Copeia

founded in 1913 by John Treadwell Nichols

Conservation to Stem Imminent Extinction: The Fight To Save Razorback Sucker *Xyrauchen texanus* in Lake Mohave and Its Implications for Species Recovery

Paul C. Marsh[1,2], Thomas E. Dowling[3], Brian R. Kesner[1], Thomas F. Turner[4], and W. L. Minckley[5]

Official Publication of the American Society of Ichthyologists and Herpetologists

Conservation to Stem Imminent Extinction: The Fight To Save Razorback Sucker *Xyrauchen texanus* in Lake Mohave and Its Implications for Species Recovery

Paul C. Marsh[1,2], Thomas E. Dowling[3], Brian R. Kesner[1], Thomas F. Turner[4], and W. L. Minckley[5]

Razorback Sucker *Xyrauchen texanus* is iconic of the plight of native ''big-river'' fishes of the Colorado River system of western North America. The species was historically widespread and abundant throughout the basin but has suffered substantial range reductions and population declines now characteristic of Western fishes. By the 1960s the largest remaining population was in Lake Mohave, a lower Colorado River reservoir where casual monitoring began in the mid-1950s and intensified to focus on Razorback Sucker in the late 1970s. The population then was comprised of several hundred thousand large adults, but recruitment past the larval stage was nil presumably because of predation by non-native fishes and potentially worsened by nutritional limitation. Remnant adults began to dwindle in the 1980s and were virtually gone within twenty years. An *ad-hoc* ''Lake Mohave Native Fishes Work Group'' initiated investigations to identify and understand the reasons for recruitment failure and launched an informal program to perpetuate Razorback Sucker in the reservoir. The initial goal was to establish a population of 50,000 adults in Lake Mohave, and the group developed an innovative and ultimately successful strategy in which Razorback Sucker larvae produced naturally by wild adults in the lake were harvested, reared in protected off-channel habitats, and repatriated. Demographic monitoring continued and expanded, providing annual census estimates of population abundance and trends of wild and repatriated fish. Critical genetic monitoring was initiated to track spatial and temporal diversity of harvested larvae and captured repatriates. Wild adults now are gone from Lake Mohave, but they have been replaced by a genetically diverse repatriate population of several thousand fish that spawn annually and provide larvae to continue the management cycle. However, the program is stymied by continued post-larval recruitment failure and predation losses of even the largest stocked Razorback Sucker. The program depends on stocking to maintain a repatriate population and for now has preserved the genetic legacy of the species. The species fares no better elsewhere in the basin where historical genetic diversity was lower, and, with the exception of Lake Mead, wild adults have perished and populations are maintained only by stocking of hatchery-produced fish. Naturally self-sustaining populations of Razorback Sucker are unlikely to ever again occupy the lower Colorado River mainstem and the species will remain ''conservation-reliant.'' A conceptual strategy that integrates use of non-native-free backwaters and the river channel has promise for this and other big-river species, and its implementation should be aggressively pursued.

RAZORBACK Sucker *Xyrauchen texanus* (Catostomidae) evolved over millennia within the progenitor habitats of the modern-day Colorado River system of Western North America. A product of selection in ancient pluvial lakes and swiftly flowing canyon-bound rivers that characterize the system today, the species was well known to Native Americans who inhabited the region before the mid-16th century arrival of Europeans. Pre-historic shoreline weirs to facilitate the capture of fishes and midden remains of fish bones (Rostlund, 1952; Gobalet and Wake, 2000) provide evidence of big-river fishes as human food and imply at least seasonal abundance and availability. Regional peoples had low technology and little influence on larger watercourses and their fishes other than diversion by temporary brush dams to support floodplain agriculture and harvest with nets, or perhaps by stranding in canals and acequias (Minckley and Marsh, 2009).

Early Europeans who settled into the region were drawn to scarce water in the arid west and likely had little more impact than residents, notable exceptions being wood-cutting along most major rivers and landscape-scale damages inflicted by herds of domestic livestock in the late 1800s (Mueller and Marsh, 2002). But even these paled in comparison to changes wrought later by water control with high dams and releases of non-native fishes that began around the turn into the 20th century. Embedded in this timeline is the Razorback Sucker from its ''discovery'' in the lower Colorado River to current status as a critically imperiled species protected and managed under the Endangered Species Act (USFWS, 1991). Here we tell its story in Lake Mohave in the lower Colorado River and as it relates to the species' conservation toward recovery throughout the basin.

DESCRIPTION OF THE SPECIES

Razorback Sucker (Fig. 1) became known to science after description and naming (as *Catostomus texanus*) by Abbott (1861); its trivial name, *texanus*, is based on misunderstanding that the first specimens came from the Colorado River in Texas. This monotypic genus in fact is endemic to the ''other'' Colorado River basin, and its historic range included larger streams from what now is Wyoming through Arizona, California, Colorado, Nevada, New Mexico, and

[1] Marsh & Associates, LLC, 5016 South Ash Avenue, Suite 108, Tempe, Arizona 85282; E-mail: (PCM) fish.dr@nativefishlab.net; and (BRK) BKesner@nativefishlab.net. Send reprint requests to PCM.
[2] School of Life Sciences, Box 4501, Arizona State University, Tempe, Arizona 85287-4501.
[3] Department of Biological Sciences, 5047 Gullen Hall, Wayne State University, Detroit, Michigan 48202; E-mail: Thomas.Dowling@wayne.edu.
[4] Department of Biology and Museum of Southwestern Biology, MSC03-2020, University of New Mexico, Albuquerque, New Mexico 87131; E-mail: turnert@unm.edu.
[5] Department of Biology, Arizona State University, Tempe, Arizona 85287-4501 (deceased).
Submitted: 18 February 2014. Accepted: 17 June 2014. Associate Editor: J. F. Schaefer.
 DOI: 10.1643/OT-14-030 Published online: March 5, 2015

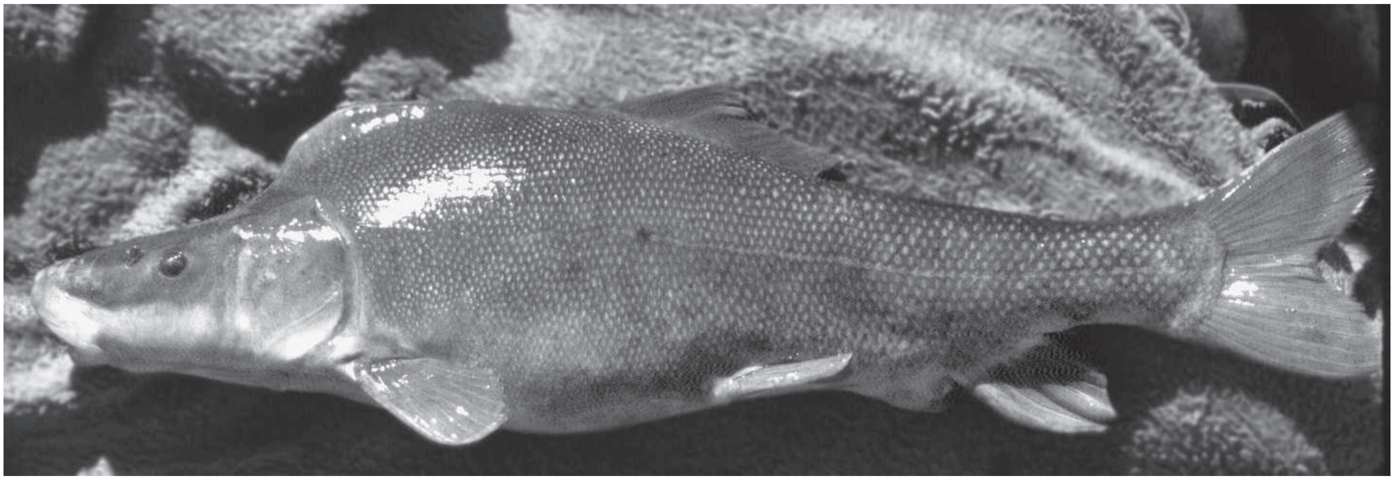

Fig. 1. Adult female Razorback Sucker *Xyrauchen texanus*, 65 cm total length, trammel netted from Lake Mohave, April 1979. Original photograph by WLM.

Utah, and to the delta in Baja California and Sonora, Mexico (Fig. 2); it also penetrated west into the Salton Sink of southern California when that basin was wetted with freshwater. It now is extirpated from many places including the Gila River basin of central Arizona and western New Mexico and is found today in only a small fraction of its former range. Occupied habitats included swift water in main channels of large rivers and peripheral eddies, backwaters, and other protected places.

Adult Razorback Sucker is unmistakably characterized by its pronounced nuchal hump or ''razorback,'' small eye, and deeply cleft lower lip. There are 68–87 lateral line scales, and typically 14 or 15 dorsal-fin rays and 7 anal-fin rays. There are 44–50 thin gill rakers on the first arch. The fish can attain total length (TL) approaching a meter although fish of such size are unknown today. Coloration in reservoir-caught specimens is brownish black above, lighter below (often bright yellow-to-orange in breeding males), and sides may have a brown-to-pink lateral stripe; fins are dark brown to yellow. Fish in turbid waters may be uniformly gray. Adult males have a distinctly sharper nuchal hump and larger, more oval-shaped caudal fin than females, while females have a distinctive genital papillus not present in the male. Both sexes may form nuptial tubercles on head, fins, and caudal peduncle but these are much more prolific and pronounced in males.

LIFE HISTORY

This fish is among the most studied of the Colorado River natives and as such there are many excellent summaries from which the following is derived (e.g., McAda and Wydoski, 1980; Minckley, 1983; Bestgen, 1990; Minckley et al., 1991; USFWS, 1998; Bestgen et al., 2012). We can only infer that Razorback Sucker life history was similar in the past to that observed today under post-development conditions. Larval Razorback Sucker eat tiny algae and microcrustaceans and detritus (Marsh and Langhorst, 1988), presumably graduating as juveniles to larger sizes of the same foods. Adults in lotic systems eat benthic and drifting macroinvertebrates plus algae and detritus, while in lentic habitats they are primarily planktivores with some benthos in the diet (Minckley, 1973; Marsh, 1987). Growth is highly variable (Minckley et al., 1991). Juvenile fish grew 4–27 cm in their first year in ponds at Ouray, Utah, while young in a Lake Mohave backwater attained 35 cm by age 1. Growth remains rapid for the next few years then slows after age six. Females grow faster than males, in recent samples reaching terminal TLs of about 75 and 60 cm, respectively, and weights of more than 5 Kg (Minckley, 1983); maximum longevity is >50 years (McCarthy and Minckley, 1987).

Males attain sexual maturity in 1 to 3 years, females in 2 to 6. Reproduction related migration distances can be substantial to access river and tributary spawning grounds, and there is good evidence for site fidelity (Tyus, 1987). Spawning is in winter into late spring, earlier in southern portions of the range, at temperatures ranging from the mid-teens into the low-to-mid-20s centigrade (McAda and Wydoski, 1980; Minckley, 1983). Population sex ratio is assumed to be 1:1 (Turner et al., 2007), but as with other catostomids, Razorback Sucker spawn in groups comprised of one (rarely two) females and two or more males aggregated over stream gravels in moderate currents; about twice as many males as females are in large collections of wild adults on spawning grounds in Lake Mohave (Minckley, 1983; unpubl. data). Successful reproduction is common over wave-washed cobble along modern reservoir shorelines (Minckley et al., 1991), and given some of its feeding adaptations and possible evolution in lacustrine environs it likely also spawned in lentic habitats prehistorically. Regardless, the act is accompanied by simultaneous discharge of gametes and by much thrashing that can excavate depressions a meter or more across and into which the fertilized ova settle and develop (Mueller, 1989). Relative fecundity is high (about 149 ova per mm TL) and increases with length. Adults vacate the area after spawning but may spawn again in the same season, or the following year. Fertilized ova are left to develop without parental care and, depending on temperature, yolk-sac larvae hatch at 7 to 9 mm TL in three to nine days; swim-up and active feeding begin at four to 13 days (Inslee, 1982; Hamman, 1985; Marsh, 1985). Post-larval survival in nature was historically low based on principles of a type III survivorship curve and today is nil in unprotected habitats, presumably because of predation, except in Lake Mead where there is some evidence of limited natural recruitment (Kegerries et al., 2009; Albrecht et al., 2010).

Movements are less common during non-reproductive times and fish are mostly sedentary. Contact rates by any

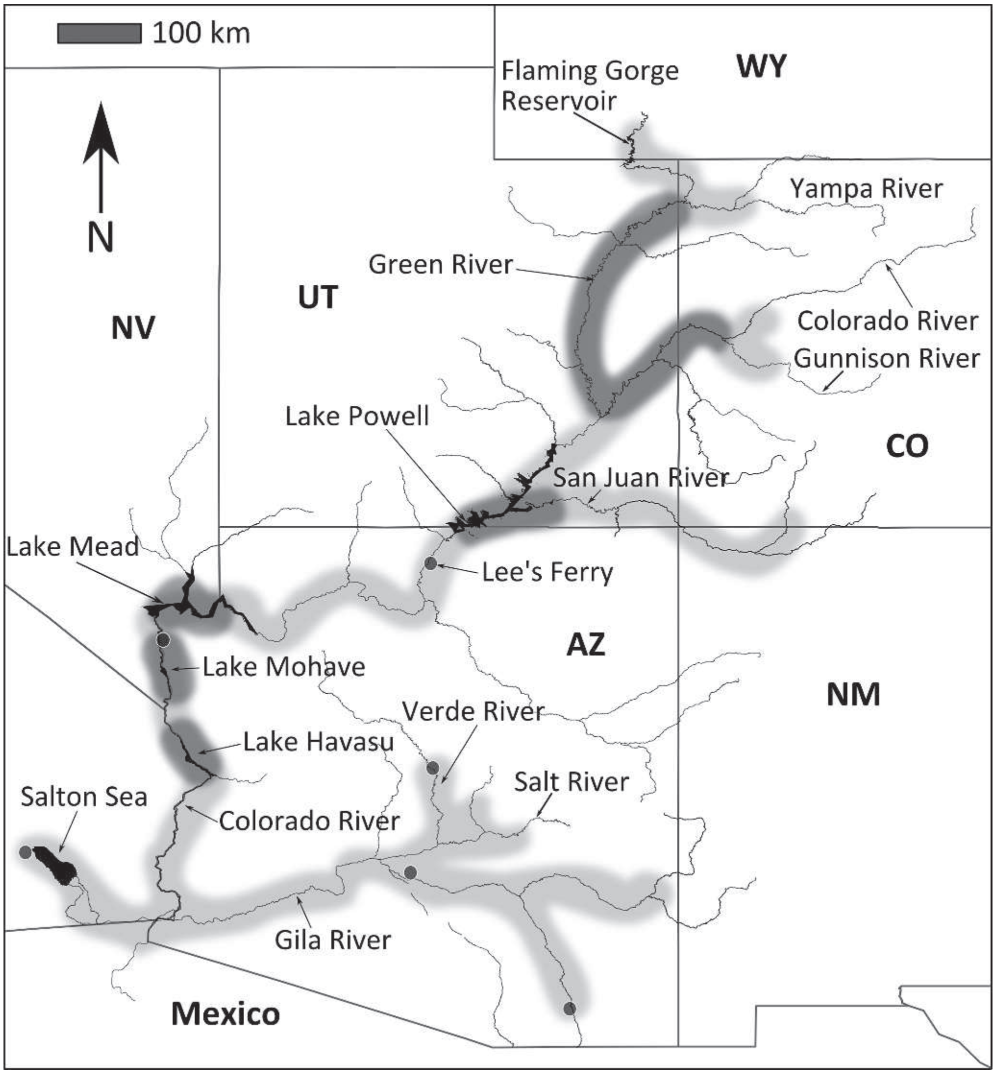

Fig. 2. Historical (light gray) and present (dark gray) distributions of Razorback Sucker *Xyrauchen texanus* in the Colorado River basin of Western North America. Point locations (circles) represent archaeological sites.

method are low and actual occupied habitats are presumed to be deeper water of rivers and reservoirs. There is little evidence of schooling (other than during reproduction) or territoriality. Co-occurring mainstem fishes historically were Bonytail *Gila elegans*, Humpback Chub *Gila cypha* (in and upstream from Grand Canyon), Roundtail Chub *Gila robusta*, Colorado Squawfish or Pikeminnow *Ptychocheilus lucius,* Speckled Dace *Rhinichthys osculus*, Flannelmouth Sucker *Catostomus latipinnis,* and Bluehead Sucker *Pantosteus discobolus* (primarily upstream of present-day Lake Mead). Other than a repatriated population of Flannelmouth Sucker, downstream of Grand Canyon all of these natives are now replaced or accompanied by a suite of non-native species (Minckley, 1979, 1991; Minckley and Marsh, 2009).

POPULATION ABUNDANCE

There are no quantitative data on pre-European abundance of Razorback Sucker in the lower Colorado River basin, but archaeological evidence and early 1900s newspaper reports and testimonials all suggest it and other big-river fishes were present in large numbers (Miller, 1961; Minckley, 1973). Abundance was substantial enough in fact that these fishes were pitch-forked from canals and loaded into wagons to be distributed for food and fertilizer (Miller, 1961). Current census estimates of adult population size basin-wide (now mostly comprised of stocked repatriates) have been calculated for each of the remnant populations (Table 1); however, largely because of low recapture rates, accuracy of these estimates is variable (Bestgen et al., 2012). All are a small fraction of what they once were and most are maintained by stocking (Marsh and Minckley, 1992; Marsh et al., 2005; Schooley and Marsh, 2007; Bestgen et al., 2012).

There also are no historical data on dynamic parameters such as growth, reproduction, recruitment, or mortality, but we assume that intrinsic and extrinsic factors influencing these dynamics were like those affecting any naturally occurring fish population. We have little information on parasites and diseases (but see Amin, 1969a, 1969b; Mpoame, 1981). Chubs (genus *Gila*) would have preyed on young-of-year Razorback Sucker but only Colorado Squawfish was large enough to eat juveniles and adults. Resource competition would likely have come only from other suckers (Flannelmouth Sucker and Bluehead Sucker in mainstem rivers, and Desert Sucker *Pantosteus clarkii* and Sonora Sucker *Catostomus insignis* in smaller tributaries). We know that Razorback Sucker was among fish remains excavated at pre-historic sites (Miller, 1955; Minckley and

Table 1. Census estimates (number and 95% confidence interval, CI) of adult Razorback Sucker in the Colorado River Basin. The Lake Mead population is reportedly comprised of wild fish, while those in other locations are stocked repatriates plus potentially an unknown but small number of wild individuals; all estimates include sub-adult and adult size fish of all ages. Field collection and computational methods vary among studies and years and may not be directly comparable. NA = estimate not provided.

Location	Year	Estimate	CI	Reference
Colorado River	2005	1066	377–3070	Bestgen et al., 2012
Green River: Lower	2006	1582	1061–2446	Bestgen et al., 2012
	2007	5153	2588–10460	Bestgen et al., 2012
	2008	2597	1595–4359	Bestgen et al., 2012
Green River: Desolation-Gray Canyons	2006	474	207–1217	Bestgen et al., 2012
	2007	3011	772–12076	Bestgen et al., 2012
	2008	836	280–2677	Bestgen et al., 2012
Green River: Middle	2006	576	227–1068	Bestgen et al., 2012
	2007	3146	1039–9764	Bestgen et al., 2012
	2008	1218	448–3514	Bestgen et al., 2012
San Juan River	2009	2047	1063–5000	USFWS, 2012
	2010	3021	2007–4940	USFWS, 2012
	2011	2928	1952–4796	USFWS, 2012
Lake Mead	2009	546	NA	Kegerries et al., 2009
Lake Mohave	2011	2577	1139–6284	Kesner et al., 2012
	2012	1854	941–3782	Kesner et al., 2014
	2013	2525	1180–5741	unpubl. data
Lake Havasu	2011	2496	1835–3220	Patterson et al., 2013
	2012	4524	4027–5081	Patterson et al., 2013

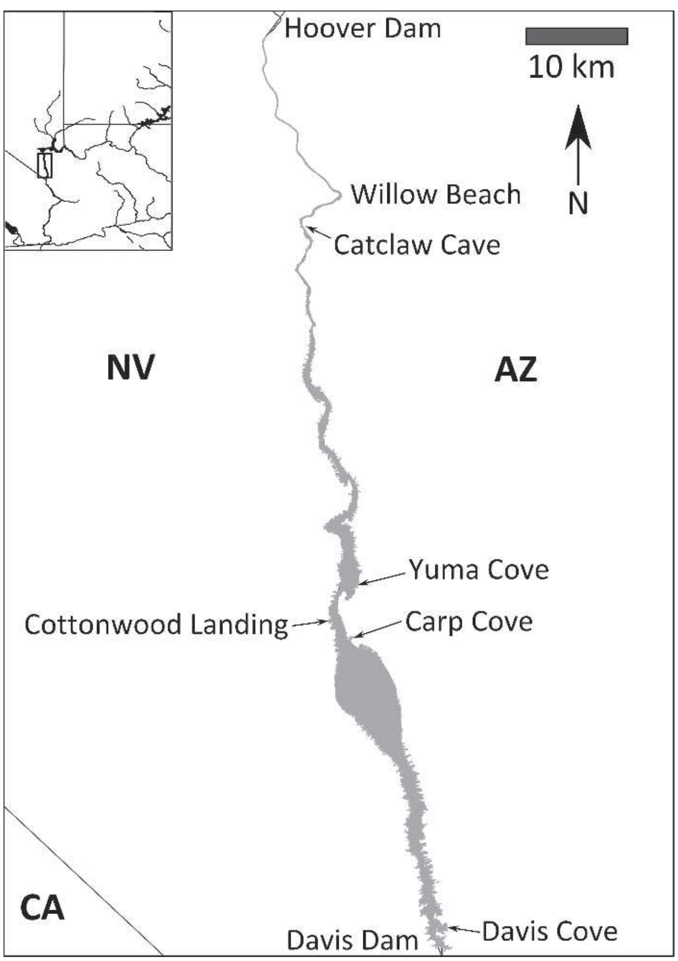

Fig. 3. Lake Mohave, Arizona and Nevada, showing place names mentioned in text, and location map (inset).

Alger, 1968; Gobalet, 1992, 1994) including one at Catclaw Cave on Lake Mohave (Fig. 3), so the human relationship with this species has been a long one.

Water use and small-scale development by Native Americans in the lower Colorado River system scarcely impacted native fishes, but imposition of mainstem dams and introductions for a variety of purposes of non-native aquatic biota, especially to support recreational fishing, had profound effects on habitats and native fishes. Razorback Sucker was widespread and abundant when Hoover (Boulder) Dam (Lake Mead) was closed in 1935 and remained so into the 1950s when Davis Dam was constructed to impound Lake Mohave (Fig. 3; Dill, 1944; Allan and Roden, 1980; Minckley, 1983). Most other mainstem natives by then were extirpated and replaced by a diverse array of two dozen documented (and established) and a dozen hypothetical (stocked or otherwise reported but never established) introduced fishes (Minckley, 1979, 1991), and wild Razorback Sucker eventually would follow. Razorback Sucker now only occurs as a few small repatriated populations in Lake Mohave and Lake Havasu in the lower basin, and in the Colorado, Green, and San Juan rivers (including the river arm of Lake Powell) in the upper Colorado River basin (Table 1). A notable exception is Lake Mead where limited recruitment to a population of uncertain origin has recently been reported (Albrecht et al., 2008, 2010).

MOLECULAR CHARACTERIZATION

The advent of molecular markers provided exceptional tools for characterization of the distribution of genetic variation within and among populations, and many of these have been applied to Razorback Sucker. Buth et al. (1995) characterized allozymic variation in all remnant populations at 38 loci, 17 of which exhibited multiple alleles. Buth

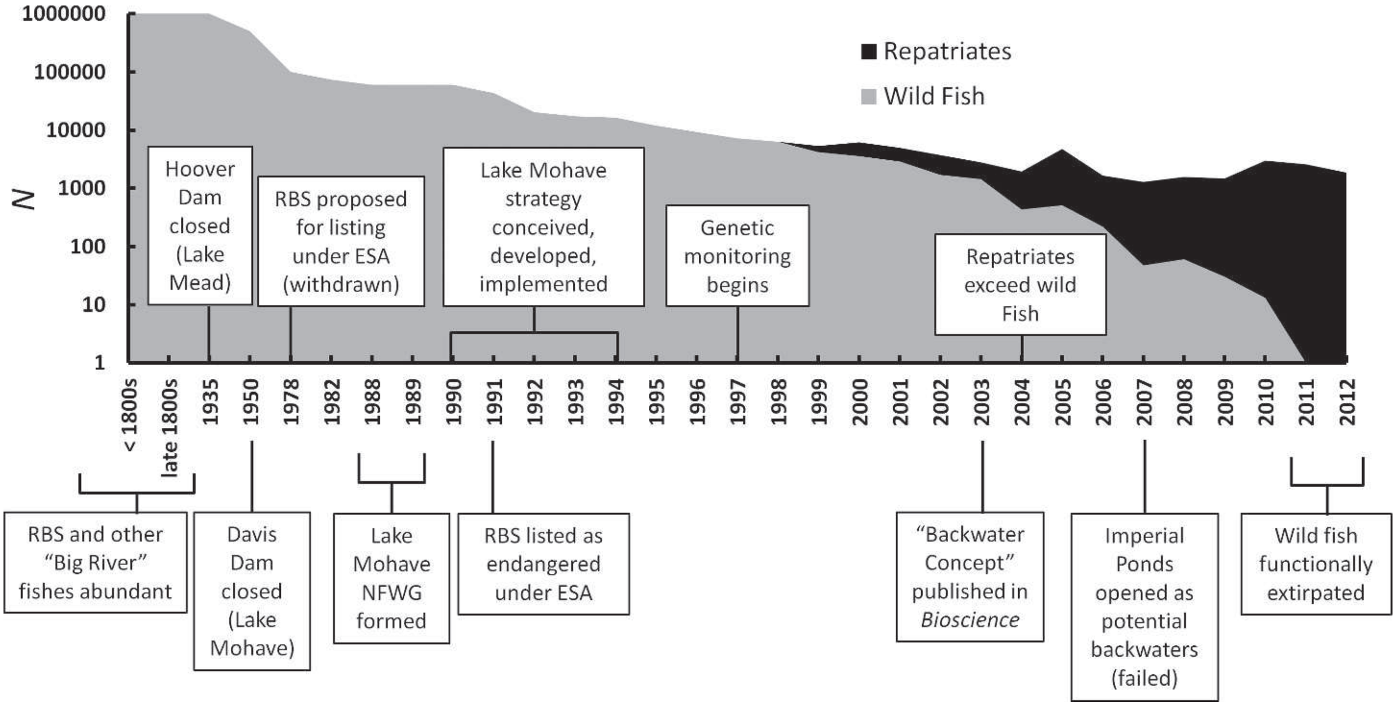

Fig. 4. Timeline of Razorback Sucker (RBS) status and conservation program events and other actions superimposed on changes in Lake Mohave census number (N; log scale) over time (non-linear prior to 1988). ESA is the U.S. Endangered Species Act; NFWG is the Lake Mohave Native Fishes Work Group (see text).

et al. (1987) characterized allozymic variation between flannelmouth and razorback sucker, demonstrating that introgression between the two species was limited. Alleles unique to individual populations were found at three of ten loci with multiple alleles; however, levels of divergence among populations were low. Dowling et al. (1996a) used restriction endonuclease analysis of mtDNA from these same populations, also finding that most variation was distributed within instead of among locations. In addition, levels of mtDNA diversity and number of haplotypes declined progressively from Lake Mohave upstream to the upper Colorado and Green-Yampa rivers, leading to a conclusion that samples represented remnants of a single population that formerly occupied the entire basin (Dowling et al., 1996a). They concluded that the species should be managed as a single population.

Dowling and coworkers (Dowling and Marsh, 2011; Dowling et al., 2012a) further characterized nuclear genome variation using 13 microsatellite loci, more sensitive markers for characterizing geographic structure. Wilson (2011), using 13 different microsatellite loci, focused on hatchery stocks from all locations except Lake Mead. Like studies of mtDNA, these analyses also indicated that the majority of variation was found within populations and identified a decrease in variation from down- to upstream localities. Even though levels of among location variation were low, F-statistic and Bayesian assignment analyses identified distinct groups above and below the Grand Canyon. Based on this information, Dowling et al. (2012a) concluded that the Grand Canyon has acted as a barrier, and a conservative approach would be to manage populations above and below independently; however, it would be appropriate to translocate individuals from the lower to upper basin if reduction in population sizes in the latter became dramatic.

These studies demonstrate that the Lake Mohave population represents the greatest amount of genetic variation in Razorback Sucker, with 49 wild individuals sampled exhibiting 33 different haplotypes and an estimated diversity of 0.98 (maximum value = 1.00; Dowling et al., 1996a). Lower levels of variation in other locations likely resulted from smaller population sizes at some time in their history, and in some cases, led to increased levels of relatedness among individuals (Lake Mead [Dowling et al., 2012a], upper Colorado River [Dowling et al., 2012b; Wilson, 2012]). Whatever the cause, the high levels of genetic variation in Lake Mohave made this population especially significant for conservation, further reinforcing its value as a target of intensive conservation efforts to preserve genetic variation in the species.

RAZORBACK SUCKER IN LAKE MOHAVE

There was early suspicion that native fishes of the lower Colorado River began to decline with closure in 1935 of Hoover Dam (Figs. 3, 4; Minckley et al., 1991 and citations therein), but reports of Razorback Sucker abundance are conflicting. Moffett (1942) provided no indication they were numerous, but Jonez et al. (1951) and Jonez and Sumner (1954) reported them as "very common." Although the population size in the river reach that was to become Lake Mohave is unknown, there is evidence of a large year class produced around the time Davis Dam was closed and the reservoir began filling (Sigler and Miller, 1963). In June 1950 more than 6,000 juvenile fish 10 to 35 mm standard length were taken in two seine hauls at Cottonwood Landing, Nevada (Fig. 3). Water temperature along the shoreline was 22–24°C while in the adjacent river it was only 14°C because of the hypolimnetic discharge from Hoover Dam. This cohort and others recruited in the early 1950s were the likely source of adults encountered by WLM when he first visited the lake in the mid-1960s (Minckley, 1983; McCarthy and Minckley, 1987), and these fish persisted without apparent decline from 1974 into the early 1990s (Minckley et al., 1991) and beyond. These recruitment events were the last documented for Razorback Sucker in the lower Colorado River basin downstream of Hoover Dam (Marsh and Minckley, 1989)—predation by non-native fishes simply eliminated larvae before they attained juvenile stage (Marsh and Langhorst, 1988; Minckley, 1991), exacerbated perhaps by food limitation in low productivity waters (Papoulias and Minckley, 1990; Horn, 1996).

Minckley et al. (1991) noted lack of a trend in trammel netting catch per unit effort data that extended back to the early 1980s and supported the idea of little change in population abundance over that time. The earliest mark–recapture census estimates of about 73,500 wild adults were from 1980–1990 Carlin-tagging data compiled largely by University of Nevada Las Vegas in the late 1980s plus 1988–1990 Floy-tag and 1991–1993 PIT tag information (Marsh and Minckley, 1992; Marsh, 1994; unpubl. data). However, subsequent estimates of 59,900 fish for 1988–1993 and 23,300 fish for 1991–1993 made it clear the population was in steep decline. Recruitment was undetected and the population was on a trajectory toward collapse.

CAPTIVE PROPAGATION

It was evident after the earliest attempts at artificial propagation that Razorback Sucker was amenable to the process (Toney, 1974). Because the population was not expected to persist, a broodstock of 281 wild fish taken from Lake Mohave in 1981 and 1982 was established at Dexter, New Mexico (Inslee, 1982) and rearing methods were developed and refined (Hamman, 1985, 1987). Hatchery production soon supported a monumental yet little documented stocking program under which millions of mostly larval-to-juvenile size fish were distributed into waters of the Gila River basin of Arizona and to the lower Colorado River downstream from Davis Dam (Marsh and Brooks, 1989; Minckley et al., 1991; Hendrickson, 1993; Schooley and Marsh, 2007). There were few recaptures of stocked fish, long-term survival was miniscule, and there was no evidence of reproduction or population persistence (Schooley and Marsh, 2007). The failed stocking program had been implemented through a USFWS–State of Arizona cooperative agreement in lieu of listing the Razorback Sucker under the Endangered Species Act (Mueller, 1995), and a result was a decade-plus delay from an initial proposal to list the Razorback Sucker as threatened (USFWS, 1978) to its eventual listing as endangered (USFWS, 1991). Nonetheless, much was learned about the mechanics and methods of propagation, and about the fate of stocked fish (reviewed in Minckley et al., 1991; Schooley and Marsh, 2007). Captive spawning and rearing now support most reintroduction programs for the lower Colorado River mainstem (LCR Multispecies Conservation Program), upper Colorado River basin streams (UCRB Recovery Implementation Program), and San Juan River (SJR Recovery Implementation Program).

THE LAKE MOHAVE NATIVE FISH WORK GROUP

Given the documented decline of the Lake Mohave population in the early 1990s and continued recruitment failure, it became clear that the population was going the route of other populations in the Gila, Salt, and Verde rivers of central Arizona (Minckley, 1983), and the species was expected to ultimately be extirpated from the lower Colorado River basin. With the failure of hatchery efforts to establish or augment populations, it became obvious that alternative approaches needed to be considered and implemented if the Razorback Sucker population in Lake Mohave were to be conserved. A cadre of seasoned field biologists, administrators, and researchers who were concerned about the failing Lake Mohave population came together in the late 1980s to address this problem (Fig. 4). The result was formation of the Lake Mohave Native Fishes Work Group (hereafter NFWG) dedicated to maintaining the Razorback Sucker in Lake Mohave and thereby saving the genetic legacy of the species. The group developed a novel strategy in 1990 that still provides the template for Razorback Sucker management in the reservoir: harvest naturally produced larvae from the lake, rear the young in protective custody, and repatriate them to the reservoir at a size thought immune to most predation (that size initially was 25 cm, now known to be much too small). Mueller (1995) described in detail the formation of the group and the initial years of implementation of its management concept. Wild adult fish remained relatively common in the reservoir in the early 1990s, and it was naively expected that a repatriate population of 50,000 adult fish could be established within a decade or less. A number of different rearing methods were attempted and evaluated to meet annual stocking targets, but grasping the golden ring of population restoration would prove elusive.

ALTERNATE APPROACHES TO CONSERVING GENETIC DIVERSITY

Several options have been considered for preservation of genetic diversity in Razorback Sucker, with programs from different regions (i.e., lower and upper Colorado River basins, which are in U.S. Fish and Wildlife Service Regions 2 and 6, respectively) applying different approaches to conservation. Programs in the upper Colorado River basin decided to focus on a hatchery based approach. Czapla (1999) recommended against the use of diallelic crosses involving all possible combinations of five males and females but promoted the use of 25 paired matings (50 individuals) for conservation of each of the upper basin stocks. The San Juan River Recovery Program recommended the generation of five sets of diallelic crosses, for a total effective broodstock population size of 50 (Crist and Ryden, 2003). Because of concerns over availability of this many wild fish from the San Juan River (including its Lake Powell arm), they recommended using fish from the upper Colorado River and Lake Mohave to achieve the desired goal of 50 individuals.

The NFWG decided on an alternative approach based on several concerns over the use of hatcheries as the major tool for conservation of Razorback Sucker (reviewed in Minckley et al., 2003). Maintenance of fishes in hatcheries has deleterious consequences, a concern that has been discussed and validated by others (Waples, 1999; Araki et al., 2008; Frankham, 2008; Fraser, 2008; McClure et al., 2008). Risks to diversity were further exacerbated by issues with the Lake Mohave Razorback Sucker broodstock and reduced fitness of their progeny in the hatchery (Dowling et al., 1996b). There were also concerns over the minimum number of individuals necessary to maintain a population. An effective size of 50 individuals was considered appropriate; however, this estimate provides the minimum effective size necessary to conserve neutral (e.g., non-adaptive) genetic variation, not the number of individuals needed to retain adaptive variation (Franklin and Frankham, 1998; Lynch and Lande, 1998). Given these issues, the NFWG reasoned that it would be best to reduce the potential impacts of domestication selection and to use as many individuals as possible in production of Razorback Sucker for conservation purposes.

Natural spawning.—The NFWG tried several methods to preserve high levels of genetic variation in Lake Mohave before settling on the one currently utilized. The first effort was in Yuma Cove backwater (Fig. 3), a natural shoreline feature formed at the mouth of a desert wash and periodically isolated from the reservoir by a wave-formed berm of coarse gravel (Marsh and Langhorst, 1988). The berm was mechanically reinforced and raised to ensure continuous isolation and the backwater then chemically treated to remove all non-native fishes; absence of non-native fishes is the primary criterion of an acceptable site to maintain native fish life cycles (Clarkson et al., 2005; Marsh and Pacey, 2005). One hundred adult Razorback Sucker, 33 female and 67 male, were captured in January 1991 from the Yuma Cove spawning grounds (Minckley et al., 1991), stocked into the adjacent Yuma Cove backwater, and allowed to reproduce. Larvae were collected in spring but for unknown reasons no young survived. The experiment was revisited in January 1992 when 28 females and 60 males were stocked. Larvae survived and 296 juveniles that averaged 35.4 cm TL were recovered in November. A sub-sample of 15 juveniles was genotyped with restriction endonucleases (as described in Dowling et al., 1996a, 1996b), yielding five haplotypes and an estimate of diversity of 0.70, significantly less variation than expected relative to the sample of wild adults in the lake (95% bootstrap confidence intervals: 7–15 for number of haplotypes and 0.78–1.00 for diversity). The 15 juveniles were produced by five females, and eight of the young were from a single female. These results indicated capture and use of adults likely would not preserve genetic diversity of Lake Mohave Razorback Sucker.

Stocking of fertilized ova.—Next was stocking of embryos. In spring 1993 spawning adults were captured from the lake, their gametes manually stripped, and ova from each of 24 females were fertilized with sperm from two or more of 60 males. The process yielded about 200,000 embryos that were stocked along the perimeter of Yuma Cove backwater, plus 50,000 that were diverted for laboratory research. The experiment was compromised by an abrupt 1 m lowering of the reservoir that exposed much of the backwater shoreline, but 17 juvenile fish were later recovered. A concomitant experiment in the same backwater was initiated when 420, 2.6 cm laboratory-reared metalarvae–early juveniles were stocked after the water level drop, and similar stockings took place into other isolated backwaters around the lake. Survival represented by juveniles later harvested from these sites ranged from 5 to 92% (Mueller, 1995) and nearly 500 fish were recovered, PIT tagged, and transferred to Lake Mohave. Nonetheless, the total number produced was considered inadequate to meet goals.

Stocking of larvae.—The next attempt to preserve diversity was to capture wild-produced larvae and rear them in protective custody. Razorback Sucker larvae are phototactic (Bozek et al., 1991; Mueller et al., 1993), and substantial numbers are readily captured on spawning grounds at night using lights and dip nets. The NFWG realized that this approach would provide the lowest levels of production (Minckley et al., 2003); however, it was likely to maintain the greatest levels of genetic diversity (Dowling et al., 1996b). More than 11,000 larvae were captured from January to March 1994, reared through yolk sac absorption to about to 2 cm TL, and 3000 stocked into Yuma Cove backwater and 500 to 1000 into each of six other lakeside backwaters, all free of non-native fishes at the time. Survival in autumn was 12 to 76% (three backwaters produced no young), and about 2200 juveniles were harvested and stocked into the lake. A subsample of 14 of 358 juveniles from Yuma Cove backwater was characterized with restriction endonucleases that identified 11 haplotypes and an estimated diversity of 0.95, levels of variation that were not significantly different from the original wild population. Additional support for the utility of this approach was provided by recapture data. Five of 153 cove-reared fish released in autumn 1992 and ten of 487 stocked in 1993 were captured as large sub-adults the spring following their release (Mueller, 1995), demonstrating the successful application of the concept of lake harvest of larvae and custodial rearing.

IMPLEMENTATION

The custodial rearing of lake-harvested larvae was adopted as the standard approach for restoring Razorback Sucker in Lake Mohave (Fig. 4). Naturally produced larvae were available in almost limitless numbers, so the primary bottleneck was identifying suitable places to rear them that were free of non-native fishes. Isolated lakeside backwaters had proven their utility, and some dried annually to ensure absence of non-natives. Predators were mechanically removed from other backwaters with limited success. Chemical treatment was expensive and time consuming and readily thwarted by illicit stocking as had been observed in Yuma Cove backwater and elsewhere. Eleven sites on Lake Mohave already had been pressed into service and there were few new opportunities there, and isolation by construction of new berms at additional existing sites was politically and economically constrained. Space, albeit limited, nonetheless was identified and secured for native fish rearing at Boulder City Golf Course, Boulder City Wetland Ponds, Floyd Lamb State Park, and Reclamation Fish Lab (all in Nevada), and the Phoenix Zoological Garden (Arizona).

Another logical choice for grow-out was the federal hatchery system. U.S. Fish and Wildlife Service Willow Beach National Fish Hatchery (Willow Beach, Fig. 3) was established in 1959 to use cold hypolimnetic release water from Hoover Dam to raise Rainbow Trout *Oncorhynchus mykiss* to support sport fishing in the Colorado River from Lake Powell downstream to Yuma. It was sited on the tailwater shoreline about 18 km downstream from the dam and played a prominent role in early work on native big-river fishes (e.g., Toney, 1974). Willow Beach received multiple transfers from NFWG of Razorback Sucker embryos and larvae for indoor rearing in tanks during the 1980s, but the primary water supply was perennially 11–12°C and too cold to support rapid growth of Razorback Sucker. Thus the water needed to be heated, which was expensive and fraught with logistical issues. Over the years the facility was expanded and upgraded with solar hot water heating, new outdoor raceways, additional well capacity, and myriad other infrastructural improvements that enhanced its warmwater fish rearing capabilities. Willow Beach has reared by far the largest proportion of Razorback Sucker repatriated to Lake Mohave, and it suspended cold-water trout operations temporarily in 2014 in favor of endangered Razorback Sucker and Bonytail. Its satellite site is Achii Hanyo Native Fish Rearing Facility, a former catfish farm adjacent to the lower Colorado River near Parker, Arizona, where Razorback Sucker grow-out is done in outdoor earthen ponds.

Dexter National Fish Hatchery (hereafter Dexter) in New Mexico (later Dexter National Fish Hatchery & Technology Center, now Southwestern Native Aquatic Resources & Recovery Center) also played a significant role in furthering the Razorback Sucker program beginning in 1980. Although primarily responsible for broodstock development and propagation and rearing of hatchery-produced fish, Dexter also was an important grow-out site for Lake Mohave Razorback Sucker. Its capabilities have expanded dramatically over the years. Bubbling Ponds State Fish Hatchery (Cornville, Arizona) and Lake Mead State Fish Hatchery (Boulder City, Nevada) also participate in the Lake Mohave program by rearing Razorback Sucker.

POPULATION MONITORING AND ASSESSMENT

Demographic monitoring.—The importance of long-term monitoring cannot be better exemplified than by the tireless efforts of the NFWG and the resultant 40+ years of data. Early attempts to assess the status of the Lake Mohave population were made in the 1980s. Between November 1982 and May 1983 tagging and fin-clipping efforts by University of Nevada Las Vegas resulted in the marking of 933 adult Razorback Sucker (Bozek et al., 1984). Recaptures of these individuals by various cooperators resulted in an estimate of 73,500 (Marsh, 1994), but the estimate was considered unreliable because tag loss and random assortment were not evaluated. Annual monitoring efforts that began in the late 1970s were renewed in earnest in March 1988 and became known as the ''March Roundup,'' timed to occur near the peak of Razorback Sucker spawning. The week-long effort consisted of deploying various entanglement nets among known spawning grounds centered around Carp Cove (Fig. 3) where WLM first visited the lake in 1967 and ever since had camped with classes, colleagues, and myriad interested parties. The roundup also was when the annual NFWG meeting was held (at Yuma Cove backwater) to discuss observations, strategies, and opportunities.

Although various tagging techniques were employed up to 1991, passive integrated transponder (PIT) tags became the standard marking technique by 1992. Since then, nearly all Razorback Sucker handled from Lake Mohave contained a PIT tag prior to release, including all of the thousands stocked annually as part of the repatriation program. This complete record of capture, release, and recapture spanning more than 30 years has provided annual estimates of population size and survival for both wild and repatriate Razorback Sucker in Lake Mohave, an unprecedented monitoring program allowing for the continuous assessment of the repatriation program.

Survival of repatriates.—While significant effort was made to collect recapture data on released Razorback Sucker in Lake Mohave and all repatriated fish were PIT tagged prior to release, estimated survival was less than 10% for the first year post-release (Marsh et al., 2005). Attempts to determine factors affecting post-stocking survival using mark–recapture techniques were hampered both by low survival and by low recapture rates, the latter estimated at 10% during the March Roundup. Although size at release was clearly identified as a significant contributor to post-stocking survival (Minckley et al., 2003; Marsh et al., 2005), no other single factor was identified through the first two decades of the repatriation program. Acoustic telemetry studies from 2006–2010 verified the size at release and survival relationship and implicated Striped Bass *Morone saxatilis* as a major cause of mortality (Karam et al., 2008). The studies also found that survival for similar sized fish could vary as much as five fold from one year to the next (Kesner et al., 2008, 2010a), and even the largest Razorback Sucker released (about 50 cm TL) was vulnerable to Striped Bass predation (Karam and Marsh, 2010). Although variation in survival of Razorback Sucker released in Lake Mohave was possibly due to fluctuating abundance of Striped Bass, no reliable data on Striped Bass abundance in Lake Mohave were available for comparison.

In 2006, when the repatriation program had entered its 15th year, it was clear that PIT tag technology had advanced considerably and a change in tag frequency would improve monitoring data. The old 400 kHz PIT tags that had been used since the inception of the program had very short read ranges and were only reliably read when the fish was in-hand. In contrast, newer 134.2 kHz PIT tags could be remotely sensed with submerged antennas. The transition from 400 to 134.2 kHz PIT tag was made in 2006, but few fish were stocked from 2007 through 2008 because release size became a prominent issue and fish were held over additional years in an attempt to release fish at 50 cm (USFWS, unpubl. data). All Razorback Sucker captured from the lake, both wild and repatriate, were implanted with the new tag even if they had the old tag already in them (double tagging) to increase potential contact rates until stocking rates increased. Stocking picked up again in 2008–2009, and remote sensing (PIT scanning) on the reservoir began in 2008 at sites of known Razorback Sucker aggregations (Kesner et al., 2010b). By 2012, the number of individuals contacted annually had increased by an order of magnitude compared to traditional sampling alone (Kesner et al., 2012), and by 2013 the total number of fish contacted was greater than 80% of the estimated population size (Kesner et al., 2014).

In addition to the increase in contacts, PIT scanning allowed for sampling in the swiftly flowing lotic waters downstream of Hoover Dam. Wild and repatriate Razorback Sucker were observed in the area long before monitoring began, but were rarely sampled due to the ineffectiveness of netting or electrofishing in the fast and fluctuating waters. PIT scanning in this area resulted in identifying a separate subpopulation that exhibited limited exchange with the subpopulation in the basin (Kesner et al., 2012), effectively doubling the population estimate for Razorback Sucker in the reservoir (Hoover Dam downstream to Davis Dam and including both river and basin reaches; Fig. 3). Monitoring currently focuses on determining the exchange rates between the two subpopulations, locating additional population centers within the reservoir, refining estimates of post-stocking survival, and identifying additional predictors of survival based on PIT scanning contact rates.

Genetic monitoring.—Genetic monitoring provides valuable insight into complex relationships of ecological, demographic, and genetic factors (e.g., Schwartz et al., 2007; Antao et al., 2011; Osborne et al., 2012), and protocols have been developed to monitor patterns of genetic variation within and among locations and years within Lake Mohave (Fig. 4; Dowling et al., 2005, 2014). Garrigan et al. (2002) estimated historical female effective population size for Lake Mohave as 940,000, noting that their coalescent approach using mitochondrial DNA (mtDNA) data indicated that the variation observed was typical of an expanding population. Genetic patterns consistent with population growth are commonly observed in rapidly declining species (Lavery et al., 1996; Garrigan et al., 2002) because of influence of past events (e.g., population growth preceding rapid decline) on coalescent-based estimates. Dowling et al. (2005) used variation in mtDNA to track levels and distribution of genetic variation in larvae, repatriates, and wild adults over time, and Turner et al. (2007) used these data to generate estimates of female effective size for the contemporary population in Lake Mohave. Turner et al. (2009) developed microsatellite markers that were applied to generate comparable measures for the male as well as female component to effective size (Dowling and Marsh, 2011; Dowling et al., 2014). These studies have shown that the program implemented by the NFWG has maintained levels of genetic variation and increased the contribution of individuals in the face of reduced census size. As a matter of fact, the Lake Mohave population is still the most diverse of all remaining populations despite having converged on similarly reduced population size (Table 1; Wilson, 2011).

While much smaller than the historical effective population size, serial estimates of contemporary genetic effective size over the last 17 years are generally greater than 1000 (Dowling et al., 2014), suggesting that the risk of population decline from genetic factors (i.e., reduced viability due to inbreeding or accumulation of deleterious alleles) is low in the Lake Mohave population. Time series analysis of sequential larval cohorts shows that the ratio of effective size to census size is increasing in Lake Mohave, despite complete turnover from remnant wild fish to repatriated fish over the last two decades (Dowling et al., 2014). This observation is important because it provides strong evidence that nearly all reproductively capable fish contribute genes to the larval pool that ultimately builds future reproductive stocks in Lake Mohave. Genetic diversity remains unchanged through the rearing process in protective custody, and to the point where fish are repatriated (Carson et al., unpubl.). The challenges now are to enhance long-term survival of repatriated fish and reduce the need for human intervention through the transition from larva to adult. The 'backwater concept' (Minckley et al., 2003) provides a potential solution to this problem.

THE BACKWATER OR ''OFF-CHANNEL'' CONCEPT

The NFWG set out with an initial expectation of replacing the senescent remnant population with an expanded and stable population of 50,000 adult Razorback Suckers. Monitoring results from the first several years of the program were encouraging because repatriate population numbers were increasing (Marsh et al., 2005). But it became painfully obvious with time and experience that reaching such a goal was unlikely. Harvesting larvae, rearing juveniles, and repatriating sub-adults were planned and executed with ever increasing efficiency, yet population size continued to decline. Recommendations for minimum stocking sizes for Lake Mohave were based largely upon post-stocking observations there and upon information from Gila River studies where ictalurid catfishes were the predators on stocked Razorback Sucker (Marsh and Brooks, 1989); it was presumed that these and Largemouth Bass *Micropterus salmoides* comprised the primary concern in the reservoir. But a wild card was thrown into the mix when the Lake Mohave population of large Striped Bass exploded. These obligate carnivores attained lengths exceeding a meter and were capable of consuming even the largest adult Razorback Suckers (Karam and Marsh, 2010). An abundance of Striped Bass at all age-size classes exerted debilitating predation pressure on both native fishes and non-natives like Rainbow Trout, so much so that less than 1% of nearly 165,000 Razorback Suckers (Pacey and Marsh, 2013) and none of the hundreds of thousands of Rainbow Trout stocked between 1999 and 2012 are thought to survive.

A strategy believed more efficient than the Lake Mohave model and closer to the definition of recovery for both Bonytail and Razorback Sucker was developed and outlined by Minckley et al. (2003). The plan consists of maintaining adult populations of these two species in the Colorado River system including Lake Mohave, and developing multiple self-recruiting populations of the species within protected off-channel habitats free of non-native fishes. The second half of the plan denoted in this paper as the backwater concept was fortuitously tested in a small remnant oxbow of the old Colorado River channel (ca. 0.25 ha), created by U.S. Bureau of Reclamation channelization efforts in the 1970s. The oxbow has a hydrologic connection to the river via the porous substrate used in the levees, and was chemically renovated and stocked with Bonytail and Razorback Sucker in 1993. Both species had naturally recruiting populations for longer than a decade until non-native Largemouth Bass invaded and eliminated recruitment (LaBarbara and Minckley, 1999; Marsh, 2000; Mueller et al., 2003).

Imperial ponds.—A panel of experts was convened in December 2004 to develop design criteria for the creation of off-channel habitats based on the backwater concept. Their finalized plan called for six experimental ponds with specific features thought to aid in Bonytail and Razorback Sucker recruitment and survival: hummocks, gravel substrate for spawning, and rip-rap shoreline for cover (USBR, 2005). The ponds would be used to test the backwater concept and the utility of each habitat feature. A series of existing ponds on USFWS Imperial National Wildlife Refuge, Arizona and California was transformed into six backwaters and named ''Imperial Native Fish Ponds'' in 2007. Although the ponds incorporated many of the special features of the design plan, the ponds failed to produce self-sustaining populations of native fishes due to the continued presence and invasion of non-native fishes that constrained recruitment by predation on early life stages.

Groundwater was initially preferred over screened river water as a secure (i.e., lacking in non-native fish eggs and larvae) water source (USBR, 2005). However, screened river water from an inlet canal to Martinez Lake on the Colorado River was piped in as the main water source (LCR MSCP, 2008). The ponds were not renovated prior to native fish stocking and a ''wait and see'' approach was established. Within the first year non-native sunfishes (Centrarchidae), Common Carp *Cyprinus carpio*, and Western Mosquitofish *Gambusia affinis* were detected in all six ponds (Kesner et al., 2011). Failure of the screens at the pumping platform to filter fish eggs and larvae was confirmed by experimental trials in 2009 (McDonald and Karchesky, 2010). Chemical renovation attempts were partially successful in two ponds, but by 2011 all Bonytail and Razorback Sucker were consolidated into a single pond supplied by well water and contaminated by only Western Mosquitofish. The other five ponds have since been dedicated to water physico-chemistry and hydrological monitoring, and it is unclear when they may come back on-line to the benefit of native fishes. Although limited Bonytail and Razorback Sucker recruitment was documented in the presence of non-native fishes, the ponds failed to provide the environment necessary to test the backwater concept.

Other places to rear young fish.—Additional off-site facilities continue to provide short-term examples of the potential of the concept. Lakeside backwaters adjacent to Lake Mohave have served since 1992 as grow-out facilities for Razorback Sucker destined to be stocked into Lake Mohave (Marsh et al., 2005). Typically, Razorback Sucker are stocked in spring and harvested in autumn with an average survival over the period of approximately 50% (Ty Wolters, U.S. Bureau of Reclamation, pers. comm.). Most of the backwaters dry during autumn–winter lake drawdowns resetting the ponds each year and limiting non-native fish presence. This drying also eliminates the potential to use these waters for self-recruiting populations of Bonytail and Razorback Sucker. Exceptions to this limitation have recently been exploited for use in experiments involving self-recruiting populations of Bonytail (Davis Cove backwater; Fig. 3) and Razorback Sucker (Yuma Cove backwater). These two lakeside backwaters have enough depth to avoid drying during drawdowns, and their isolation from the lake is ensured by mechanically maintained berms. Observations on habitat use, survival, population size structure, and water quality are ongoing in Davis Cove backwater, and Yuma Cove backwater is being used to estimate adult contributions to offspring per year and generation using genetic techniques and remote PIT scanning.

Additional sites for backwaters are currently in various stages of development, but the full potential of the concept to restore Razorback Sucker remains unrealized. The LCR MSCP calls for the creation of off-channel habitats based on the backwater concept downstream of Lake Mohave. However, the plan gives no preference to backwaters that are devoid of non-native fish species (i.e., the plan does not specify their absence as a requirement). Backwaters under this plan that were allowed to contain non-native fishes would ''count'' toward the goals of the LCR MSCP but not contribute significantly to the conservation or recovery of either Bonytail or Razorback Sucker. Examples of recruitment failure in waters with non-native fishes are pervasive and undisputed (Marsh and Langhorst, 1988; Mueller et al., 2003; Marsh and Pacey, 2005; Kesner et al., 2011).

POLITICAL REALITIES: REGIONAL AND BASINWIDE IMPACTS

NFWG partnerships continue to be strong and effective under auspices of the LCR MSCP, which now has broad purview over Razorback Sucker management in Lake Mohave (LCR MSCP, 2006). All of the founding entities still participate. However, at the onset of the program, management decisions were made at the lowest possible level (field biologists actually working on the fish). Programmatic decision-making is now done by LCR MSCP signatory parties who determine the direction of (and funding for) the program with input from field biologists, including those in the NFWG. Nonetheless, core functions of the program, including annual spring and autumn adult (repatriate) monitoring and winter–spring larval harvest still are conducted as joint operations with broad participation across agencies and interested parties.

While the situation for the lower Colorado River basin is relatively straightforward, conservation range-wide is fraught with complications. There are several different groups responsible for conservation of Razorback Sucker, specifically divided along geo-political boundaries. Lower and Upper Colorado River basins are administratively divided at Lee's Ferry, 1.6 km downstream from the mouth of Paria River at the head of Grand Canyon. Programs to benefit native fishes are separate and distinct in the two basins, and sources and allocations of resources are different and sometimes disparate. Unfortunately for all involved, and especially so for the fishes that do not recognize political boundaries, there has long been a lack of communication and an undercurrent of mistrust among workers in the two basins. A result is a sense that not all interests are equally represented in policy decisions such as designation of critical habitat or determination of recovery goals, or implementation of effective conservation strategies. Open dialogue and improved cooperation at all levels would improve the situation.

These geo-political issues have had a direct impact on formulation of landmarks for recovery. Recovery goals articulated in the initial Razorback Sucker recovery plan (USFWS, 1998) were qualitative and obvious: in the short term prevent extinction, in the long term recover the fish so it no longer needs protection of the Endangered Species Act. The former would be attained when decline of the Lake Mohave and two upper Colorado River basin stocks was reversed, as evidenced by natural recruitment leading to increasing population sizes. The plan was amended by quantitative goals (USFWS, 2002) that for downlisting required, among other things, maintenance of a genetic refuge in Lake Mohave and of multiple, self-sustaining populations each numbering more than 5800 adults. The prognosis at the time was that ''Based on current information and associated uncertainties, it is estimated that self-sustaining populations of Razorback Sucker will become established over the next 15 years.'' (USFWS, 2002:56). Another recovery plan revision is in process. For political reasons recovery leadership was placed with USFWS Region 6 in Denver, Colorado, at least in part because the Upper Colorado River Recovery Implementation Program (USFWS, 1987; Wydoski and Hamill, 1991) for recovery of Razorback Sucker and other big-river fishes also was located there. Also for political reasons, meaningful participation of many knowledgeable individuals and leading species experts from USFWS Region 2, which includes the lower Colorado River basin, was largely excluded from the recovery planning process. In light of current status of Razorback Sucker in Lake Mohave and throughout its range, timely attainment of current recovery goals is improbable. Considering the massive expenditures on behalf of the big-river fishes ($293 million from 1989 to 2013 for the upper basin RIP [Tart, 2014] and part of a projected >$626 M over 50 years for the lower basin [LCR MSCP, 2004]), it seems more likely that legislators and funding partners will tire of investing in programs that have failed to benefit the species than recovery or conservation will actually be attained. It may transpire that new recovery goals present a lower bar and thereby preserve existing programmatic infrastructure and process but still fail to serve the needs of the species, but we hope for better.

PAST, PRESENT, AND FUTURE OF RAZORBACK SUCKER IN LAKE MOHAVE

The Razorback Sucker is at a crossroads relative to its evolutionary history and ability to persist in the dramatically altered environment of the Colorado River basin. This makes it an excellent time to look at what can and needs to be done to maintain this species into the future.

Razorback Sucker has declined precipitously range-wide and is currently maintained by repatriation programs in all locations where it currently resides, with a possible and notable exception of Lake Mead. The population in Lake Mohave is still one of the largest, and conservation efforts have maintained its high level of genetic diversity; therefore, it likely remains the most genetically diverse. This combination of features makes this population the cornerstone for Razorback Sucker conservation.

Like most other locations, the presence of non-native fishes has made it impossible to gain any headway toward re-establishment of a self-sustaining population in Lake Mohave. While this reservoir is still important, it and other currently and formerly occupied places could be replaced by other "natural" locations (e.g., big rivers) that are more hospitable for maintaining "wild" populations. Note, however, as species are extirpated it becomes less important to manage them in these systems (e.g., Colorado pikeminnow in the lower Colorado River basin; Miller, 1961; Minckley, 1973), and such locations could be completely lost as "natural" ecosystems for native fishes. Therefore, it is important to keep Razorback Sucker in Lake Mohave as a placeholder for its former habitat.

When the NFWG developed its protective custody program in the early 1990s, the key assumption was that " . . . Razorback Sucker of approximately 30 cm TL and longer are essentially immune to existing predators" (Minckley et al., 2003). The thought at that time was that a large population of Razorback Sucker could be established in Lake Mohave, with self-sustaining populations present in protected backwater habitats. This combination of populations would include a large population of adults in Lake Mohave and all life history stages in isolated backwaters, producing stable demographic and genetic structure. Given the longevity of this species, this situation could provide time to solve the problem posed by predation of non-native species on early life stages.

Unfortunately, the situation in Lake Mohave has changed for the worse. Striped Bass has become abundant in the reservoir, and they are known to consume Razorback Sucker >50 cm TL (Karam and Marsh, 2010). Their presence makes it difficult, perhaps impossible, to establish and maintain a large population of adult Razorback Sucker in Lake Mohave (Marsh et al., 2005). Other regions have this and/or other similarly effective, large predators (e.g., Flathead Catfish *Pylodictis olivaris*, Northern Pike *Esox lucius*); therefore, this issue will impact conservation efforts throughout its range. At this time, there are no known methods to eradicate non-native fishes from large river systems; therefore, it is currently not possible to re-establish Razorback Sucker in native habitats because the threats are still in place.

Role of hatcheries in conservation.—Hatcheries have played an increasingly important role in on-the-ground conservation efforts, and to a lesser extent in recovery of endangered fishes. The challenge in a conservation hatchery is threefold: (1) to produce sufficient numbers of fishes to significantly bolster numbers in the wild, (2) to match or enhance genetic diversity of wild populations, and (3) to remove effects of hatchery-imposed selection regimes such that fitness in the wild is not compromised. Over the last few decades, spawning and rearing practices have been honed, developed, and tested through research programs at Dexter (e.g., Wilson, 2011, 2012) and elsewhere. Based on these efforts, it is clear that challenges 1 and 2 can be adequately met and addressed. However, effects of hatchery-imposed selection are impossible to remove completely (Waples, 1999; Frankham, 2008), and there are unavoidable trade-offs between maintaining 'neutral' genetic diversity (e.g., by reducing variance in family size) and hatchery-imposed selection (Fraser, 2008).

It is for these reasons that we advise resistance to the temptation to use hatchery culture to quickly produce large quantities of individuals to replace the existing Lake Mohave stock. Population size can clearly be maintained through stocking hatchery-cultured fish but at a substantial potential cost to survivorship and viability in the wild, and with unknown future results.

It is possible, if not likely, that rearing larval fishes in protective custody also alters natural selective regimes or imposes a new selective environment. However, because this strategy permits mate choice in the wild, deposition of gametes over natural substrates, and at least an opportunity for a natural foraging strategy, we suggest that it is the preferred alternative for minimizing effects of hatchery-imposed selection. Implementation of strategies that further reduce human intervention, such as those detailed in the backwater concept, could be an important advance toward restoring quasi-natural evolutionary forces acting upon this managed population.

A second and arguably more important function of conservation hatcheries is that they provide a measure of insurance against catastrophic loss in the wild, particularly when wild populations are geographically restricted (such as in Lake Mohave). Thus, we do not advocate an end to the hatchery program because it is imperative that a large, diverse broodstock be maintained in case other efforts fail. The present broodstock at Dexter should be periodically replaced through augmentation with wild-caught individuals, however, and production should be designed to maintain documented genetic variability in offspring produced for any future purpose. Progeny of the current broodstock should not be released to replace the existing Lake Mohave population. Instead, the backwater culture program should be continued and expanded, if for no other reason than to provide additional habitat where both backwater culture and wild-caught larvae can grow. Rearing should be geographically as near Lake Mohave as possible to minimize transport expense and fish losses through handling. The safest course would be to keep all three options open, if economics allow and if dedication and mandate are sufficient incentives, so that if one method fails the others may be attempted.

Role of backwaters in conservation.—The backwater approach has more positive attributes than a hatchery based approach. Use of larvae captured in the lake utilizes many more parents than it is possible to maintain in a hatchery, maximizing the genetic contribution of potential parents. Rearing fishes in more natural habitats minimizes the impact of domestication selection imparted by raising them in captivity. Most importantly, backwater populations can be managed as self-perpetuating, with stable demographic and genetic features.

Can such backwater populations be used to supplement "wild" populations? That depends on our ability to produce backwater populations with the appropriate features. Razorback Sucker are known to reproduce in ponds, and their progeny can themselves become reproductive (Mueller et al., 2003; Kesner et al., 2011; unpubl. data). Unfortunately, such ponds have never been allowed to perpetuate, so it is not certain what conditions would be necessary to generate stable, self-replicating populations. If they can, these backwater populations will be miniature replicates of what are considered to be wild populations, albeit on a smaller scale and linking them together in a metapopulation network could provide a powerful tool for conservation of this species.

CONCLUSIONS AND RECOMMENDATIONS

Proactive management of Razorback Sucker in Lake Mohave has thus far conserved the genetic diversity of the species, but the once abundant wild population is gone, and both a relatively small repatriate population and the program itself depend on stocking (Fig. 4). Absent the current program or a successful alternative, the species will disappear from the lower basin. We believe the future of Razorback Sucker and other big-river fishes such as Bonytail in the lower Colorado River lies in application through aggressive implementation of an off-channel management concept (Minckley et al., 2003; USFWS, 2005) that separates them from harmful non-native fishes. In this regard some successes of the Lake Mohave conservation program may be measured best in terms of lessons learned and knowledge gained. We now know that Razorback Sucker cannot perpetuate itself regardless of fish size or abundance because the extant predator load is simply too great. We know that numbers and genetic diversity can be maintained by harvest from the wild of naturally produced fish, and case studies demonstrate that life cycle completion is possible where non-native fishes are excluded but that recruitment fails where non-natives are present.

Ability to eliminate non-native fishes is an absolute requirement of any successful native fish management program, and realistically this means that we must be able to desiccate any habitat where Razorback Sucker and Bonytail are expected to reproduce and recruit. This is because there is no other practical treatment that can ensure eradication of non-native fishes. As articulated before, we envision a number of off-channel sites where the species can live, with periodic exchange of individuals to maintain genetic heterogeneity. These populations also could contribute adults to mainstem habitats, including Lake Mohave, and vice versa, where life cycle completion is not possible. The necessary number of off-channel populations and requirements for movement of individuals among them would be determined by demographic and genetic studies in currently available sites.

The Lake Mohave repatriation program must continue unabated until adequate off-channel habitats are in place and reliably functioning as determined by appropriate monitoring and assessment. Moving the recommended program forward will require participation and cooperation of all entities currently committed to the LCR MSCP but especially those who own or manage the resources of land and water that must be allocated to provide needed habitat. All parties must be proactive and responsive, and willing to make adjustments indicated by new information—"adaptive management" must be a reality rather than a rhetorical catch-phrase. The technology is available to conserve the Razorback Sucker; we need only the will to implement it.

While levels of genetic diversity in Lake Mohave clearly identify its importance for conservation, this does not diminish the significance of other populations that occupy a variety of different habitats and environmental regimes. Unfortunately, recovery effort for the species has suffered from geo-political division. Minimally, representatives from both basins need to be communicating to share their considerable knowledge and experience. Ideally, a composite of these groups should attempt to generate a cohesive vision for conservation of the species. Such a joint venture should include representatives from all regions and disciplines and would allow us to move beyond regional approaches and to generate a more inclusive approach to conservation of Razorback Sucker.

ACKNOWLEDGMENTS

Founding members of the Lake Mohave Native Fishes Work Group included T. Burke (Reclamation, retired), M. Burrell (NVDOW, retired), G. Devine (USFWS, retired), R. Haley (NPS), T. Liles (AZGFD, retired), PCM, C. Minckley (USFWS, retired), WLM, G. Mueller (USGS, retired), and J. Sjoberg (NVDOW), and others too numerous to thank individually participated in meaningful ways over the years. We thank R. Clarkson, C. Pacey, and T. Wolters for their constructive reviews of the manuscript.

LITERATURE CITED

Abbott, C. C. 1861. Descriptions of four new species of North American Cyprinidae. Proceedings of the Philadelphia Academy of Natural Sciences 12:473–474.

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 26:336–344.

Albrecht, B., T. Sanderson, and P. B. Holden. 2008. Razorback sucker studies on Lake Mead, Nevada and Arizona, 1996–2007 Comprehensive Report. Prepared for the U.S. Department of the Interior, Bureau of Reclamation, and the Department of Resources, Southern Nevada Water Authority by BIO-WEST, Inc., Logan, Utah. PR-1093-2.

Allan, D. C., and D. L. Roden. 1980. Fishes of Lake Mead and Lake Mohave. Nevada Department of Wildlife Biological Bulletin 7:1–105.

Amin, O. M. 1969a. Helminth fauna of suckers (Catostomidae) of the Gila River system, Arizona. I. *Nematobothrium texomenis* McIntosh and Self, 1955 (Trematoda) and *Glaridacris confusus* Hunter, 1929 (Cestoda) from buffalofish. American Midland Naturalist 82:188–196.

Amin, O. M. 1969b. Helminth fauna of suckers (Catostomidae) of the Gila River system, Arizona. II. Five parasites from *Catostomus* spp. American Midland Naturalist 82:429–443.

Antao, T., A. Pérez-Figueroa, and G. Luikart. 2011. Early detection of population declines: high power of genetic monitoring using effective population size estimators. Evolutionary Applications 4:144–154.

Araki, H., B. A. Berejikian, M. J. Ford, and M. S. Blouin. 2008. Fitness of hatchery-reared salmonids in the wild. Evolutionary Applications 1:342–355.

Bestgen, K. R. 1990. Status review of the razorback sucker, *Xyrauchen texanus*. Final Report, Bureau of Reclamation, Salt Lake City, Utah. Larval Fish Laboratory Contribution 44.

Bestgen, K. R., K. A. Zelasko, and G. C. White. 2012. Monitoring reproduction, recruitment, and population status of razorback suckers in the Upper Colorado River Basin. Final Report, Upper Colorado River Endangered Fish Recovery Program, U.S. Fish and Wildlife Service, Denver, Colorado. Larval Fish Laboratory Contribution 170.

Bozek, M. A., L. J. Paulson, and J. E. Deacon. 1984. Factors affecting reproductive success of bonytail chubs and razorback suckers in Lake Mohave. Final Report, U.S. Fish and Wildlife Service Contract 14-16-0002-81-251. University of Nevada, Las Vegas.

Bozek, M. A., L. J. Paulson, and G. R. Wilde. 1991. Spawning season of the razorback sucker, *Xyrauchen texanus,* in Lake Mohave, Arizona and Nevada. Journal of Freshwater Biology 6:61–73.

Buth, D. G., T. R. Haglund, and S. L. Drill. 1995. Allozyme variation and population structure in the razorback sucker, *Xyrauchen texanus*. Proceedings of the Desert Fishes Council 26:28–29.

Buth, D. G., R. W. Murphy, and L. Ulmer. 1987. Population differentiation and introgressive hybridization of the flannelmouth sucker and of hatchery and native stocks of razorback sucker. Transactions of the American Fisheries Society 116:103–110.

Clarkson, R. W., P. C. Marsh, S. E. Stefferud, and J. A. Stefferud. 2005. Conflicts between native fish and nonnative sport fish management in the southwestern United States. Fisheries 30:20–27.

Crist, L. W., and D. W. Ryden. 2003. Genetics management plan for the endangered fishes of the San Juan River. Final report, San Juan River Recovery Implementation Program, 24 March 2003.

Czapla, T. E. 1999. Genetics management plan (Revised Final). Recovery Implementation Program for Endangered Fish Species in the Upper Colorado River Basin. U.S. Fish and Wildlife Service, Denver, Colorado.

Dill, W. A. 1944. Fishery of the lower Colorado River. California Fish and Game 30:109–211.

Dowling, T. E., and P. C. Marsh. 2011. Work task C31 of the LCR MSCP–RASU Genetic Diversity Assessment. Report, Lower Colorado River Multi-Species Conservation Office, Bureau of Reclamation, Agreement Number R09AP30001.

Dowling, T. E., P. C. Marsh, A. T. Kelsen, and C. A. Tibbets. 2005. Genetic monitoring of wild and repatriated populations of endangered razorback sucker (*Xyrauchen texanus*, Catostomidae, Teleostei) in Lake Mohave, Arizona–Nevada. Molecular Ecology 14:123–135.

Dowling, T. E., W. L. Minckley, and P. C. Marsh. 1996a. Mitochondrial DNA diversity within and among populations of razorback sucker (*Xyrauchen texanus*) as determined by restriction endonuclease analysis. Copeia 1996:542–550.

Dowling, T. E., W. L. Minckley, P. C. Marsh, and E. Goldstein. 1996b. Mitochondrial DNA diversity in the endangered razorback sucker (*Xyrauchen texanus*): analysis of hatchery stocks and implications for captive propagation. Conservation Biology 10:120–127.

Dowling, T. E., M. J. Saltzgiver, D. Adams, and P. C. Marsh. 2012b. Assessment of genetic variability in a recruiting population of endangered fish, the razorback sucker (*Xyrauchen texanus*, family Catostomidae), from Lake Mead, AZ–NV. Transactions of the American Fisheries Society 141:990–999.

Dowling, T. E., M. J. Saltzgiver, and P. C. Marsh. 2012a. Genetic structure within and among populations of the endangered razorback sucker (*Xyrauchen texanus*) as determined by analysis of microsatellites. Conservation Genetics 13:1073–1083.

Dowling, T. E., T. F. Turner, E. W. Carson, M. J. Saltzgiver, D. Adams, B. Kesner, and P. C. Marsh. 2014. Time-series analysis reveals genetic responses to intensive management of razorback sucker (*Xyrauchen texanus*). Evolutionary Applications 7:339–354.

Frankham, R. 2008. Genetic adaptation to captivity in species conservation programs. Molecular Ecology 17:325–333.

Franklin, I. R., and R. Frankham. 1998. How large must populations be to retain evolutionary potential? Animal Conservation 1:69–70.

Fraser, D. J. 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. Evolutionary Applications 1:535–586.

Garrigan, D., P. C. Marsh, and T. E. Dowling. 2002. Long-term effective population size of endangered Colorado River fishes. Animal Conservation 5:95–102.

Gobalet, K. W. 1992. Colorado River fishes of Lake Cahuilla, Salton Basin, southern California: a cautionary tale for zooarchaeologists. Bulletin of the Southern California Academy of Sciences 91:70–83.

Gobalet, K. W. 1994. Additional archaeological evidence for Colorado River fishes in the Salton Basin of southern California. Bulletin of the Southern California Academy of Sciences 93:8–41.

Gobalet, K. W., and T. A. Wake. 2000. Archaeological and paleontological fish remains from the Salton Basin, southern California. The Southwestern Naturalist 45: 514–520.

Hamman, R. L. 1985. Induced spawning of hatchery-reared razorback sucker. Progressive Fish-Culturist 47:187–189.

Hamman, R. L. 1987. Survival of razorback sucker cultured in earthen ponds. Progressive Fish-Culturist 49:135–140.

Hendrickson, D. A. 1993. Evaluation of the razorback sucker (*Xyrauchen texanus*) and Colorado squawfish (*Ptychocheilus lucius*) reintroduction programs in central Arizona based on surveys of fish populations in the Salt and Verde rivers from 1986 to 1990. Final Report, Arizona Game and Fish Department, Phoenix.

Horn, M. J. 1996. Nutritional limitation of recruitment in the razorback sucker (*Xyrauchen texanus*). Unpubl. Ph.D. diss., Arizona State University, Tempe, Arizona.

Inslee, T. D. 1982. Culture of endangered Colorado River fishes. Section III: spawning of razorback sucker, p. 145–157. *In*: Final Report. Reclamation Contract No. 9-07-40-L-1016. W. H. Miller, J. J. Valentine, D. L. Archer, H. M. Tyus, R. A. Valdez, and L. R. Kaeding (eds.). U.S. Fish and Wildlife Service, Salt Lake City, Utah.

Jonez, A., R. D. Beland, G. Duncan, and R. A. Wagner. 1951. Fisheries report of the lower Colorado River. Arizona Game and Fish Commission, Phoenix, Arizona.

Jonez, A., and R. C. Sumner. 1954. Lakes Mead and Mohave investigations: a comparative study of an established reservoir as related to a newly created impoundment.

Final Report, Federal Aid Project F-1-R. Nevada Fish and Game Commission, Reno, Nevada.

Karam, A. P., B. R. Kesner, and P. C. Marsh. 2008. Acoustic telemetry to assess post-stocking dispersal and mortality of razorback sucker *Xyrauchen texanus* (Abbott). Journal of Fish Biology 73:1–9.

Karam, A. P., and P. C. Marsh. 2010. Predation of adult razorback sucker and bonytail by striped bass in Lake Mohave, Arizona–Nevada. Western North American Naturalist 70:117–120.

Kegerries, R., B. Albrecht, and P. Holden. 2009. Razorback sucker studies on Lake Mead, Nevada and Arizona 2008–2009. Final Report, U.S. Bureau of Reclamation and Southern Nevada Water Authority, PR-1161-2. Bio-West, Logan, Utah.

Kesner, B. K., J. S. Fencl, G. Ley, and P. C. Marsh. 2011. Imperial Ponds native fish monitoring 2011 final report October 2008–August 2011. Final Report, Reclamation Agreement No. R09AP30002. Marsh & Associates, Tempe, Arizona.

Kesner, B. R., A. P. Karam, C. A. Pacey, and P. C. Marsh. 2008. Demographics and post-stocking survival of repatriated razorback sucker in Lake Mohave. Final Report. Bureau of Reclamation Agreement No. 06-FC-300003, Boulder City, Nevada. Arizona State University, Tempe, Arizona.

Kesner, B. R., A. P. Karam, C. A. Pacey, and P. C. Marsh. 2010a. Demographics and post-stocking survival of repatriated razorback sucker in Lake Mohave. Annual Report. Bureau of Reclamation Agreement No. 09-FG-30-0002, Boulder City, Nevada. Marsh & Associates, Tempe, Arizona.

Kesner, B. R., A. P. Karam, C. A. Pacey, J. W. Warmbold, and P. C. Marsh. 2012. Lake Mohave razorback sucker monitoring 2012 annual report. Reclamation Agreement No. R12PD30001. Marsh & Associates, Tempe, Arizona.

Kesner, B. R., W. A. Massure, C. A. Pacey, and P. C. Marsh. 2014. Lake Mohave razorback sucker monitoring 2013 annual report. Reclamation Agreement No. R12PD30001. Marsh & Associates, Tempe, Arizona.

Kesner, B. R., J. R. Nelson, M. K. Fell, G. Ley, and P. C. Marsh. 2010b. The development of two portable remote (PIT) scanning systems. Colorado River Basin Science and Resource Management Symposium. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.

LaBarbara, M., and C. O. Minckley. 1999. Report on native fish growout facilities at Cibola and Imperial National Wildlife Refuges 1993-1995. U.S. Fish and Wildlife Service, Parker Fishery Resources Office, Parker, Arizona.

Lavery, S., C. Moritz, and D. R. Fielder. 1996. Genetic patterns suggest exponential population growth in a declining species. Molecular Biology and Evolution 13:1106–1113.

LCR MSCP. 2004. Final habitat conservation plan. Volume II. Lower Colorado River Multi-Species Conservation Program Office, Boulder City, Nevada.

LCR MSCP. 2006. Final fish augmentation plan. Lower Colorado River Multi-Species Conservation Program Office, Boulder City, Nevada.

LCR MSCP. 2008. Imperial Ponds Conservation Area Restoration Development Plan. January, Boulder City, Nevada.

Lynch, M., and R. Lande. 1998. The critical effective size for a genetically secure population. Animal Conservation 1:70–72.

Marsh, P. C. 1985. Effect of incubation temperature on survival of embryos of native Colorado River fishes. The Southwestern Naturalist 30:129–140.

Marsh, P. C. 1987. Food of adult razorback sucker in Lake Mohave, Arizona–Nevada. Transactions of the American Fisheries Society 116:117–119.

Marsh, P. C. 1994. Abundance, movements, and status of adult razorback sucker, *Xyrauchen texanus*, in Lake Mohave, Arizona and Nevada. Proceedings of the Desert Fishes Council 25:35–36.

Marsh, P. C. 2000. Fish population status and evaluation in the Cibola High Levee Pond. Final Report, U.S. Bureau of Reclamation Agreement No. 99-FG-30-00051. Arizona State University, Tempe, Arizona.

Marsh, P. C., and J. E. Brooks. 1989. Predation by ictalurid catfishes as a deterrent to re-establishment of hatchery-reared razorback suckers. The Southwestern Naturalist 34:188–195.

Marsh, P. C., B. R. Kesner, and C. A. Pacey. 2005. Repatriation as a management strategy to conserve a critically imperiled species. North American Journal of Fisheries Management 25:547–556.

Marsh, P. C., and D. R. Langhorst. 1988. Feeding and fate of wild larval razorback sucker. Environmental Biology of Fishes 21:59–67.

Marsh, P. C., and W. L. Minckley. 1989. Observations on recruitment and ecology of razorback sucker: lower Colorado River, Arizona–California–Nevada. Great Basin Naturalist 49:71–78.

Marsh, P. C., and W. L. Minckley. 1992. Status of bonytail (*Gila elegans*) and razorback sucker (*Xyrauchen texanus*) in Lake Mohave, Arizona–Nevada. Proceedings of the Desert Fishes Council 23:18–23.

Marsh, P. C., and C. A. Pacey. 2005. Immiscibility of native and nonnative fishes, p. 59–63. *In*: Restoring Native Fish to the Lower Colorado River: Interactions of Native and Nonnative Fishes. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, and U.S. Bureau of Reclamation, Boulder City, Nevada.

McAda, C. W., and R. S. Wydoski. 1980. The razorback sucker, *Xyrauchen texanus*, in the upper Colorado River basin, 1974–1976. Technical Paper U.S. Fish and Wildlife Service Series 99:1–15.

McCarthy, M. S., and W. L. Minckley. 1987. Age estimation for razorback sucker (Pisces: Catostomidae) from Lake Mohave, Arizona and Nevada. Journal of the Arizona–Nevada Academy of Science 21:87–97.

McClure, M. M., F. M. Utter, C. Baldwin, R. W. Carmichael, P. F. Hassemer, P. J. Howell, P. Spruell, T. D. Cooney, H. A. Schaller, and C. E. Petrosky. 2008. Evolutionary effects of alternative artificial propagation programs: implications for viability of endangered anadromous salmonids. Evolutionary Applications 1:356–375.

McDonald, R. D., and C. M. Karchesky. 2010. Evaluation of the cylindrical wedge-wire screen system at the Imperial National Wildlife Refuge, Arizona 2009. U.S. Bureau of Reclamation Contract No. GS10F0319M, Boulder City, Nevada. Normandeau Associates Inc., Stevenson, Washington.

Miller, R. R. 1955. Fish remains from archeological sites in the lower Colorado River basin, Arizona. Papers of the Michigan Academy of Science, Arts, and Letters XL:125–136 + plates.

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

Minckley, W. L. 1973. Fishes of Arizona. Arizona Game and Fish Department, Phoenix, Arizona.

Minckley, W. L. 1979. Aquatic habitats and fishes of the lower Colorado River, southwestern United States. Reclamation Contract No. 14-06-300-2529. Arizona State University, Tempe, Arizona.

Minckley, W. L. 1983. Status of the razorback sucker, *Xyrauchen texanus* (Abbott), in the lower Colorado River basin. The Southwestern Naturalist 28:165–187.

Minckley, W. L. 1991. Native fishes of the Grand Canyon region: an obituary?, p. 124–177. *In*: Colorado River Ecology and Dam Management. National Academy Press, Washington, D.C.

Minckley, W. L., and N. T. Alger. 1968. Fish remains from an archaeological site along the Verde River, Yavapai County, Arizona. Plateau 40:91–97.

Minckley, W. L., and P. C. Marsh. 2009. Inland fishes of the greater southwest: chronicle of a vanishing biota. The University of Arizona Press, Tucson, Arizona.

Minckley, W. L., P. C. Marsh, J. E. Brooks, J. E. Johnson, and B. L. Jensen. 1991. Management toward recovery of the razorback sucker, p. 303–317. *In*: Battle Against Extinction: Native Fish Management in the American West. W. L. Minckley and J. E. Deacon (eds.). University of Arizona Press, Tucson, Arizona.

Minckley, W. L., P. C. Marsh, J. E. Deacon, T. E. Dowling, P. W. Hedrick, W. E. Matthews, and G. A. Mueller. 2003. A conservation plan for native fishes of the lower Colorado River. BioScience 53:219–234.

Moffett, J. W. 1942. A fishery survey of the Colorado River below Boulder Dam. California Fish and Game 28:76–86.

Mpoame, M. 1981. Parasites of some fishes native to Arizona and New Mexico, with ecological notes. Unpubl. Ph.D. diss., Arizona State University, Tempe, Arizona.

Mueller, G. A. 1989. Observations of spawning razorback sucker (*Xyrauchen texanus*) utilizing river habitat in the lower Colorado River, Arizona–Nevada. The Southwestern Naturalist 34:147–149.

Mueller, G. A. 1995. A program for maintaining the razorback sucker in Lake Mohave. American Fisheries Society Symposium 15:127–135.

Mueller, G. A., J. Carpenter, P. C. Marsh, and C. O. Minckley. 2003. Cibola High Levee Pond Annual Report 2003. Project Report, U.S. Geological Survey, Fort Collins Science Center, Fort Collins, Colorado.

Mueller, G. A., M. Horn, J. Kahl, Jr., T. Burke, and P. C. Marsh. 1993. Use of larval light traps to capture razorback sucker (*Xyrauchen texanus*) in Lake Mohave, Arizona–Nevada. The Southwestern Naturalist 38:399–402.

Mueller, G. A., and P. C. Marsh. 2002. Lost, a desert river and its native fishes: a historical perspective of the lower Colorado River. U.S. Geological Survey Information and Technology Report USGS/BRD/ITR-2002-0010, Denver, Colorado.

Osborne, M. J., E. W. Carson, and T. F. Turner. 2012. Genetic monitoring and complex population dynamics: insights from a 12-year study of the Rio Grande silvery minnow. Evolutionary Applications 5:553–574.

Pacey, C. A., and P. C. Marsh. 2013. Lower Colorado River native fish database October 1, 2012 to September 30, 2013. Annual Report, Reclamation Agreement No. R12AP30002. Marsh & Associates, Tempe, Arizona.

Papoulias, D., and W. L. Minckley. 1990. Food limited survival of larval razorback suckers in the laboratory. Environmental Biology of Fishes 29:73–78.

Patterson, K. A., B. R. Kesner, A. P. Karam, and P. C. Marsh. 2013. Comparative survival of repatriated razorback sucker in lower Colorado River Reach 3. Final Report, Reclamation Agreement No. R12AP30013. Marsh & Associates, Tempe, Arizona.

Rostlund, E. 1952. Freshwater fish and fishing in native North America. University of California Publications in Geography 9:1–313.

Schooley, J. D., and P. C. Marsh. 2007. Stocking of endangered razorback suckers in the lower Colorado River basin over three decades: 1974–2004. North American Journal of Fisheries Management 27:43–51.

Schwartz, M. K., G. Luikart, and R. S. Waples. 2007. Genetic monitoring as a promising tool for conservation and management. Trends in Ecology & Evolution 22:25–33.

Sigler, W. F., and R. R. Miller. 1963. Fishes of Utah. Utah State Department of Fish and Game, Salt Lake City, Utah.

Tart, J. K. 2014. The upper Colorado River endangered fish recovery program: twenty-five years in the making. University of Denver Water Law Review, January 16, 2014. http://duwaterlawreview.com/tag/upper-colorado-river-basin-endangered-fish-recovery-program/

Toney, D. P. 1974. Observations on the propagation and rearing of two endangered fish species in a hatchery environment. Proceedings of the Annual Conference of the Western Associations of Fish and Game Commissioners 54:252–259.

Turner, T. F., T. E. Dowling, P. C. Marsh, B. R. Kesner, and A. T. Kelsen. 2007. Effective size, census size, and genetic monitoring of the endangered razorback sucker, *Xyrauchen texanus*. Conservation Genetics 8:417–425.

Turner, T. F., T. E. Dowling, M. J. Osborne, M. V. McPhee, R. E. Broughton, and J. R. Gold. 2009. Microsatellite markers for the endangered razorback sucker, *Xyrauchen texanus*, are widely applicable to genetic studies of other catostomine fishes. Conservation Genetics 10:551–553.

Tyus, H. M. 1987. Distribution, reproduction, and habitat use of the razorback sucker in the Green River, Utah, 1979–1986. Transactions of the American Fisheries Society 116:111–116.

USBR. 2005. Design workshop Imperial National Wildlife Refuge Imperial native fish habitat reconstruction. Final Report, U.S. Bureau of Reclamation, Boulder City, Nevada.

USFWS. 1978. Proposed endangered status for the bonytail chub and threatened status for the razorback sucker. Federal Register 43:17373–17377.

USFWS. 1987. Final recovery implementation program for endangered fish species in the upper Colorado River basin. U.S. Fish and Wildlife Service, Denver, Colorado.

USFWS. 1991. Endangered and threatened wildlife and plants; the razorback sucker (*Xyrauchen texanus*) determined to be an endangered species; final rule. Federal Register 56:54957–54967.

USFWS. 1998. Razorback sucker (*Xyrauchen texanus*) recovery plan. U.S. Fish and Wildlife Service, Denver, Colorado.

USFWS. 2002. Razorback sucker (*Xyrauchen texanus*) recovery goals: amendment and supplement to the razorback sucker recovery plan. U.S. Fish and Wildlife Service, Denver, Colorado.

USFWS. 2005. Management plan for the big river fishes of the Colorado River basin: amendment and supplement of the bonytail, humpback chub, Colorado pikeminnow, and razorback sucker recovery plans. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.

USFWS. 2012. Razorback sucker (*Xyrauchen texanus*) 5-year review: summary and evaluation. Upper Colorado River Endangered Species Program, Denver, Colorado.

Waples, R. S. 1999. Dispelling some myths about hatcheries. Fisheries 24:12–21.

Wilson, W. 2011. Annual report Dexter National Fish Hatchery and Technology Center razorback sucker broodstock evaluation and genetic monitoring. Report to Lower Colorado River Multi-Species Conservation Office, Bureau of Reclamation, Inter-agency Acquisition R11PG30006.

Wilson, W. 2012. Razorback sucker broodstock evaluation and genetic monitoring, 2012 annual report. Report to Lower Colorado River Multi-Species Conservation Office, Bureau of Reclamation, Inter-agency Acquisition R11PG30006.

Wydoski, R. S., and J. Hamill. 1991. Evolution of a cooperative recovery program for endangered fishes in the upper Colorado River basin, p. 123–140. *In*: Battle Against Extinction: Native Fish Management in the American West. W. L. Minckley and J. E. Deacon (eds.). University of Arizona Press, Tucson, Arizona.