The Colorado River and its tributaries have undergone drastic alterations from their natural states over the past 125 years. These alterations include both physical change or elimination of aquatic habitats and the introductions of numerous non-native species, particularly fish. Ironically, several more species occur at most localities today than were historically present before these alterations. This situation complicates the use of biodiversity as a litmus test for monitoring trends of either the deterioration or the health of an aquatic ecosystem.

An Altered Ecosystem

Over its entire basin (Figure), the Colorado River has been changed from its natural state perhaps as much as any river system in the world. The demands for water and power in the arid West have drastically altered the system by impoundments, irrigation diversions, diking, channelization, pollutants, and destruction of bank habitats by cattle grazing and other practices. Some reaches, ranging from desert spring runs to main rivers, have been completely dewatered or, seasonally, their flows consist almost entirely of irrigation return laden with silt and chemical pollutants. The Gila River of Arizona, one of the Colorado's largest tributaries, has not



flowed over its lower 400 km (248 mi) since the early 1900's. These alterations and their effects on the fish fauna have been discussed by several authors (Miller 1961; Minckley and Deacon 1968; Stalnaker and Holden 1973; Carlson and Muth 1989; Minckley and Deacon 1991). Only a few small tributaries, mostly at higher elevations, retain most of their natural characteristics.

Native Fish Fauna

Despite the expansive drainage basin (631,960 km² [243,937 mi²]) of the Colorado River, the system supported only a relatively small number of native fish species compared with basins of much smaller size east of the Continental Divide. The Colorado Basin's native fauna, however, was nearly unique. If two former marine invaders are removed from the 51 native taxa known from the system (Table 1), 42 of the 49 that remain (86%) are considered endemic to the system. The greatest diversity of taxa (44) was distributed in the Lower Basin downstream of the Arizona-Utah border, in a variety of habitats that include mainstem rivers, smaller tributaries, and isolated springs. The Upper Basin was much less diverse, containing 14 species, including a subset of the Lower Basin fauna plus 4 headwater species that occur in cooler water and a warm spring endemic. Basinwide, about 5 species occurred mostly in mainstem river or larger tributary habitats, 37 were restricted to smaller, in some cases isolated, habitats, and 7 were more generally distributed among different habitat types.

Trends

As a consequence of habitat alterations, the prevailing trend among native fish populations in the Colorado River Basin has been drastic

Colorado River Basin Fishes

by Wayne C. Starnes Smithsonian Institution



Figure. Colorado River Basin.

reductions that include decreased abundance in all or part of their ranges, overall range reductions, or virtual or actual extinctions (Tables 1 and 2). Presently, 40 of the 49 strictly freshwater, native species are considered either possibly or actually jeopardized or are extinct (Table 1). Of the 40, 12 are of special concern, 25 are considered endangered or threatened, and 3 are believed extinct.

In the Lower Basin, only 3 of the 10 native species that inhabited the mainstem of the lower Colorado River remained by the 1940's but by the 1960's, none remained. In the lower Salt River portion of the Gila River system, the original complement of 14 taxa was also reduced to 3 by the 1940's and to 2 by the 1960's; today, they are probably extirpated. In the early 1900's, the isolated springs of the Pluvial White River system in southern Nevada harbored 17 endemic taxa; today, 1 of those taxa is extinct, 9 endangered, 3 threatened, and the remainder of **Table 1.** Native fish taxa of the Colorado River Basin including currently recognized subspecies. Taxa denoted by * may eventually prove genetically distinct from populations outside the Colorado River Basin. Those denoted "(m)" are marine invaders. Status of jeopardized and extinct species appears in parentheses: E = endangered; T = threatened; SC = special concern; X = extinct (based, in part, on Carlson and Muth 1989; Williams et al. 1989; and the National Biological Service's Category 2 list). Common names bracketed with quotation marks indicate that those species are undescribed and not officially named.

Scientific name	Common name		
Family Elopidae			
Elops affinis (m)	Machete		
Family Cyprinidae			
Agosia chrysogaster	Longfin dace		
Gila cypha (E)	Humpback chub		
G. elegans (E)	Bonytail		
G. intermedia (SC)	Gila chub		
G. robusta jordani (E)	Pahranagat chub		
G. robusta robusta (SC)	Houndtail chub		
G. seminuda (E)	Virgin chub		
Lepidomeda albivallis (E)	White Hiver spinedace		
L. altivelis (X)	Pahranagat spinedace		
L. mollispinis mollispinis (1)	Virgin spinedace		
L.m. pratensis (E)	Big Spring spinedace		
L. vittata (T)	Little Colorado spinedace		
Meda fulgida (T)	Spikedace		
Moapa coriacea (E)	Moapa dace		
Plagopterus argentissimus (E)	woundfin		
Ptychocheilus lucius (E)	Colorado squawtish		
Hninichthys cobitis (T)	Loach minnow		
R. deaconi (X)	Las Vegas dace		
R. osculus osculus	Speckled dace		
R. osculus ssp.(SC)	"Preston speckled dace"		
R. osculus ssp. (SC)	"Meadow Valleys speckled dace"		
R. osculus ssp. (SC)	"White River speckled dace"		
R.o. thermalis (SC)	Kendall Warm Springs dace		
R.o. velifer (SC)	Pahranagat speckled dace		
Family Catostomidae			
Catostomus clarki clarki	Desert sucker		
C.c. intermedius (E)	White River sucker		
C. clarki ssp. (E)	"Meadow Valley sucker"		
C. discobolus discobolus	Bluehead sucker		
C.d. yarrowi (SC)	Zuni sucker		
C. insignis	Sonora sucker		
C. latipinnis (SC)	Flannelmouth sucker		
C. platyrhynchus	Mountain sucker		
<i>C.</i> sp.(SC)	"Little Colorado sucker"		
Xyrauchen texanus (E)	Razorback sucker		
Family Salmonidae			
Oncorhynchus apache (T)	Apache trout		
O. clarki pleuriticus (SC)	Colorado cutthroat trout		
O. gilae (T)	Gila trout		
Prosopium williamsoni*	Mountain whitefish		
Family Goodeidae			
Crenichthys baileyi albivallis (E)	Preston springfish		
C.b. baileyi (E)	White River springfish		
C.b. grandis (E)	Hiko springfish		
C.b. moapae (T)	Moapa springfish		
C.b. thermophilus (T)	Moorman springfish		
C. nevadae (T)	Railroad Valley springfish		
Family Cyprinodontidae			
Cyprinodon macularius macularius (E)	Desert pupfish		
C. sp. (X)	"Monkey Springs pupfish"		
Family Poeciliidae			
Poeciliopsis occidentalis (SC)	Gila topminnow		
Family Cottidae			
Cottus bairdi*	Mottled sculpin		
C. beldingi*	Paiute sculpin		
Family Mugilidae			
Mugil cenhalus (m)	Striped mullet		

special concern. On the other hand, a few small tributaries, by virtue of their isolation, rare intermittent flows in lower reaches, and physical barriers, have been spared significant alterations or invasions by non-native species and retain an intact native fauna (e.g., Redfield Canyon, Arizona, Table 2).

In the larger rivers of the Upper Basin, such as the Green, lower Yampa, and most of the upper Colorado, most native taxa are extant but one or two (razorback sucker [Xyrauchen texanus], possibly bonytail [Gila elegans]), are represented by very rare individuals that may not be reproducing; all native fishes are greatly exceeded in numbers and kind by non-native taxa. In smaller tributaries of that region, varied numbers of native taxa persist; in the worst affected streams (e.g., most Green River tributaries in Utah), most taxa have been replaced by non-native taxa (author's observation).

Case studies of two endangered Colorado River species, which are hallmarks to conservationists, further elucidate patterns of decline among these fishes. They are large, long-lived (20-50 years) species that inhabit larger streams. The Colorado squawfish (*Ptychocheilus lucius*) is a highly migratory (Tyus 1990) predatory minnow. Perhaps because of fragmentation or impediment of migratory routes, its original extensive range has been reduced by roughly two-thirds, and it is uncommon where it remains. The last confirmed report in the Gila River was in 1950 and the last in the Lower Basin in 1975 (Miller 1961; Minckley 1973; Maddux et al. 1993).

The fourth species, the humpback chub (Gila cypha), is strictly a denizen of turbulent canyon reaches so difficult to sample that it was not discovered until 1946; it ranged from Boulder Canyon on the lower Colorado throughout canyon reaches of the Upper Basin well into Wyoming. Today, it occurs only in Grand Canyon, Arizona (Maddux et al. 1993), near the confluence of the Colorado and Little Colorado rivers, and in five Upper Basin canyon areas (rare in three), although the genetic "purity" of the Upper Basin populations is questioned. Recovery plans are in place for these fish as well as the bonytail and the razorback sucker. These fish are all easily propagated in captivity. It is otherwise difficult to find anything positive in the history of these or other Colorado Basin native fishes over the past several decades.

Non-native Species

Concomitant with the pervasive physical alteration of the Colorado River ecosystem has been both purposeful and accidental introductions of at least 72 non-native fish taxa (Maddux et al. 1993), including those indigenous to other North American basins and more exotic species. Alterations of the ecosystem's natural characteristics have apparently tipped the ecologic balance in favor of many of the non-native species that now vastly outnumber natives in numbers of species (Table 2), population density, and often biomass at most localities. There is evidence that some, such as the extremely pervasive red shiner (Cyprinella lutrensis), displace native taxa (Douglas et al. 1994) while others, such as channel and flathead catfish (Ictalurus punctatus and Pylodictis olivaris), are known predators on larval and juvenile native species (several references in Maddux et al. 1993). The introduced white sucker (Catostomus commersoni) is hybridizing extensively with native suckers throughout much of the Upper Basin (author's observation), possibly threatening the genetic integrity of those taxa. These and other interactions between nonnative and native taxa may have significant negative effects on native fishes. The dominance held by non-native fishes may be symptomatic of the overall degree of alteration of the Colorado River ecosystem and could potentially confound future studies of biodiversity.

Table 2. Overall and relative abundance of native and nonnative fishes from various localities in the Colorado River Basin. Numbers for 1800's represent original complements of native taxa. For subsequent years, total abundance is followed by ratio of non-native to native taxa in parentheses. Sources: Miller 1961; Taba et al. 1965; Vanicek et al. 1970: Stalnaker and Holden 1973: Cross 1975; Holden and Stalnaker 1975a,b; Suttkus et al. 1976; Carlson et al. 1979; Miller et al. 1982; Valdez et al. 1982; Valdez 1984,1990; Wick et al. 1985; Platania and Bestgen 1988; Griffith and Tiersch 1989.

Survey date						
1800's	1940's	ca. 1965	ca. 1975	ca.1985		
10	-	21(12/9)	22(13/9)	24(15/9)		
9	-	-	13(7/6)	12(5/7)		
9			11(7/4)	16(12/4)		
10		15(9/6)	29(19/10)	31(23/8)		
9	-	-	•	18(12/6)		
10	-	-	19(15/4)	-		
6		-	19(13/6)			
10	12(9/3)	11(11/0)	-	-		
14	9(6/3)	22(20/2)	-	-		
5	-	•	-	5(0/5)		
	1800's 10 9 9 10 9 10 6 10 14 5	1800's 1940's 10 - 9 - 9 - 10 - 9 - 10 - 9 - 10 - 6 - 10 12(9/3) 14 9(6/3) 5 -	Survey data 1800's 1940's ca. 1965 10 - 21(12/9) 9 - - 9 - - 10 - 15(9/6) 9 - - 10 - 15(9/6) 9 - - 10 - 15(9/6) 9 - - 10 - - 6 - - 10 12(9/3) 11(11/0) 14 9(6/3) 22(20/2) 5 - -	Survey date 1800's 1940's ca. 1965 ca. 1975 10 - 21(12/9) 22(13/9) 9 - - 13(7/6) 9 - - 13(7/6) 9 - - 13(7/6) 9 - - 11(7/4) 10 - 15(9/6) 29(19/10) 9 - - - 10 - 19(15/4) 6 - 19(15/4) 6 - 19(13/6) 10 12(9/3) 11(11/0) - 14 9(6/3) 22(20/2) - 5 - - -	Survey date 1800's 1940's ca. 1965 ca. 1975 ca. 1985 10 - 21(12/9) 22(13/9) 24(15/9) 9 - - 13(7/6) 12(5/7) 9 - - 11(7/4) 16(12/4) 10 - 15(9/6) 29(19/10) 31(23/8) 9 - - - 18(12/6) 10 - 19(15/4) - 18(12/6) 10 - 19(15/4) - - 6 - 19(13/6) - - 10 12(9/3) 11(11/0) - - 14 9(6/3) 22(20/2) - - 5 - - 5(0/5) -	

Altered Species Diversity and Biodiversity Studies

While native taxa have declined, there have actually been two- to threefold increases in the number of species at most localities in the Colorado Basin because of the success of introduced taxa (Table 2). If future biodiversity monitoring is to truly gauge positive and negative shifts in the health of the Colorado River ecosystems, then an accurate baseline is necessary. A baseline describing unaltered native fauna might be an ideal but unattainable goal. That line could be approached, however, by divesting faunal lists of all non-native taxa and determining, as much as possible, the true extent of diversity of that which remains. In fish, it is practical to do so to the level of distinctive populations through studies of genetic variability. With luck, it is even possible to include extirpated populations through DNA studies of museum specimens if historic material is available.

Once a baseline is determined, researchers and managers can know where to try to "hold the line" in maintaining diversity through management and protection. Of course, on a systemwide basis, the baseline diversity of a pristine system can never be reattained because genetically unique populations have already been lost. On a more local basis, however, positive increments and recovery of the habitat are indicated if monitoring reveals increased diversity resulting from the successful reestablishment of taxa which were conserved in other, less altered, portions of the system.

For monitoring purposes, when non-native species are added to biodiversity determinations, we must carefully tease out the cause of shifts toward or from the "desired baseline" which, in the case of the Colorado River, is probably a value far less than the present overall number of species. Thus, "desirable" outcomes may be indicated by overall decreases in diversity caused by the disappearance of nonnative taxa as an indicator of habitat "healing," but not so by the loss of native taxa. Conversely, actual increases may yet be positive if caused by reestablishment of native taxa, but may be an indicator of further degradation if caused by success of additional non-natives. Realistically, monitoring will have to include, in addition to determinations of diversity, attention to shifts in dominance among native and nonnative species, which can be indicative of both positive and negative trends.

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