. 2013–3104. U.S. Geological Survey, Flagstaff, AZ. 4 pp.

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.

STEVENS, D.L., AND A.R. OLSEN. 1999. Spatially restricted surveys over time for aquatic resources. Journal of Agricultural, Biological, and Environmental Statistics 4:415–428.

STEVENS, D.L., AND A.R. OLSEN. 2003. Variance estimation for spatially balanced samples of environmental resources. Environmetrics 14:593–610.

STEVENS, D.L., AND A.R. OLSEN. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262–278.

STONE, J.L., AND N.L. RATHBUN. 1968. Tailwater fisheries investigations: creel census and limnological study of the Colorado River below Glen Canyon Dam, July 1, 1967–June 30, 1968. Arizona Game and Fish Department, Phoenix, AZ.

SUTTKUS, R.D., G.H. CLEMMER, C. JONES, AND C.R. SHOOP. 1976. Survey of the fishes, mammals and herpetofauna of the Colorado River in Grand Canyon. Colorado River Research Series Contribution 34. Grand Canyon National Park, Grand Canyon, AZ. 48 pp.

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. USGS Professional Paper 1677. U.S. Geological Survey, Denver, CO. 118 pp.

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. SWCA, Inc., Environmental Consultants, Flagstaff, AZ.

VALDEZ, R.A., B.R. COWDELL, AND E.E. PRATS. 1995. Effects of interim flows from Glen Canyon Dam on the aquatic resources of the lower Colorado River from Diamond Creek to Lake Mead. Phase II Report to the Hualapai Natural Resources Department, Peach Springs, AZ.

VALDEZ, R.A., AND R.J. RYEL. 1997. Life history and ecology of the Humpback Chub in the Colorado River in Grand Canyon, Arizona. Pages 3–31 *in* C. van Riper III and E.T. Deshler, editors, Proceedings of the Third Biennial Conference of Research on the Colorado Plateau. National Park Service Transactions and Proceedings Series 97/12.

VOICHICK, N., AND S.A. WRIGHT. 2007. Water-temperature data for the Colorado River and tributaries between Glen Canyon Dam and Spencer Canyon, northern Arizona, 1988–2005. USGS data series 251. U.S. Geological Survey, Reston, VA. 24 pp.

WARD, D.L., R. MORTON-STARNER, AND B.M. VAAGE. 2016. Effects of turbidity on predation vulnerability of juvenile Humpback Chub to Rainbow Trout and Brown Trout. Journal of Fish and Wildlife Management 7:205–212.

WARD, D.L., AND B.M. VAAGE. 2019. What environmental conditions reduce predation vulnerability for juvenile Colorado River native fishes? Journal of Fish and Wildlife Management 10:196–205.

WILLIAMSON, R.S., AND C.F. TYLER. 1932. Trout propagation in Grand Canyon National Park. Grand Canyon Nature Notes 7(2):1–15.

WOODBURY, A.M. 1959. Ecological studies of flora and fauna in Glen Canyon. University of Utah Anthropological Papers, No. 40. University of Utah Press, Salt Lake City, UT. 226 pp.

YARD, M.D., L.G. COGGINS JR., C.V. BAXTER, G.E. BENNETT, AND J. KORMAN. 2011. Trout piscivory in the Colorado River, Grand Canyon: effects of turbidity, temperature, and fish prey availability. Transactions of the American Fisheries Society 140(2):471–486.

Received 26 June 2019
Revised 23 October 2019
Accepted 29 October 2019
Published online 3 June 2020