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STATUS OF THE RAZORBACK SUCKER, *XYRAUCHEN TEXANUS* (ABBOTT), IN THE LOWER COLORADO RIVER BASIN

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ABSTRACT.—The razorback sucker population of the lower Colorado River basin is now reduced to scattered individuals in all but Lake Mohave, Arizona-Nevada. That population consists of large, slowly-growing fish, which are proposed to be nearly 30 years old, presumably having hatched when the reservoir was filling in the early 1950s. The species comprised about 12.5% of all fishes taken by trammel netting in Lake Mohave in the period 1974-82. No recruitment into the population has been detected in that period, despite repeated observations of spawning and records of fertilized eggs and hatched larvae. Sex ratios, sexual dimorphism, and fecundity all indicate the fish to be reproductively capable despite a high incidence of disease. The species is now under artificial propagation, and is being reintroduced within its native range. Predation by introduced fishes on early life-history stages of razorback sucker is considered the most important factor in their decline.

Of four endemic "big-river" fishes of the Colorado River basin, Colorado squawfish (*Ptychocheilus lucius* Girard), humpback chub (*Gila cypha* Miller), bonytail chub (*Gila elegans* Baird and Girard), and razorback sucker (*Xyrauchen texanus* [Abbott]), only the last has yet to be listed as endangered by the U.S. Department of Interior (Johnson and Rinne, 1982). Habitats for all these fishes have been reduced by development of the river for domestic and industrial (including agricultural) water supplies and power, and further reductions may be expected as human demands increase (Wydoski et al., 1980).

Sampling of fish populations by myself, students, and colleagues since 1963, throughout the lower Colorado River basin, has documented changes in distribution and abundance of indigenous species (Minckley, 1965, 1973, 1979; Minckley and Deacon, 1968). Although all native fishes have demonstrated reductions in range, local populations of many species yet remain abundant. Razorback suckers have become increasingly rare in all but Lake Mohave, Arizona-Nevada, and systematic sampling to determine life-history characteristics of that population was commenced in 1974. Lake Mohave is inhabited mostly by introduced fishes, with only two native species, razorback sucker and bonytail chub, persisting as a small percentage of the overall fauna. Proposed changes in powerplant specifications and operations of Hoover Dam, development of pump-storage facilities, and re-regulation of water levels in Lake Mohave (Paulson el al., 1980a-b) soon may influence these fishes, and little is known of their requirements in the system. In fact, there has long been a critical lack of information of these and other big-river fishes of the Colorado River basin (Miller, 1946, 1961; Branson, 1966; Minckley and Deacon, 1968; Minckley, 1965, 1973, 1979; Wydoski et al., 1980).

This report reviews information on razorback sucker in the lower Colorado River basin, presents results of studies of the species in Lake Mohave during the period 1974-82, and examines reasons for decline of the "big-

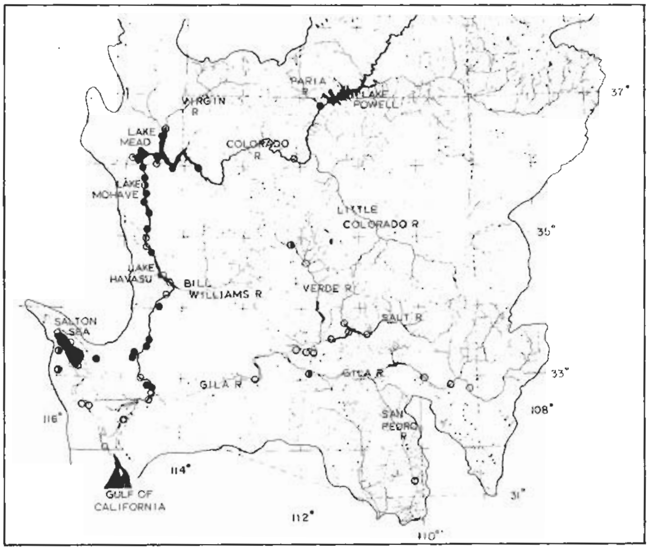

FIG. 1.—Sketch map of the lower Colorado River basin, United States and Mexico, showing features mentioned in text and locality records for razorback sucker. Symbols: ● = record localities, 1972-81; O = record localities, 1850-1971; and ◑ = records from archaeological sites. This map supercedes and corrects that published by Holden (1980).

river" fishes in general. Current attempts to perpetuate and re-establish the species also are reviewed. It is concluded that predation by introduced fishes on early life-history stages of razorback sucker is the most important single factor in their extirpation.

STUDY AREA.—The lower Colorado River is defined as that portion of the system downstream from Lees Ferry, Arizona. The mainstream lies within some of the most arid lands in North America, and flows through alternating reaches of spectacular canyons and broader structural valleys. Only four major tributaries enter this reach, from up- to downstream the Little Colorado, Virgin, Bill Williams, and Gila rivers (Fig. 1).

Lake Mohave is a mainstream reservoir about midway on the lower Colorado River. It was filled in the early 1950s to form a long (ca. 104 km) and relatively deep (43 m maximum) impoundment. The lake is generally less than 1.5 km wide between canyon walls, but widens to just more than 6.0 km at a central basin. Surface area at full pool (197 m elevation) is about 114 km^2 (Jonez and Sumner, 1954; LaRivers, 1962). The shoreline (length ca. 300 km) is complex and irregular as a result of numerous washes, and the surroundings are typical Mohave desertscrub vegetation (Brown and Lowe, 1978). The reservoir is subject to severe, seasonal wind action as a result of its long south-north fetch and prevailing winds from south-southwest. Bottoms along shore are gravel and cobble, resulting from waves (to >1.5 m high) exhuming ancient riverine terraces. Deeper areas have sand-silt substrates. Near-shore turbidity is caused by wave action, but the lake otherwise remains clear since water enters directly from the hypolimnion of Lake Mead. The reservoir is stable by southwestern standards, with a seasonal draw-down of only about 5.0 m.

METHODS AND Materials.—Review of past and present records for razorback sucker in the lower Colorado River basin depended heavily on LaRivers (1962), Minckley (1973), reports by the U.S. Fish and Wildlife Service (Anonymous, 1980, 1981), and on unpublished reports and personal communications from workers active in the region (noted in text). William Loudermilk, California Fish and Game Department (CFGD), provided data from California not otherwise acknowledged in text. Robert R. Miller, University of Michigan Museum of Zoology (UMMZ), provided data on specimens housed at that institution.

Fishes were sampled from 1975-1977 and 1979-82. Field work was concentrated within 5.0 km up- and downlake from Carp Cove, Mohave County, Arizona (east of Cottonwood Landing, Clark County, Nevada), in March 1975 immediately south of Hoover Dam, in March 1981 on the Nevada side west-southwest of Carp Cove, and in January 1982 in Arizona Bay. Collections from throughout the central basin of the reservoir yielded similar data. Voucher specimens are housed in the Arizona State University Collection of Fishes (ASU).

Trammel nets from 30.5 to 213.3 m long were used to collect fishes. They were 1.9 to 2.4 m deep and had meshes (bar measure) of 25.4 to 35.6 cm outer walls and 2.5 to 4.1 cm inner walls (most were 30.5 and 3.8 cm, respectively). Nets were set horizontally, 25 to 200 m offshore with float lines 0.5 to 5.0 m beneath the surface, bouyed at intervals along their lengths, and marked with appropriate identification as navigation hazards and scientific devices. A few were set near or on bottom on each sampling date. Attempts were made to equitably sample coves, open lake, and areas of turbulence downwind of submerged terraces. Nets were generally set at right angles to prevailing waves, which most often resulted in angles of about 60° relative to local shorelines. Nets were run and cleared of fishes at 2- to 8-hour intervals, day and night, depending upon catch rates and weather, and generally were allowed to fish in the same position for at least two 24-hour periods. Catch rates are expressed as numbers of individuals per 100 m^2 of netting per 24-hour period.

Other gear employed to compile a species list, attempt to catch smaller fishes, and to collect adults for hatchery stocks included experimental gill nets with meshes that varied from 1.3 to 5.1 cm, fyke and hoop nets of various sizes and meshes, seines varying from 1.0 to 22.9 m long, and with meshes from 3.2 mm to 1.5 cm (all bar measure), and 110- and 220-volt, A.C./D.C. electrofishing gear. Data collected by these methods were rarely quantified. Fishes taken by Arizona Game and Fish Department (AGFD) were by electrofishing barge at night, generally in shallow water along shore. All reported lengths of fishes are to the nearest cm from snout to tip of depressed caudal fin (TL; total length). Standard lengths (SL; snout to end of hypural plate) were used for some morphological comparisons and for computation of relative fecundity. SL = 0.783 ± 0.012 TL in 100 fish 42 to 69 cm TL. Mean values of length and other features are given ± one standard error unless otherwise noted.

Scales for attempts at aging razorback suckers were removed from midway between the dorsal fin and lateral line, cleaned of tissue in potassium hydroxide solution, and mounted between glass slides for examination at appropriate magnification on a Bausch and Lomb Scale Reader. Back calculation of ratios of scale radius to TL was by direct proportion. Laboratory and hatchery information on growth of razorback suckers was obtained at ASU and at Willow Beach and Dexter National Fish hatcheries (in part Toney, 1974).

A total of 83 adult razorback suckers was analyzed for sexual dimorphism; all were collected from Lake Mohave between 1966 and 1975 and are housed at ASU or UMMZ. Measurements of body parts followed methods of Hubbs and Lagler (1974). Breeding coloration and tuberculation were recorded in the field.

Mature ovaries of five female razorback suckers were excised for investigation of fecundity. Number of eggs within ovaries was estimated volumetrically (Kandler and Piriwitz, 1957). Eggs were separated from ovarian tissue, total volume of ova for each fish was recorded, and two 1.0 ml subsamples were counted. Relative fecundity estimates are expressed in terms of ova cm SL (Bagenal and Braum, 1978).

RESULTS.—*Historical and Present Distributions.*—Razorback suckers have been widely recorded in the lower Colorado River basin. Early distributional records include the original description (Abbott, 1861) from the "Colorado and New Rivers," and a re-description (as *Catostomus cypho*) by Lockington (1881) from the Yuma area. The species penetrated far onto the Colorado Delta in Mexico (Follett, 1961), and upstream throughout the mainstream Colorado River (Jordan, 1891; Jordan and Evermann, 1896; Evermann and Rutter, 1895; Gilbert and Scofield, 1898; Grinnell, 1914; Snyder, 1915; Douglas, 1952; Rostlund, 1952; Miller, 1955, 1961; Stewart, 1957). The fish occupied the Salton Sea in aboriginal times (Wilke, 1980), supporting a lakeshore fishery until presumably extirpated by evaporative concentration of salts. Hubbs (1960) found archaeological remains of young razorback suckers about 32.5 km upstream from the Salton Sea in Fish Creek California, indicating successful reproduction in that system during high lake stages. The species re-entered the Salton Sea when it re-filled in 1905-07 (Evermann, 1916), but disappeared with increasing salinity by 1929 (Coleman, 1929). In the mainstream Gila River, razorback suckers occurred near Yuma (Evermann and Rutter, 1895), in the now-dry reach between Yuma and Gila Bend (Bartlett, 1854), in the Phoenix area where they were called "buffalo" or "buffalofish" (Miller, 1961; Minckley, 1973), in archaeological sites near Casa Grande (Minckley, 1976), and almost to New Mexico (Kirsch, 1889; Chamberlain, 1904) (Fig. 1). They also ranged far upstream in the Verde River (Minckley and Alger, 1968; Wagner, 1954), to well above the present Roosevelt Lake on Tonto Creek (Hubbs and Miller, 1953) and the Salt River (Ellison, 1980), and to the upper San Pedro River (Miller, 1955, 1961).

Razorback suckers remained locally abundant until recently. They were common in irrigation channels of the Palo Verde Valley, California, until the 1940s (Loudermilk, pers. comm.). In the early 1900s they were so common in canals in the Phoenix area and in the Salt River above Roosevelt Lake that "wagon loads" were collected by local people (Miller, 1961; Ellison, 1980). Carl L. Hubbs collected an adult in Roosevelt Lake in 1926 (UMMZ 94749, 71.5 cm TL). T. T. Fraizer, local resident, considered the species extirpated in Roosevelt Lake by 1950 (Hubbs and Miller, 1953; R. R. Miller, pers. comm.). As late as 1949 a commercial fishery for razorback suckers that ranged to 6 kg individual weight existed in Saguaro Lake, central Arizona (Hubbs and Miller, 1953). In 1966 that reservoir was drained and none was present (Minckley and Deacon, 1968). The species persisted as adults in the Verde River until at least 1954 (Wagner, 1954), and in canals northeast of Mesa, Arizona, to about that same time (Vardell Blau, Mesa, Arizona, pers. comm.). Young razorback suckers were last preserved from the Gila River drainage in 1926 (Hubbs and Miller, 1953; 5 specimens, 52-100 mm TL, UMMZ 94877).

In the Colorado River mainstream, razorback suckers "were doing well" in the 1940s and early 1950s (Wallis, 1951; Jonez and Sumner, 1954). Large concentrations of spawning adults were observed in Lake Mohave and in the river below that reservoir (Douglas, 1952), and the species was considered common (Moffett, 1942; Dill, 1944; Jonez et al., 1951; Wallis, 1951).

Minckley and Deacon (1968) noted that no specimens shorter than about 40 cm TL had been caught from the lower Colorado River "in recent years," and this pattern of only large individuals being present has generally persisted to date. Few razorback suckers were taken or observed in Lake Mead in the 1970s (Anonymous, 1973), and McCall (1980) and Sue Morgenson (AGFD, pers. comm.) recorded only 18 large individuals (55.2 to 67.0 cm TL for 11 fish measured) while sampling that reservoir in 1976-80. Between Davis Dam and Lake Havasu, 8 adult razorback suckers (54.5-68.0 cm TL for 7 fish measured) were recorded by CFGD in 1972-76. Lake Havasu populations also are low (Guenther and Romero, 1973; Mike Donahoo, USFWS, pers. comm.); none was taken there or in the river below in a 1975-76 survey by Minckley (1979). Downstream from Lake Havasu a 2.05 kg razorback sucker (not measured) was taken in 1969 near Blythe, California, an angler caught a 56.0 cm TL specimen in the Palo Verde Valley in 1976, and another *ca.* 60 cm fish was found dead there in 1977. A trammel-net survey by Loudermilk (pers. comm.) from Parker to Morelos dams in 1980-81, specifically for razorback suckers, caught none, but a small population persists in Senator Wash Reservoir, California. Two small individuals (32.7 and 37.1 cm TL) were caught from canals in the Blythe-Parker area in 1980 (Donahoo, in Anonymous, 1981), an adult was netted from Imperial Reservoir in March 1973 (ASU 6283), and five young fish (ca. 15 cm TL) were caught from the East Highline Canal and from commercial fish ponds filled from that canal near Niland, California, in 1973 and 1974 (St. Amant et al., 1974). Over the past 5 years, 1 or 2 individuals per year have been reported by fishermen from the Imperial-Coachella Valley irrigation system. The fish remains common in Lake Mohave as large adults (Gustafson, 1975a-b), as will be detailed below.

Young-of-the-year or juvenile razorback suckers were collected in 1950 from the Colorado River from pools below Laguna Dam (2 individuals, 17 and 20 mm TL, UMMZ 162645), below Davis Dam (3 individuals, 80-135 mm TL, UMMZ 160730; Douglas, 1952), near Cottonwood Landing (6,100 specimens, 12-42 mm TL, UMMZ 162845 and ASU 3719), and in Lake Havasu (Douglas, 1952). Jonez and Sumner (1954) also identified young razorback suckers from below Davis Dam in 1950. One larva was caught by University of Nevada, Las Vegas (UNLV), biologists below Hoover Dam in 1979 (ASU 8455), larvae have been collected in Senator Wash Reservoir, and from along the shoreline of Lake Mohave in 1981 (Loudermilk, pers. comm.), and in plankton tows in Lake Mohave in 1982 (Larry Paulson, UNLV, pers. comm.).

Fishes of Lake Mohave.—Twenty-nine species of fishes have been reliably reported from Lake Mohave, of which only six are native (Table 1). Four of the six, speckled dace, Colorado squawfish, humpback chub, and flannelmouth sucker, have almost certainly been long extinct in the reservoir. Of introduced species, the Pacific salmons, goldfish, golden shiner, and fathead minnow also are rare or extirpated. Utah chub (*Gila atraria* [Girard]) was reported below Lake Mead and in bait shops along the lower Colorado River by Jonez et al. (1951) and Miller (1952), but has yet to become established and is tentatively excluded. Other introduced fishes are both up- and downstream from the reservoir and are thus to be expected. Native fishes that occurred both north and south of the area and were thus at least transient include roundtail chub (*Gila robusta* Baird and Girard) and woundfin (*Plagopterus argentissimus* Cope).

Net Catches.—Carp dominated catches in trammel nets in Lake Mohave (Table 2). They were relatively rare only in cold water below Lake Mead. In 1979, carp used nets as spawning substrate, and in May were so abundant that sampling was curtailed when catches exceeded an average of 40 carp per 100 m^2 of netting per day.

Catfish and bass were relatively consistent in occurrence, but trout dominated only in cold water below Hoover Dam. Surface temperatures of Lake

TABLE 1.—*Common and scientific names of fishes represented by specimens or otherwise reliably reported from Lake Mohave, Arizona-Nevada.*

Threadfin shad, *Dorosoma petenense* (Gunther)
Silver (coho) salmon, *Oncorhynchus kisutch* (Walbaum)
Sockeye (kokanee) salmon, *O. nerka* (Walbaum)
Brook trout, *Salvelinus fontinalis* (Mitchill)
Rainbow trout, *Salmo gairdneri* Richardson
Cutthroat trout, *S. clarki* Richardson
Carp, *Cyprinus carpio* Linnaeus
Goldfish, *Carassius auratus* (Linnaeus)
Golden shiner, *Notemigonus crysoleucus* (Mitchill)
Bonytail chub, *Gila elegans* Baird and Girard[1]
Humpback chub, *G. cypha* Miller[1,2]
Colorado squawfish, *Ptychocheilus lucius* Girard[1]
Speckled dace, *Rhinichthys osculus* (Girard)[1]
Red shiner, *Notropis lutrensis* (Baird and Girard)
Fathead minnow, *Pimephales promelas* Rafinesque
Razorback sucker, *Xyrauchen texanus* (Abbott)[1]
Flannelmouth sucker, *Catostomus latipinnis* Baird and Girard[1]
Utah sucker, *C. ardens* Jordan and Gilbert [3]
Channel catfish, *Ictalurus punctatus* (Rafinesque)
Yellow bullhead, *I. natalis* (LeSueur)
Black bullhead, *I. melas* (Rafinesque)
Mosquitofish, *Gambusia affinis* (Baird and Girard)
Smallmouth bass, *Micropterus dolomieui* (Lacepede)
Largemouth bass, *M. salmoides* (Lacepede)
Green sunfish, *Lepomis cyanellus* Rafinesque
Bluegill, *L. macrochirus* Rafinesque
Redear sunfish *L. microlophus* (Gunther)
Black crappie, *Pomoxis nigromaculatus* (LeSueur)
Striped bass, *Morone saxatilis* (Walbaum)

[1]Native species.
[2]Recorded from the area from an archaeological site (Catclaw Cave; Miller 1955) now flooded by Lake Mohave.
[3]This constitutes the first record of Utah sucker from open waters of Arizona (ASU Collection of Fishes).

Mohave south of the influence of Lake Mead become too warm in April (ca. 21° C) to be preferred by salmonids, and they were common only in winter months. Small centrarchids were consistently in low numbers. Bluegill were netted in all but 2 sampling sessions, but green sunfish were caught in only 4 of the 12 collections. Threadfin shad, caught by thousands in fine-meshed gill and fyke nets, were obviously selected against by mesh sizes of trammel nets, and were taken only three times. Bonytail chubs were exceedingly rare, with only 18 individuals caught in the 8-year period.

Razorback suckers were collected or observed in Lake Mohave in water varying from 0.5 to 10+ m deep over essentially all available types of substrate. However, largest concentrations were in water <5.0 m deep over gravel or cobble bottoms. They were strongly second to carp in relative abundance in 1975-6 (Table 2), decreased to third or fourth to channel catfish, largemouth bass, and/or rainbow trout in subsequent years, then again were abundant in 1981. Sampling in January and November 1981 was biased toward razorback suckers, since netting was specifically for acquistition of a hatchery brood stock and nets were set low in the water column. Netting near the surface to catch bonytail chubs for brood stock in March 1981 still caught relatively large numbers of razorback suckers. There are

TABLE 2.—*Numbers and percentages (in parentheses) of fishes taken per 100 m² of trammel netting per 24-hour period, Lake Mohave, Arizona-Nevada, 1975-81.*

Dates	m² Nets Fished	Threadfin shad	Rainbow trout	Cutthroat trout	Brook trout	Carp	Bonytail chub	Razorback sucker	Razorback X Flannelmouth	Channel catfish	Largemouth bass	Black crappie	Green sunfish	Bluegill	Striped bass	Totals
III-75[1]	1,561		5.19			1.15		1.35			0.19			0.57		8.46
			(61.42)			(13.61)		(15.98)			(2.25)			(6.75)		
IV-75	1,784	0.28	0.78			11.16		4.48	0.28	2.13	1.07	1.51	0.06	0.90		22.65[2]
		(1.24)	(3.44)			(49.27)		(19.78)	(1.24)	(9.40)	(4.72)	(6.67)	(0.26)	(3.97)		
XI-75	1,561		1.09			13.20		5.64		1.47	1.09		0.13	0.13		22.75
			(4.79)			(57.98)		(24.79)		(6.46)	(4.70)		(0.57)	(0.57)		
II-76	2,452		1.18			4.85	0.12	2.32		0.86	0.73	0.16		0.94		11.16
			(10.57)			(43.46)	(1.08)	(20.79)		(7.71)	(6.54)	(1.43)		(8.42)		
III-77	2,675		0.49			6.39		0.86		1.23	2.28	0.07	0.07	0.64		12.03
			(4.07)			(53.12)		(7.15)		(10.22)	(18.95)	(0.58)	(0.58)	(5.32)		
IV-79	1,784		0.11			28.92	0.11	0.34		0.95	1.01					31.44
			(0.35)			(91.98)	(0.35)	(1.08)		(3.02)	(3.21)					
V-79	1,561		0.13			42.09				4.16	0.64			0.19		47.21
			(0.28)			(89.15)				(8.81)	(1.36)			(0.40)		
III-80	1,784		1.46			13.85		1.74		1.68	3.98	0.06		0.06		22.83
			(6.40)			(60.67)		(7.62)		(7.36)	(17.43)	(0.26)		(0.26)		
IV-80	5,202	0.33	0.21			9.38	0.10	0.77		1.13	1.19		0.02	0.13		13.26
		(2.49)	(1.58)			(70.74)	(0.75)	(5.81)		(8.52)	(8.97)		(0.15)	(0.98)		
I-81	2,970		0.47	0.10		2.59		2.83		0.40	2.05			0.07		8.51
			(5.52)	(1.18)		(30.43)		(33.25)		(4.70)	(24.09)			(0.82)		
III-81	4,710	0.04	4.20	0.23		9.62	0.17	3.14		0.64	1.04	0.04				19.12
		(0.21)	(22.00)	(1.20)		(50.39)	(0.89)	(16.45)		(3.35)	(5.45)	(0.05)				
XI-81	2,006		0.84	0.30	0.19	4.53		3.64		0.55	1.15	0.05		0.10	0.38	11.73
			(7.16)	(2.56)	(1.62)	(38.62)		(31.03)		(4.69)	(9.80)	(0.43)		(0.85)	(3.24)	
Total	30,050	0.08	1.20	0.07	0.01	10.79	0.06	2.17	0.02	1.13	1.37	0.12	0.02	0.27	0.02	17.33
		(0.46)	(6.92)	(0.40)	(0.06)	(62.26)	(0.35)	(12.52)	(0.12)	(6.52)	(7.91)	(0.69)	(0.12)	(1.56)	(0.12)	

[1]Samples on this date were from immediately below Hoover Dam. All subsequent collections were from the vicinity of Carp Cove, Mohave County, Arizona, on the east shore across from Cottonwood Landing, Clark County, Nevada, or in March 1981, partially on the Nevada side, west-southwest of Carp Cove.
[2]A single specimen of Utah sucker (*Catostomus ardens*) also was taken.

TABLE 3.—*Catches of razorback suckers per 100 m² of trammel netting per 24-hour period at various localities in the upper Colorado River basin. Data re-calculated from McAda and Wydoski (1980); percentages are in parentheses.*

Localities	Total No. Fish	Catch per Unit Effort	
		Razorback	All Fish
Echo Park, UT			
May 1975	102	0.24 (1.2)	19.90
Walker Wildlife Area, CO			
April 1975	543	5.95 (4.2)	140.64
May 1975	514	1.25 (3.5)	35.52
June 1975	600	0.46 (3.5)	38.52
Green River, UT			
December 1975	103	1.13 (0.5)	24.36
April 1976	61	0.24 (3.6)	6.74

thus no indications of a population decline in razorback suckers in Lake Mohave based on trammel netting.

Hybrids between razorback and flannelmouth suckers comprised a small percentage of the total catch in 1975. They were not again taken by me, but Paulson (UNLV, pers. comm.) captured hybrids in 1982. All were large, >50 cm TL, indicating ages comparable to those of the razorback sucker population. Flannel mouth suckers have not been collected from Lake Mohave since the 1950s. This hybrid combination has previously been recorded from the upper Colorado River basin (Hubbs and Miller, 1953), and from the Grand Canyon region (Suttkus and Clemmer, 1979).

McAda and Wydoski (1980) provided the only other quantitative data known to me on relative abundance of razorback suckers. They used similar trammel nets at various locations in the upper Colorado River basin in 1974-76, finding the sucker as 3.3 to 9.0% of all fishes caught at Echo park, Colorado (near the confluence of the Green and Yampa rivers), 0.8 to 4.2% in a gravel pit near Grand Junction, Colorado (Colorado River), and 0.0 to 3.3% on the Green River, Utah, at various localities. Some of their data on catch per unit effort are reproduced in Table 3.

Age and Growth.—I have no evidence for recruitment into the adult razorback sucker population of Lake Mohave since sometime prior to 1964. On the basis of size-frequency distributions of wild-caught fish, growth since 1964 has proceeded at an average of about 0.5 cm per year (Fig. 2). Larger fish are females (47 to 74 cm TL) and smaller ones are males (37 to 64 cm). McAda and Wydoski (1980) reported similar size limits for adult fish from the upper Colorado River basin, with females from the Colorado River between 50 and 62 cm TL and those from the Yampa and Green rivers from 46 to 54 cm. Males from those areas were from 48 to 52 cm and 44 to 52 cm TL, respectively.

Bias toward large fishes by major sampling techniques used in Lake Mohave (trammel nets and electrofishing) may be rejected since numerous

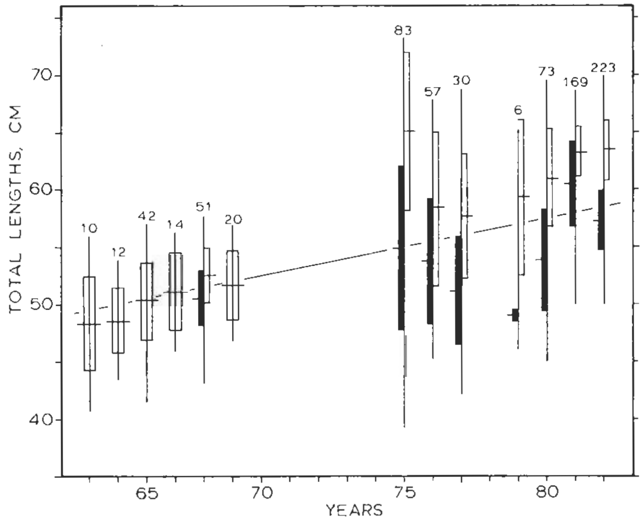

FIG. 2.—Total lengths of razorback suckers collected in Lake Mohave, Arizona-Nevada, in 1964-69 and 1975-81. Horizontal lines are means, bars represent ±1 standard error, and vertical lines represent the range of lengths; numbers are total sample sizes; open bars are females, closed bars are males, when sexes were determined.

fishes of other species <15 cm TL are readily caught by both methods. Variation in TL for razorback suckers taken by trammel nets in the period 1975-81 was, however, far greater than that indicated from electrofishing in earlier years. Perhaps the former technique samples more diversity of habitats than the latter, providing a broader picture of the population. Hubbs and Miller (1953) also noted a "paucity of young in collections," and suggested that young moved with adults "into larger and deeper waters, which have been neglected by collectors." It is possible that young razorback suckers live at great depth in Lake Mohave, and have thus avoided capture. They have not occurred inshore. No razorbacks <37 cm TL have been collected in extensive seining operations by myself and others (Gail Kobetich, Don Toney, and Jerry Burton, USFWS, pers. comm.), in annual electrofishing surveys by AGFD or Nevada Game and Fish Department (NGFD) (Kraig Burkstrand, pers. comm.), or in my sampling with devices other than trammel nets.

Any occurrence of small razorbacks suckers in Lake Mohave after 1978 may result, unfortunately, from the escape of a substantial number of individuals (ca. 200) <30 cm TL from Willow Beach (James E. Johnson, USFWS, pers. comm.). This perhaps explains the report of "25-30 cm" razorback suckers by Paulson et al. (1980b) and Liles (1981) in upper Lake Mohave near Hoover Dam, in the vicinity of the hatchery.

Scales of razorback suckers are highly variable, small in size and irregular in shape on an individual fish. Width of posterior, anterior, and lateral radii was determined for each of 2 to 5 scales of 20 fish sacrificed in 1975. Regression for each of these variables against TL gave correlation coefficients of 0.55, 0.57 and 0.61 for each radius, respectively. The regression for lateral radius (LR) against TL was LR = 2.893 + 0.126 (TL). Agreement among

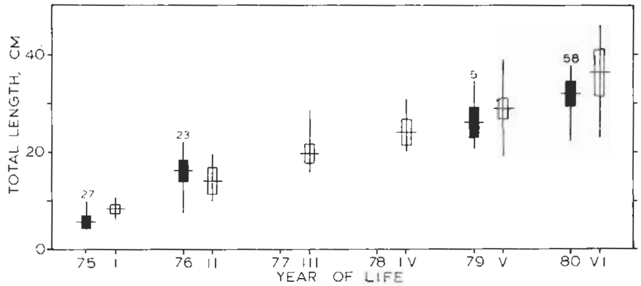

FIG. 3.—Comparisons of growth of known-age razorback suckers (numbers indicate sample sizes), with growth estimates back-calculated from scale annuli for 20 fish sacrificed in 1975. Horizontal lines are means, bars represent ±1 standard error, and vertical lines represent the range of lengths (darkened - known-age fish; open - estimated from annuli).

investigators could not be achieved for more than the first six apparent annular marks on scales. After that point dense circuli were over-lapping, obscure, or obviously lacking, with scales often appearing to have grown uniformly except for random "checks" that could not be interpreted as annuli. Most scales were deeply worn on the margins, and regenerated scales (excluded from further consideration) were common. Minimum estimates for ages of fish with possible annuli were 11 to 14 years, and maxima ranged to >20 years. Estimates of growth rates for the first six years of life compare favorably, however, with growth of known-age fishes under hatchery and laboratory conditions (Fig. 3).

Variation in length of individuals from the hatchery cohort is remarkably high, and this is shared by estimates of growth made from scales of wild-caught adults. Multiple or protracted spawning in nature may result in a similar size distribution, but the hatchery cohort all were spawned the same day in 1974. A similar size range (7.1 to 13.5 cm TL at 5 months of age) in hatchery produced fish reared in ponds at Dexter, New Mexico, in 1981 (J. E. Johnson, pers. comm.) provides further evidence for inate variability in this life-history character. Size variation in the 1974 cohort resulted in some hatchery individuals becoming sexually mature at six years of age and 35-39 cm TL, while siblings <35 cm TL had no sexual development.

McAda and Wydoski (1980) similarly found little relationship between scale radius and body lengths of razorback suckers. They assigned ages of 4 to 9 years to fish 44 to 61 cm TL, but doubted accuracy of their determinations. Evidence against validity of their data was a report by James St. Amant (in McAda and Wydoski, 1980) of a 66.2 cm TL male from the lower Colorado River estimated to be 22 years old and another large fish (length unknown) that was 17 years old, both on the basis of sagitta analysis. McAda and Wydoski also noted a fish recaptured 1.5 years after original tagging in the upper river had not grown at all, and a second specimen (50.8 cm TL) had grown only 8 mm when recaptured 3.5 years later.

I am of the opinion that razorback suckers currently in Lake Mohave hatched when the reservoir was filling in the early 1950s. If this is so, mean growth between 1956 and 1963 would have slowed from ca. 7.0 cm in their seventh year of life (Fig. 3) to less than a cm per year in 1964 (Fig. 2). Males may have essentially ceased to grow after 1968 or before (Fig. 2), tending to suppress the apparent growth rate of the over-all population. Death of larger, faster growing fish, and slow growth by smaller fish toward the mean for the cohort(s), might also serve to explain the remarkably slow average growth rate in recent years. An average of 7.3 carcasses/km of large (>50 cm TL) razorback suckers were along the shoreline of Lake Mohave in spring 1979. Sagittae have now been obtained from a representative sample of razorback suckers from Lake Mohave, so accurate aging will hopefully soon be accomplished.

Reproduction.—McAda and Wydoski (1980) recently summarized information on reproduction by razorback suckers. Before large dams, razorback suckers migrated in early spring, evidently to spawn (Hubbs and Miller, 1953). Jordan (1891) reported such a migration into the Animas River, Colorado, and Chamberlain (1904) cited early reports that they congregated in tributaries to larger streams. Minckley and Carothers (1979) collected a gravid female razorback sucker and observed two other individuals in the Paria River, Arizona, in June 1978. Concentrations in the Salt River of Arizona in the 1920s (Ellison, 1980) were presumably spawning aggregations.

Douglas (1952) specifically described spawning by razorback suckers in shallow coves of Lake Havasu in March 1950. Water depths ranged from 0.25 to 1.5 m and temperatures were between 14° and 16°C. Individual females were accompanied by 2 to 6 males as they swam in small circles over the bottom. Males remained close to responsive females and the fish occasionally settled to the bottom and vibrated their bodies rapidly. Gamete emission was not visible because of silt disturbed by the fish. Jonez and Sumner (1954) observed razorback suckers spawning in Lake Mead between 1 March and 15 April 1953, and described extensive shoreward movements at that time. There was a tendency for the fish to concentrate near inflowing rivers. Water temperatures were between 12° and 18°C. Spawning was widespread along gravel shorelines in water 0.6 to 5 m deep. My extensive observations corroborate those of Douglas (1952). I have most often observed spawning razorback suckers in shallow (<5 m) waters along gravelly, submerged terraces in bays and inlets, and once along canyon walls and on a gravel-cobble bar among boulders in current about 1.6 km below Hoover Dam. The last fish were concentrated in an area of inflowing hot springs (Gustafson, 1975a).

McAda and Wydoski (1980) collected razorback suckers in spawning condition from water about 1 m deep and at the upstream ends of gravel bars in the upper Colorado River basin. Substrate was predominately cobble, and water velocity was about 1 m/sec. Females captured over bars were ripe, but those from other places were not; all males over or near bars were ripe. They also observed behavior resembling that described by Douglas (1952) in the gravel pit at Walker Wildlife Area, but no successful reproduction was indicated. Linda Ulmer and Loudermilk (pers. comm.) have confirmed spawning activity and hatching of eggs on small, gravelly, wave-cut terraces of Senator Wash Reservoir, California.

Holden (in McAda and Wydoski, 1980) collected a few subadult fish in the upper Colorado River basin before 1977, and Holden (1978) reported tentative identification of two juvenile razorback suckers. Apparently poor reproductive success by razorback suckers in that area was attributed in part by McAda and Wydoski (1980) to possible confusion of young-of-the-year with young of flannelmouth sucker. This is not the case in the lower river, since no similar sucker species now are present.

Factors directly contributing to failure of successful reproduction by razorback sucker include occasional stranding of eggs by reservoir fluctuations in Lake Mohave (Gustafson, 1975b), but more importantly, predation by introduced piscivores. Jonez and Sumner (1954) similarly believed that predation by carp and other fishes on freshly spawned eggs limited reproductive success in Lake Mohave, and McAda and Wydoski (1980) attributed failure of reproduction in Walker Wildlife Area to the presence of "sizable numbers of introduced predaceous fishes..." Ulmer and Loudermilk (pers. comm.) have documented direct predation by recording razorback sucker ova in stomachs of channel catfish and carp in Senator Wash Reservoir, observed bluegill feeding on the substrate in spawning areas, and found smallmouth and largemouth bass and redear sunfish in substantial numbers near spawning razorback suckers. William Rinne and Gordon Mueller (U.S. Bureau of Reclamation, pers. comm.) also confirmed carp predation on razorback eggs in Lake Mohave in 1982.

Sex Ratios.—Sex ratios are biased toward females in offshore netting samples of razorback suckers (males/females, *n* in parentheses): 1975 - 0.29-0.86 (3 samples, $\bar{X} = 0.58 \pm 0.28$, 189 fish); 1976 - 0.43 (57); 1977 - 0.21 (23); 1979 - 0.20 (6); 1980 - 0.21-0.29 (2 samples, 69 fish), and 1981 - 0.46 (73 fish). In 1968, AGFD personnel sexed 30 fish collected by electrofishing, of which only 9 were females (ratio 2.33). Males are regularly more abundant than females on spawning areas (Douglas, 1952). Sex ratio for 97 fish collected while spawning in 1981 was 3.57, and for 258 fish seined from pre-spawning aggregation in 1982 the ratio was 1.8. The 1968 electrofishing collection presumably reflected similar circumstances.

Sexual Dimorphism.—Six sexually dimorphic characters are obvious in razorback suckers. Dimorphic coloration and tuberculation are apparent only during the spawning period, January through March, although some expression has been noted as early as November. Four sexing criteria are independent of season: 1) size (both length and weight); 2) pelvic and 3) anal fin lengths; and 4) length and morphology of the urogenital papillae. An additional character reported by McAda and Wydoski (1980), curvature of the last anal fin-ray in male razorback suckers while the ray remains straight in females, was not studied by me.

Male and female razorback suckers exhibit strongly dimorphic pigmentation and tuberculation during the breeding season (Douglas, 1952; Minckley, 1973). Males are dark-olivaceous to black dorsally, with a bright-orange belly and a dark-pink to reddish lateral band. Females remain olivaceous dorsally, lightening to off-white, yellowish, or mottled ventrally. In males, large conical tubercles are produced on the anal fin and lower lobe of the caudal fin, and smaller, conical tubercles are on the pectoral and pelvic fins, and both above and below the lateral line along sides, and on the ventrum, of the caudal peduncle. Branson (1961) erroneously reported tubercles only on the

TABLE 4.—*Sexual dimorphism in adult razorback suckers from Lake Mohave, Arizona-Nevada, 1975; means followed by ± one standard error.*

Characteristic	Males (n)	Females (n)
Standard Lengths	43.1 ± 5.5 cm	50.6 ± 6.5 cm
	(29)	(54)
Total Weights	2.07 ± 0.42 kg	3.01 ± 0.70 kg
	(19)	(44)
Pelvic Fin Length	14.5 ± 7.3%	11.5 ± 1.6%
(% SL)	(29)	(54)
Anal Fin Length	20.2 ± 4.2%	16.1 ± 1.6%
(% SL)	(29)	(54)
Urogenital Papillus Length	5.6 ± 1.8%	8.0 ± 1.3%
(% SL)	(23)	(48)

anal fins of males. Small, lower-profile tubercles are often, although not invariably, present on the anal fin and lower lobe of the caudal fin of breeding females, and below the lateral line on their caudal peduncles. Tubercles on anal fin-rays of females may be tiny and sub-cutaneous. Tubercles were not found on the pelvic and pectoral fins of females.

Female razorback suckers are larger than males in terms of both length and total weight (Fig. 2, Table 4). Males, on the other hand, have relatively longer pelvic and anal fins. Females have a distinctly longer, more fleshy and distally rounded urogenital papillus; in males the papillus is thinner and accuminate. Differences between sexes for all four morphological features are significant at the 0.05% level (two-tailed t-test; percentage data were subjected to an arcsine transformation to normalize distributions; Zar, 1974).

Fecundity.—Results of fecundity investigations are often expressed in terms of "relative" fecundity, or number of eggs per unit weight of fish. However, statistical difficulties often arise when gonad weights are either included or excluded from total weights, and false statistical relations may result when changes in condition of the fish occur with the approach of spawning, or when physiological and environmental changes occur through successive years or in different localities (Bagenal and Braum, 1978). For these reasons, relative fecundity of razorback suckers are considered most reliably expressed in terms of number of ova per unit SL.

Total numbers of ova in five ripe females between 39.1 and 57.0 cm SL $\bar{X}$ = 50.4 ± 6.8) ranged from 74,600 to 144,000 ($\bar{X}$ = 100,800 ± 26,170), and the correlation coefficient between total ova and length was $r = 0.55$. Ovary weight was relatively uniform, ranging from 9.2 to 11.5% of body weight less gonads ($\bar{X}$ = 10.1 ± 0.95%). Correlation between body weight less gonad and total ova was $r = 0.68$. Relative fecundity also was uniform among females, ranging from 1,680 to 1,908 ova/cm SL ($\bar{X}$ = 1,812 ± 90.5 ova/cm).

McAda and Wydoski (1980) presented data for 10 female razorback suckers from various localities in the upper Colorado River and taken at various times of year. Their fish varied from ca. 41 to 46 cm SL (calculated from total lengths) and contained an estimated 27,614 to 76,576 ova ($\bar{X}$ = 46,791 ± 19,076). They likewise found a low correlation between length and fecundity (I calculated $r = 0.31$). Gonad weights were not given, but I calculated relative fecundity from their data and derived a range of ca. 600 to 2,000 ova/cm SL ($\bar{X}$ = 1,166 ± 490.6).

Injuries and Disease.—Incidence of injury and disease was remarkably high in razorback suckers from Lake Mohave (Table 5), another possible indication of great age and/or stress for the population. A large number of individuals were blind in one or both eyes, and 11.5% of fish so afflicted had their orbit(s) totally overgrown with epidermis. A progressive deterioration was indicated, with eyes first becoming opaque, then swollen and protruding from the skull, followed by rupture and shrinkage into the orbit, and overgrowth by skin. The reasons for this condition are unknown, but unitl about 1976 an eye fluke was a major problem in trouts in the Colorado River (Loudermilk, pers. comm.). In 1973, B. D. Roselund (USFWS, pers. comm.) found some bacteria (*Aeromonas hydrophila*) in aqueous humor of two infected eyes, plus large numbers of the protozoan *Myxosoma* sp. in macerated tissues of the choroid-sclera region. Four of eight eyes (four fish) examined in 1974 also yielded *Myxosoma* sp. G. Hoffman (USFWS) could not identify the spores, which "measured 7.5 × 9 μ in face view," and were probably undescribed (Roselund, pers. comm.). Few fish appeared emaciated, even when totally blinded, indicating a highly developed gustatory system (Miller and Evans, 1965). Deformations of the vertebral column also were relatively common, as were infestations of parasitic copepods (*Lernaea* sp.). Roselund (USFWS, pers. comm.; also in Wydoski et al., 1980 and Anonymous, 1981) similarly recorded *Lernaea* sp., and also identified an internal monogenetic trematode of the suborder Polyopistocotyles, pathogenic protozoans of the genera *Ichthyophthirius* and *Myxosoma* (see above), and pathogenic bacteria of the genera *Aeromonas* and *Pseudomonas* from razorback suckers in Lake Mohave. Mpoame (1981) found remarkably few parasites in his sample from that lake. One of 18 fish had a cestode (*Isoglaridacris bulbocirrus*), and 17 hosted immature nematodes of the genus *Dacnitoides*.

Higher incidences of gross bacterial infections and external lesions were in samples taken during or following breeding. These maladies were conspicuously low in pre-breeding fish in 1982. External damage from tubercles of males and from contact with the bottom presumably lead to these secondary infections.

Attempted Recovery of the Species.—In 1974, the USFWS commenced experimental propagation of razorback suckers at Willow Beach National Fish Hatchery (Toney, 1974). As already discussed, progeny from the 1974 and 1975 stocks provided growth and size data (Fig. 3), information on size at sexual maturity, embryological and larval developmental sequences (Minckley and Gustafson, 1982), and a few escaped into Lake Mohave. Some of these young fish were retained for breeding purposes, and they, plus additional brood stock from Lake Mohave, were moved to Dexter National Fish Hatchery in 1981, where 20,000 fingerlings (about 8 cm TL) were produced. Some of these were stocked into historic habitats in Arizona. Additional adults were obtained in 1982, more than 1.8 million larvae were produced, and survivors were released in appropriate habitats (Table 6; Johnson, 1982). Viable populations will hopefully result from these reintroductions, especially in stream reaches were non-native fishes are rare. If reproduction con-

TABLE 5.—*Incidence of parasites and disease in razorback suckers from Lake Mohave, Arizona-Nevada, 1974-1982. Percentages are in parentheses and do not equal 100% since some fish had more than one affliction.*

Condition	1975	1976	1977	1979	1980	1981	1982	Total
Blind (right eye only)	11	9	5	2	6	28	34	95
	(14.7)	(19.1)	(21.7)	(28.6)	(19.4)	(19.4)	(13.6)	(15.8)
Blind (left eye only)	6	8	1	0	5	16	39	74
	(7.7)	(17.0)	(4.3)	(0.0)	(16.1)	(9.7)	(15.6)	(12.3)
Blind in both eyes	5	4	2	0	1	12	16	41
	(6.4)	(8.5)	(8.6)	(0.0)	(3.2)	(7.2)	(6.4)	(6.8)
Curvature of spinal	3	2	2	0	4	4	7	22
column	(3.8)	(4.3)	(8.6)	(0.0)	(12.9)	(2.4)	(2.8)	(3.7)
External lesions	2	1	0	1	1	17	1	23
	(2.6)	(2.1)	(0.0)	(14.3)	(3.2)	(10.3)	(0.4)	(3.8)
External tumerous	6	1	0	0	2	4	5	18
tissues	(7.7)	(2.1)	(0.0)	(0.0)	(6.4)	(2.4)	(2.0)	(3.0)
Bacterial infections	12	17	9	2	9	24	3	76
	(15.4)	(36.2)	(39.1)	(28.6)	(29.0)	(14.5)	(1.2)	(12.6)
Lernaea sp.	9	3	6	2	4	19	no	43[1]
	(11.6)	(6.4)	(26.1)	(28.6)	(12.9)	(11.5)	data	(12.3)
Total Fish	78	47	23	7	31	165	205	601

[1]Based on 351 fish, 1975-81.

tinues to fail, we will at least have some riverine stocks of this long-lived species to study in further attempts to alleviate its precarious situation.

DISCUSSION AND SUMMARY.—The razorback sucker population in the lower Colorado River drainage is now reduced to scattered individuals in all but Lake Mohave, Arizona-Nevada. That population consists of large, slowly-growing fish, which are proposed to be nearly 30 years old, presumably having hatched when the reservoir was filling in the early 1950s. The species remains abundant in Lake Mohave, comprising about 12.5% of all fishes taken by trammel netting in the period 1974-82. No recruitment into the population has been detected in that period, despite repeated observations of spawning. Ova are fertile since fertilized eggs and hatched larvae have been recorded in nature, and hatchery and laboratory production of the species has been achieved. There are no data, however, on the percentages of ova which are fertile, or ova survival to the larval stage. Nevertheless, sex ratios, sexual dimorphism, and fecundity all indicate the fish to be reproductively capable despite high incidences of injury and disease.

A pattern exists that large, presumably old, fish persist for many years in reservoirs. They did so in Roosevelt Lake from 1913 to near 1950, and in Saguaro Lake from 1930 to past 1949 (but not until 1966). They now appear to be disappearing from Lake Mead, which was closed in 1935, and Lake Havasu, closed in 1938. They remain common in Lake Mohave, which began filling in 1950, yet there is no evidence of subsequent, successful reproduction in that reservoir. It is notable in this regard that Wallis (1951) considered razorback suckers far less abundant in the newly-impounded Lake Mohave than in Lake Mead, indicating that a strong year class had not yet been produced in the former reservoir. He considered the species "to be holding its own and reproducing abundantly in Lake Mead." These data

TABLE 6.—*Reintroductions of razorback suckers in Arizona 1981-82 (Johnson 1982, Johnson and Rinne 1982, orig. data provided by James Brooks, AGFD).*

Locality	Date	No.
GRAHAM CO.		
Eagle Creek, S26, T4S, R28E	6/30/81	1,000
Eagle Creek, S26, T4S, R28E	7/14/82	3,000
Gila River, S3, T6S, R30E	6/30/81	1,000
Gila River, S3, T6S, R30E	9/9/81	1,344
Gila River, S3, T6S, R30E	7/14/82	3,000
Gila River, S3, T6S, R30E	10/12/82	4,146
Gila River, S32, T6S, R31E	10/12/82	8,297
Bonita Creek, Unsurv., T6S, R28E	9/9/81	1,344
GILA CO.		
Cherry Creek, S3, 10, 15, T4N, R15E	6/30/81	2,000
Cherry Creek, S3, 10, 15, T4N, R15E	4/6/82	100,159
Coon Creek, S8-9, T4N, R15E	3/16/82	2,500
Coon Creek, S8-9, T4N, R15E	4/6/82	25,500
Salt River, S2, T3N, R15E	9/9/81	1,344
Salt River, S9, T3N, R14E	9/9/81	1,344
Salt River, S9, T3N, R14E	4/6/82	100,000
Salt River, S4-5, T3N, R14E	3/16/82	62,500
Salt River, S6-7, T3N, R14E	3/16/82	277,500
YAVAPAI CO.		
Oak Creek, S23, T16N, R4E	7/1/81	1,000
Oak Creek, S23, T16N, R4E	7/14/82	6,000
Oak Creek, S12, T16N, R4E	7/1/81	1,000
West Clear Creek, S14, T13N, R6E	7/1/81	1,000
West Clear Creek, S14, T13N, R6E	7/14/82	3,000
Verde River, S7, T13N, R5E	9/15/82	6,763
Verde River, S3, 11, T11N, R6E	9/10/81	2,688
Verde River, S3, 11, T11N, R6E	9/15/82	6,762

suggest a highly successful spawn just after impoundment of southwestern mainstream reservoirs, then long persistence of adults. A similar pattern exists in some other large cyprinoid fishes elsewhere in western United States (Moyle, 1976).

Size variation in a single cohort of razorback suckers (Fig. 3) may well be adaptive to the predictably variable Colorado River. Low adult mortality would lead to selection for iteroparity and large size, yet high mortality after a brief period of growth would favor reproduction by young (smaller) size classes (G. R. Smith, 1981a). In razorback suckers, fast-growing (large) fish that could reproduce at a young age might be more fit in cycles of high discharge, while slow-growing (smaller) fish might best survive under intermittent conditions during long periods of drought, then reproduce when conditions of higher flow are again realized. G. R. Smith (1981a) demonstrated an intraspecific tendency for large-volume aquatic habitats in the intermountain deserts to produce larger fishes than small volume ones, and proposed the evolution of alternative stategies as follows:

> If adult mortality is variable because of unpredictable variation in the severity of seasonal fluctuations, individuals that invest in early reproduction will leave more descendents after destructively dry years; those that grow larger and produce more offspring later will leave more descendants in a series of wetter years.

Postpluvial habitat instability in western North America may have allowed maintenance of alternative genotypes that result in growth and reproductive placticity among and within populations of western fishes. Perhaps the stability of reservoirs has allowed such inherent variation to be expressed in year classes of razorback suckers that have achieved adulthood.

Destruction of the native fauna of the lower Colorado River has before been attributed mostly to physical modifications of the environment, such as de-watering, channelization, and impoundment (Beland, 1953; Miller, 1961; Minckley and Deacon, 1968; Vanicek et al., 1970; Holden and Stalnaker, 1975; Moyle, 1976; Behnke, 1980). Considering the great age of the Colorado River, and correspondingly great ages of at least some of the genera of fishes inhabiting it (dating at least from Pliocene; Uyeno and Miller, 1963, 1965; G. R. Smith, 1981a-b; M. L. Smith, 1981), sufficient time has been available for them to have experienced as much, and likely far more physical change than has recently been effected by man. Desertification has de-watered much of western North America, undoubtedly in a cyclical fasion, for millenia, yet stream fishes persist in desert basins (Hubbs and Miller, 1948; Hubbs et al., 1974; G. R. Smith, 1978, 1981a-b). Channel-straightening floods (Burkham, 1972) produce changes in habitat similar to man's channelization projects. Tectonic or volcanic events have repeatedly impounded desert rivers, even within the Grand Canyon (McKee et al., 1967), as evidenced by strandlines, terraces, and lacustrine deposits (Nations et al., 1982).

De-watering kills fishes directly when complete, and thus requires no further discussion. Channelization or major floods decrease environmental heterogeneity and speed time-of-flow in more uniform channels. Impoundment also obviously suppresses variability, and in doing so may, more than channelization, modify environmental cues required by an animal to feed, grow, and reproduce to fulfill its life cycle. Yet fishes of the genera *Ptychocheilus*, *Gila*, and *Catostomus*, plus other forms, lived under lacustrine conditions in Pliocene times (Uyeno and Miller, 1965; G. R. Smith, 1975, 1978, 1981a-b).

High dams on canyon rivers of southwestern North America differ from natural impoundments in their release of water from cold hypolimnia of upstream reservoirs. Physiological tolerances of native biotic elements may therefore be exceeded by direct effects of temperature downstream; cold water precludes reproduction in many lowland southwestern fishes. Yet, long reaches of stream exist that warm sufficiently in summer to duplicate conditions in natural systems (Minckley, 1979). Blockage of spawning runs by dams and diversions also has been cited as a factor in the decline of riverine species, a direct effect in the case of salmonids, but far more subtle with most other groups. A "run" is obviously not necessary for successful spawning in razorback suckers since they do so under reservoir conditions. At present, if native catostomids did move upstream from reservoirs to spawn, movement of juveniles downstream after hatching would end in a reservoir, where concentrations of predators would minimize or preclude survival. Also, as pointed out by Moyle and Nichols (1973), dams may be more important in blocking re-dispersal of native, warmwater fishes back into areas where local extirpation has occurred. Re-establishment of stocks may therefore be physically impossible.

Indigenous minnows and suckers of southwestern North American have been essentially free of the influence of other major groups of fishes, especially Perciformes, for millenia. It is my impression, based on field observations, that they are naive toward predators, showing little avoidance even when under attack. Predator-avoidance responses seem quickly learned in salmonid fishes (Patten, 1977), and would logically be so in most species, or should be strongly selected for in a relatively simple system and given adequate time. However, unique features of present environmental changes include great speed of occurrence and a great diversity of predatory species.

Declines in the western fauna are directly proportional to establishment of predatory non-native fishes (Minckley and Deacon, 1968; Hubbard, 1980). Most of the these are lentic in habitat preferences, and introductions of such species into the region have succeeded as a result of the construction of suitably stable reservoirs. Extirpation of now re-established families such as Esocidae, Centrarchidae, and Ictaluridae from western North American before Plio-Pleistocene times has been attributed to a reduction in non-erosive, lentic or semi-lentic, lowland habitats, following mountain building (Miller, 1959). Reservoirs and stabilized flows again allow species of those families to flourish when introduced. Other alien, often piscivorus fishes such as cichlids, percichthyids, percids, and poeciliids now also have been introduced. Western rivers that remain unmodified resist incursions and continuous occupation by other than native fish species (Moyle and Nichols, 1973; Moyle, 1976; orig. data), with notable exceptions being generalized, stream-adapted fishes like red shiner, carp, and channel and flathead (*Pylodictis olivaris*) catfishes. The abundance of reservoirs, however, provides a constant source of introduced fishes for rivers (Molles, 1980), so that even when riverine reproduction is lacking or minimal, populations may persist.

Interactions of native and non-native animals may result in elimination of one or the other. Generalization on these interactions commonly include nebulous statements of competition, both by myself and others, to help explain declines in western fishes. However, I now consider competition for resources that are in short supply a secondary cause of extirpation. Excluding special cases such as genetic swamping of endemic trouts by non-native trouts (Rinne and Minckley, 1983), and cold water below dams that terminates reproduction, declines in native fish populations are largely attributable to predation by adults or juveniles of introduced kinds upon early life-history stages of indigenous forms (Myers, 1965; Minckley, 1973; Minckley et al., 1977; McAda and Wydoski, 1980; Meffe et al., 1982). The primary impact of man's development of reservoirs has provided habitat for predators as a secondary, but now prevalent, force in extirpation of native fishes. Ova are directly eaten by offshore predators such as carp and channel catfish. Shoreline and backwater habitats once exclusively available to non-piscivorous juveniles of suckers and minnows are now inhabited by young centrarchids and mosquitofish, and others. Predation by these introduced animals destroys the native faunal elements. It is predictable, as theory and practice demonstrating the role of predation in shaping animal communities matures (Macan, 1977; Zaret, 1980), that predation by introduced species on "naive" prey will be recognized as a major force in faunal change (*e.g.* Eckhardt, 1972; Diamond and Veitch, 1981; Simberloff, 1981).

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