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The Colorado River: Lifeline of the American Southwest[1]

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Abstract

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In less than a century, the wild Colorado River has been drastically and irreversibly transformed into a tamed, man-made system of regulated segments. The pristine Colorado, characterized by widely fluctuating flows and physico-chemical extremes, supported unique assemblages of indigenous flora and fauna. Closure of Hoover Dam in 1935 marked the end of the free-flowing river. The system has since become one of the most altered and intensively controlled in the United States; many mainstem and tributary dams, water diversions, and channelized river sections now exist in the basin. Despite having one of the most arid drainages in the world, the river supplies more water for consumptive use than any river in the United States. Its biota is dominated by non-native organisms, and about one third of its native fishes are threatened, endangered, or extinct. This paper treats the Colorado River holistically as an ecosystem and summarizes current knowledge on its ecology and management. Little has been published on productivity and fisheries of the mainstream river.

Résumé

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En moins d'un siècle, le cours sauvage du Colorado a été irrévocablement et très fortement modifié en un système artificiel de tronçons à débit régularisé. À son état vierge, le Colorado abritait des assemblages uniques d'animaux et de plantes indigènes; on y observait des fluctuations importantes du débit et des facteurs physico-chimiques. Depuis l'achèvement en 1935 du barrage Hoover qui a marqué la fin de l'état sauvage du fleuve, le système est devenu l'un des cours d'eau les plus perturbés et intensivement harnachés des États-Unis. Il existe maintenant dans le bassin versant de nombreux barrages, ouvrages de déviation et tronçons canalisés dans le tronçon principal et les tributaires. Malgré que son bassin hydrographique soit l'un des plus arides du globe, le Colorado fournit un plus grand volume d'eau à des fins de consommation que tout autre cours d'eau américain. Son biote est composé en grande partie d'organismes exotiques et environ un tiers de sa faune piscicole indigène est menacée, en danger de disparition ou disparue. On présente une vue globale du Colorado à titre d'écosystème et on résume les connaissances actuelles sur son écologie et sa gestion. Peu de données ont été publiées sur la productivité et les pêcheries dans le tronçon principal.

Introduction

"In a little over two generations, the wild Colorado has been harnessed by a series of dams strung like beads on a thread from the Gulf of California to the mountains of Wyoming. The living river that Powell knew has been sectioned into placid desert lakes throughout much of its length, and the river's primordial task of carrying the *massif* of the Colorado Plateau to the sea, bit by grainy bit, has been interrupted, and will remain interrupted for the lifetimes of our children's children and beyond." — Watkins (1969).

Despite years of study, the Colorado River has rarely been viewed holistically as an ecosystem (sensu Minshall et al. 1985), and much information on its biota is available only in the "gray" literature. This case history is intended to introduce the reader to the Colorado River System, with emphasis on current literature, including recent reviews by Graf (1985) and Stanford and Ward (1986a, 1986b, 1986c). We have drawn upon only the most significant elements of the extensive non-peer-reviewed literature.

Description of the Basin

The Colorado heads on the Never Summer Range in Rocky Mountain National Park, Colorado, and flows 2 320 km to the Gulf of California in Mexico (Fig. 1). The Green River, which joins the Colorado in Canyonlands National Park, Utah, originates in the Wind River Range of

[1]Contribution 33, Colorado State University Larval Fish Laboratory.

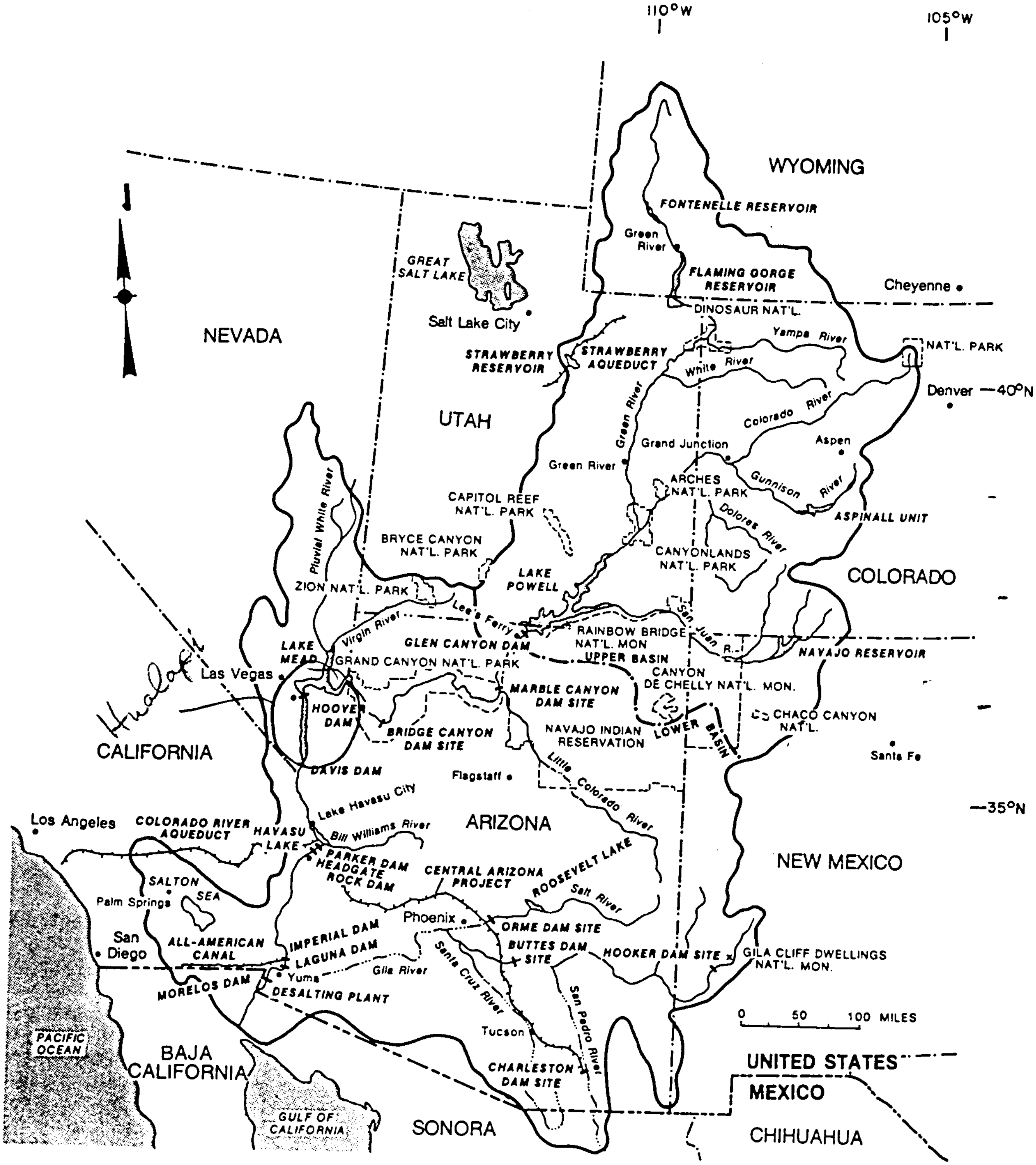

Fig. 1. The Colorado River Basin (redrawn from Hely 1969 and Fradkin 1981).

southwestern Wyoming, 2 735 km from the Gulf of California.

The Colorado River Basin encompasses 632 000 km² in the United States and Mexico (Plummer 1983) and ranges in elevation from sea level to above 4 000 m (Carlson and Carlson 1982). It occupies one-twelfth of the land area of the contiguous United States and is divided into upper and lower basins for water management purposes. Sub-basins and conditions in the basin were reviewed by LaRue (1916), Sykes (1937), Iorns et al. (1965), Bishop and Porcella (1980), Carlson and Carlson (1982), Graf (1985), and Stanford and Ward (1986a).

The Colorado River drainage spans three geologic provinces: Rocky Mountains, Colorado Plateau, and Basin and Range (Hunt 1974). Igneous and metamorphic rock underlie headwater regions, but the river contacts marine deposits containing salts and fine-grained sediments downstream (Miller et al. 1983). Major geologic strata were summarized by Stanford and Ward (1986a). Various portions of the river system originated from 3.3 to over 20 million years ago (Minckley et al. 1986).

Human occupation of the Colorado River Basin dates to some of the earliest records of man as a nomadic hunter in the Western Hemisphere over 10 000 yr ago. Agricultural Anasazi, Fremont, Mogollon, and Hohokam cultures flourished at various times into the 1200s, creating extensive irrigation systems (Masse 1981) and exploiting fishes and game along watercourses (Bolton 1919). They declined and were succeeded by their descendants (Hopi, Taos, Zuni, and Pima-Papago) and immigrant Navaho, Apache, Southern Paiute, Havasupai, and Hualapai people (Watkins 1969; Fradkin 1981; Graf 1985). Spanish explorers in search of riches encountered the lower Colorado River in 1540 (LaRue 1916). The river was given several names before Father Kino applied the name 'Colorado' on a 1705 map of his passage westward in search of religious converts (Bolton 1919; Hughes 1967). White trappers continued exploration of the canyon country in the early 1800s, and William Ashley's party first navigated the upper Green River in 1825 (LaRue 1916; Watkins 1969). Mormon colonizers established towns along the river, and John Lee was sent by church leaders to establish a crossing below Glen Canyon (Fradkin 1981). Lee's ferry site has played a prominent role in the law of the river. John Wesley Powell's scientific investigations of the Colorado began in 1869, when he floated from Green River, Wyoming, through the Grand Canyon (Stegner 1982). Watkins (1969) and Fradkin (1981) have contributed excellent comprehensive reviews of subsequent Colorado River history. The first high dam on the mainstream river (Hoover Dam) was closed in 1935, marking the free-flowing Colorado's demise (Stanford and Ward 1986a). In the remainder of this paper, we summarize the status of the Colorado River ecosystem prior to 1935, briefly describe human manipulation of the basin's waterways, and assess the current condition and future of the river system and its biota.

The Colorado River before 1935

Prior to 1935, the river flowed essentially unchecked from its sources to the sea, ending in a "live delta" of meandering streams, silt, and shifting land patterns (Hundley 1966). Then, as now, much of its basin consisted of relatively barren deserts. High relief, sparse vegetation, and desert storms combined with montane snowmelt to produce spectacular variations in discharge (Minckley 1979; Table 1). The upper basin produced most of the river's discharge, and peak flows occurred after snowmelt in spring and early summer (Bishop and Porcella 1980). Maximum runoff in the lower basin often followed winter rainstorms (Sykes 1937). Lowest discharge typically occurred in mid to late summer, but long periods of low flows accompanied droughts.

At times of moderate flows and during droughts, the river ran clear, but sediment transport was remarkably high during floods. In high-gradient reaches, alluvial rubble from side channels resulted in formation of rapids between long, sand-bottom pools (Stanford and Ward 1986a). Unstable flows and other conditions resulted in arroyo cutting in small and medium-sized streams, and floods and droughts resulted, over time, in alternating braided and meandering channels (Graf 1985). Oxbow lakes and extensive, transitory marshes formed where the lower river occupied broad valleys. Minckley (1979) characterized the lower Colorado before regulation as "a broad, meandering, sandy-bottomed, periodically erosive, yet often aggrading stream".

TABLE 1. Selected physicochemical characteristics of the Colorado River before 1935 (Deacon and Minckley 1974; Dolan et al. 1974; US Geological Survey 1975; Weatherford and Jacoby 1975; Pillsbury 1981; Graf 1985; Stanford and Ward 1986a).

Discharge, range at Yuma, AZ	0 to 7 000 $m^3 \cdot s^{-1}$
Virgin flow, long-term annual mean from upper basin	16.65 km^3
Sediment transport, daily maximum in Grand Canyon	$25 \cdot 10^6 t$
Seasonal water temperature ranges:	
Headwaters	0-20°C
Low-elevation desert streams	5->30°C
TDS:	
Headwaters	>50 $mg \cdot L^{-1}$
Lower mainstream	250–380 $mg \cdot L^{-1}$

Water temperatures in the pristine Colorado River probably resembled those recorded today in reaches far from mainstream reservoirs, and wide diurnal fluctuations were common (Minckley 1979). Chemical conditions before 1935 must have been almost as variable as discharge. Dissolved solids (TDS) concentrations differed with the geology of various sub-basins, but calcium, sulphate, and bicarbonate were predominant ions (Stanford and Ward 1986a). Local oxygen depletions probably were common in deeper backwaters along the lower river (Minckley 1979).

The biota of the Colorado River before 1935 is generally poorly documented. Headwater streams probably harbored plant and invertebrate communities like those currently present. Riverine algae were diverse but sparse, and nutrient levels were adequate to support considerable primary production during clear flows (Stanford and Ward 1986a). Autochthonous production was probably particularly important in areas on the lower river where marshy backwaters and oxbow lakes provided plant production that supplied organic detritus (Minkley 1979). Ward et al. (1986) stated that a highly adapted riverine zoobenthos existed at potamon sites in the upper basin but not in the Lower Mainstem Colorado. The trophic structure of the lower river probably was direct and simple. Chironomids and oligochaetes were the predominant benthic organisms. Only soft bottoms of backwaters and woody debris in main channels could have supported diverse and abundant invertebrate communities.

The Colorado River Basin has an unique indigenous fish fauna. The drainage was established long ago and has had no major connections with surrounding river basins for millions of years (Behnke and Benson 1983). As Molles (1980) noted, the Colorado River System may be considered "an aquatic island in a terrestrial sea". Because of long isolation, the fish fauna consists of species distinctly different from their nearest relatives, and relationships are evolutionarily and geographically distant (Miller 1959; Minckley et al. 1986). Many native genera probably existed in the basin by Miocene time, and present-day species occurred by the Plio-Pleistocene (Smith 1978; Minckley et al. 1986).

The fish fauna was first described in the middle to late 1800s in reports by naturalists assigned to military or exploratory expeditions (summarized by Evermann and Rutter 1895). Fishes native to the basin include 36 species, 20 genera, and 9 families (Table 2). Many species are polytypic within the basin.

Machete, striped mullet, and spotted sleeper are marine or brackish-water fishes that enter the Colorado's delta and ascend into the Lower Mainstem Colorado. Occurrence of spotted sleeper in the lower basin was documented by a single specimen (Hubbs 1953), and Minckley (1979) listed this species as "hypothetically" present. Ten of the remaining freshwater species are known from adjacent river basins. Of these, cutthroat trout, speckled dace, and Sonoran topminnow have subspecific representatives that are endemic to the basin. One isolated population of desert pupfish occurs naturally outside the basin (Miller 1943; Hubbs and Miller 1948; Miller 1981). The other 23 freshwater species are endemic and form an unique assemblage of highly specialized and unusual fishes. Endemic fishes account for 64 % of all native species (35 % of all native genera), constituting one of the highest levels of endemism known in North America (Miller 1959). Most other native species are represented by endemic subspecies.

Native fishes were never ubiquitously distributed throughout the basin and were associated with specific subbasins and habitat types. Many species had extremely narrow distributions within the basin (Table 2). An average of about 10 species probably occurred per major river drainage, with a range of 5 (Bill Williams drainage) to 18 or 19 (Gila River drainage). Except for mainstream species, there have always been distinct differences between upper and lower basin fish faunas. Five species (cutthroat trout, mountain whitefish, mountain sucker, mottled sculpin, and Paiute sculpin) occurred only in the upper basin and were essentially restricted to headwaters. These fishes are very similar

TABLE 2. Native fishes of the Colorado River Basin, including their current federal legal status and historic distribution/location in the basin (Evermann and Rutter 1895; Ellis 1914; Beckman 1952; Koster 1957; Miller 1959, 1961, 1972; Sigler and Miller 1963; Miller and Lowe 1964; Rinne 1976; Bailey et al. 1970; Baxter and Simon 1970; Rinne and Minckley 1970; Deacon and Bradley 1972; Minckley 1973, 1979; Holden and Stalnaker 1975; Cross 1976; Moyle 1976; Joseph et al. 1977; Behnke 1979; Deacon et al. 1979; Hubbard 1980; Lee et al. 1980; Molles 1980; Robins et al. 1980; Carothers and Minckley 1981; Parenti 1981; Behnke et al. 1982; Tyus et al. 1982; U. S. Department of the Interior 1982, 1983, 1985a-e, 1986a-e, 1987; Behnke and Benson 1983; Williams et al. 1985; Minckley et al. 1986; Stanford and Ward 1986c; Johnson 1987). X - indicates species has occurred; ? - indicates presence questionable; * - indicates endemic genera, species, or subspecies.

Species	Federal legal status[c]	Historic distribution by major river drainage[a]								Historic location
		Upper basin[b]			Lower basin[b]					
		CO	GR	SJ	CO	VR	LC	BW	GI	
ELOPIDAE										
Machete										
Elops affinis	N				X				?	sporadic in lower section of Lower Mainstem Colorado River, AZ-CA-Mexico; mouth of Gila River, AZ
SALMONIDAE										
Mountain whitefish										
Prosopium williamsoni	N		X							headwaters of Green River drainage, UT-WY-CO
Apache trout										
*Salmo *apache*	T						X		X	restricted to headwaters of Little Colorado and Salt rivers, AZ-NM
Colorado River cutthroat trout										
*S. clarki *pleuriticus*	U	X	X							headwaters of Upper Mainstem Colorado and Green river drainages, WY-CO
Gila trout										
*S. *gilae*	E								X	restricted to headwaters of Verde River, AZ and Gila River, NM
CYPRINIDAE										
Longfin dace										
Agosia chrysogaster	N							X	X	Bill Williams and Gila river drainages, AZ-NM, south to Rio Sonora, Mexico
Humpback chub										
*Gila *cypha*	E	X	X	?	X		X			larger river channels; primarily in canyon-bound segments

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Species	Federal legal status[c]	Historic distribution by major river drainage[a]								Historic location
		Upper basin[b]			Lower basin[b]					
		CO	GR	SJ	CO	VR	LC	BW	GI	
Bonytail *G. *elegans*	E	X	X	X	X		X		X	larger river channels of the basin; widespread
Colorado roundtail chub *G. *robusta robusta*	N	X	X	X				X	X	medium to large-sized river channels of the basin; widespread
No common name *G. *r. grahami*[d]	U								X	status questionable; Gila River drainage
Pahranagat roundtail chub *G. *r. jordani*	E					X				restricted to springs and spring-streams of Pahranagat Valley, pluvial White River, NV
Virgin river roundtail chub *G. *r. seminuda*	P-E					X				restricted to Virgin River, AZ-NV-UT
Moapa roundtail chub *G. *r. robusta* spp. [e]	U					X				restricted to Moapa River, NV
Gila chub *G. *intermedia*[f]	U								X	restricted to upper Gila River drainage, AZ-NM
White River spinedace **Lepidomeda albivallis*	E					X				restricted to pluvial White River, NV
Pahranagat spinedace **L. altivelis*	O					X				restricted to cool springs and spring-streams of Pahranagat Valley, Virgin River drainage, NV
Virgin river spinedace **L. mollispinis mollispinis*	U					X				restricted to Virgin River drainage, AZ-NV-UT
Meadow Valley spinedace **L. m. pratensis*	P-T					X				restricted to Meadow Valley Wash, Virgin River drainage, NV
Little Colorado spinedace **L. vittata*	P-T						X			restricted to upper Little Colorado River drainage, AZ
Spikedace **Meda fulgida*	T								X	moderately restricted to upper Gila River drainage, AZ-NM
Moapa dace **Moapa coriacea*	E					X				highly restricted to thermal springs of Moapa River, NV
Woundfin **Plagopterus argentissimus*	E				X	X			X	lower and middle sections of Lower Mainstem Colorado, Virgin, Salt, and Gila rivers

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		Upper basin[b]			Lower basin[b]					
		CO	GR	SJ	CO	VR	LC	BW	GI	
Colorado squawfish *Ptychocheilus *lucius*	E	X	X	X	X		X		X	larger river channels of the basin; widespread
Las Vegas dace *Rhinichthyes *deaconi*	O					X				restricted to Las Vegas Valley, Virgin River drainage, NV
Southern speckled dace *R. osculus[g] * osculus*	N								X	southern Gila River drainage
Colorado speckled dace *R. o. *yarrowi*	N	X	X	X	X	X	X	X		middle and upper Colorado River Basin
Moapa speckled dace *R. o. *moapae*	U					X				restricted to Moapa River, NV
Pahranagat speckled dace *R. o. *velifer*	U					X				restricted to Pahranagat Valley, Virgin River drainage, NV
Kendall Warm Springs dace *R. o. *thermalis*	E		X							restricted to Kendall Warm Springs, upper Green River drainage, WY
Meadow Valley speckled dace *R. osculus*spp.*	U					X				restricted to Meadow Valley Wash, Virgin River drainage, NV
Preston Spring speckled dace *R. osculus*spp.*	U					X				restricted to Preston Spring, Virgin River drainage, NV
Loach minnow **Tiaroga cobitis*	P-T								X	moderately restricted to upper Gila River drainage, NV
CATOSTOMIDAE										
Sonora sucker *Catostomus *insignis*	N							X	X	moderately restricted to Bill Williams and Gila river drainages, AZ-NM
Flannelmouth sucker *C. *latipinnis*	N	X	X	X	X	X	X		X	medium to large-sized river channels of the basin; widespread
Gila mountain sucker *C. (Pantosteus[i]) *clarki clarki[j]*	N							X	X	Bill Williams and Gila river drainages, AZ-NM
White River sucker *c. (P.) *c. intermedius[j]*	U					X				pluvial White River, NV
Colorado bluehead sucker *c. (p.) discobolus[k] discobolus*	N	X	X	X	X		X			medium to large-sized river channels; widespread

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Species	Federal legal status[c]	Historic distribution by major river drainage[a]								Historic location
		Upper basin[b]			Lower basin[b]					
		CO	GR	SJ	CO	VR	LC	BW	GI	
Zuni bluehead sucker *c. (P.) d. *yarrowi*	U						X			restricted to upper Zuni River drainage, AZ-NM
Mountain sucker *c. (P.) platyrhynchus*	N	X	X							headwaters of Upper Mainstem Colorado and Green river drainages, UT-WY-CO
Little Colorado sucker *Catostomus* *sp.[h]	N						X			restricted to Little Colorado River drainage, AZ-NM
Razorback sucker **Xyrauchen texanus*	U	X	X	X	X				X	larger river channels of the basin; widespread
CYPRINODONTIDAE[i]										
Northern springfish **Crenichthys baileyi albivallis*	U					X				restricted to isolated springs and spring-streams of pluvial White river, NV
Pahranagat springfish **C. b. baileyi*	N					X				restricted to isolated springs and spring-streams of Pahranagat Valley, pluvial White River, NV
Great springfish **C. b. grandis*	N					X				restricted to isolated springs and spring-streams of Pahranagat Valley, pluvial White River, NV
Moapa springfish **C. b. moapae*	U					X				restricted to isolated springs and spring-streams of pluvial White River, NV
Thermal springfish **C. b. thermophilus*	N					X				restricted to isolated springs and spring-streams of pluvial White River, NV
Railroad Valley springfish **C. nevadae*	T					X				Railroad Valley, a former connective of the Virgin River drainage, NV
Sonoran Desert pupfish *Cyprinodon macularius *macularius*	E				X				X	lower section of Lower Mainstem Colorado River and Gila River drainage
Salton Sea pupfish *C. m. *californiensis*	E				X					Salton Sea Basin, CA
POECILIIDAE										
Sonoran topminnow *Poeciliopsis occidentalis occidentalis*	E								X	moderately restricted to Gila River drainage south into Mexico

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Species	Federal legal status[c]	Historic distribution by major river drainage[a]								Historic location
		Upper basin[b]			Lower basin[b]					
		CO	GR	SJ	CO	VR	LC	BW	GI	
MUGILIDAE										
Striped mullet										
Mugil cephalus	N				X				X	sporadic in lower section of Lower Mainstem Colorado river, AZ-CA-Mexico; mouth of Gila River, AZ
ELEOTRIDAE										
Spotted sleeper										
Eleotris picta	N				?					extreme lower section of Lower Mainstem Colorado River, AZ-CA-Mexico
COTTIDAE										
Mottled sculpin										
*Cottus bairdi *punctulatus*	N	X	X	X						headwaters of upper basin drainages, UT-WY-CO
Paiute sculpin										
C. beldingi	N	X								headwaters of Upper Mainstem Colorado River drainage, CO
NUMBER OF SPECIES		12	12	8 (9?)	11 (12?)	12	9	5	18 (19?)	

[a]Major river drainages: CO — Mainstem Colorado, GR — Green, SJ — San Juan, VR — Virgin, LC — Little Colorado, BW — Bill Williams, GI — Gila.
[b]Dividing line at Lee Ferry, AZ.
[c]Federal legal status under the 1973 Endangered Species Act as amended: T — threatened, E — endangered, P — proposed for listing, U — under review (candidate), N — no federal status (however, certain of these taxa are variously protected by one or more basin states) O — extinct.
[d]Included here are populations referred by Rinne (1976) to *Gila robusta grahami* Girard; problematic fishes currently under study.
[e]This distinctive form may be worthy of subspecific rank, but remains under study.
[f]This taxon was raised to specific rank by Rinne (1976); an action followed by several western biologists (Rinne and Minckley 1970; Minckley 1973; Minckley et al. 1986).
[g]Many distinctive forms of speckled dace occur in the Lower Colorado River Basin, especially as "big-river" forms in most major streams and also as isolated populations in headwaters and springs. Status of these may never be determined because of complexities of their variation.
[h]The Little Colorado sucker, proposed as an undescribed species related to flannelmouth sucker by Minckley (1973), is yet to be formally described.
[i]Minckley (1973) provided reasoning for retaining *Pantosteus* as a valid genus (see Smith 1966 for the alternative view).
[j]Certain *Pantosteus* of the Bill Williams and Virgin rivers are distinctive and may represent valid species. This is especially true for the Bill Williams River, where *P. clarki* typical of the Gila River drainage co-occur with another form (Minckley 1973).
[k]As with *P. clarki*, this highly available taxon may include a number of unrecognized species.
[l]Parenti (1981) demonstrated that the United States genera *Crenichthys* and *Empetrichthys* belong to the family Goodeidae, an otherwise live-bearer family of central Mexico.

to conspecifics in adjacent river basins. Twenty species are known only from the lower basin and (excluding marine forms) were largely confined to small to medium-sized river channels. The Virgin and Gila river drainages represent centers of endemism. Only eight species were common to both the upper and lower basins. Of these, humpback chub, bonytail, Colorado squawfish, flannelmouth sucker, and razorback sucker, the so-called "big river" fishes, were generally restricted to large, mainstream channels. Biology, ecology, and habitat requirements of the basin's native fishes have been reviewed in detail by Minckley (1973, 1979), Deacon and Minckley (1974), Behnke et al. (1982), Behnke and Benson (1983), Stanford and Ward (1986c), and contributors to Spofford et al. (1980) and Miller et al. (1982a).

Merriam's vegetation zones were employed in Graf's (1985) description of natural riparian vegetation. At upper elevations in the basin, riparian communities were dominated by willows. In lower (Transition, Upper Sonoran, and Lower Sonoran) zones, riparian vegetation was a complex mix of willows (*Salix* sp.), cottonwood (*Populus* sp.), mesquite (*Prosopis* sp.), seepwillow (*Baccharis salicifolia*), and arrowweed (*Tessaria sericea*). Specific communities were described in detail by Brown et al. (1977) and Stanford and Ward (1986a). The exotic tamarisk (also known as salt cedar), *Tamarix gallica*, had been introduced to the basin and occurred in riparian communities of most drainages by 1935 (Graf 1985). A well-developed riparian community along the lower Colorado provided allochthonous organic input to the stream and furnished habitat for terrestrial insects which served as fish food. Ohmart et al. (1977) estimated that at least 2 023 ha of cottonwood communities existed along 322 km of potentially suitable habitat on the lower river in the 1600's. Overgrazing and cutting of cottonwoods and mesquite for fuel had caused significant changes in pristine riparian communities before regulation of the river (Ohmart et al. 1977). Riparian vegetation was important then, as now, in supplying habitat for terrestrial vertebrates (Johnson and Jones 1977).

Management of the Colorado River System

Native Americans began diverting water from rivers in the Colorado River Basin to irrigate crops around 1000 AD, and sophisticated canal systems existed on floodplains of the Salt, Gila, San Juan, and other streams by 1200 (Graf 1985). The early irrigators vanished by 1400, and interest in diverting water for agriculture in the Colorado basin was not renewed until the middle to late 1800s, when small diversions abounded and discussions of major diversion projects began (Fradkin 1981). Levees were constructed to contain the lower Colorado River, and jetties and frontworks were built to deflect currents and protect streamside development. Major diversions of Colorado River water to the Imperial Valley, California, began just after the turn of the century, and the Salton Sea was created when the flooding Colorado broke through restraints in 1905 (Sykes 1937; Watkins 1969).

TABLE 3. Selected decisions and projects influencing the Colorado River System (Hughes 1967; Watkins 1969; Spofford 1980; Fradkin 1981; Carlson and Carlson 1982; Harris et al. 1982; Plummer 1983; Valentine 1983; Coats 1984; Upper Colorado River Commission 1984; Graf 1985; Welsh 1985; Hundley 1986; Bureau of Reclamation data).

A. Laws, compacts, treaties and other decisions

Year	Action	Rationale/effect
1902	Reclamation (Newlands) Act passed	Created U.S. Reclamation service (Bureau of Reclamation)
1903	Salt River Project (Colorado R. to central AZ) authorized	Irrigation agriculture near Phoenix, AZ; authorized Roosevelt Dam
1904	Yuma Project (Laguna Dam) authorized	Irrigation of Yuma Valley, AZ/CA
1908	Grand Canyon National Monument established	—
1915	Dinosaur National Monument and Rocky Mountain National Park established	—
1919	Grand Canyon National Park established	—
1922	Colorado River Compact signed (AZ joined 1944)	Divided Colorado R. water between upper and lower basins[a]
1929	Boulder Canyon Project Act passed	Authorized Hoover Dam and all-American Canal; Congress approved Compact of 1922
1934	Fish and Wildlife Coordination Act passed	Provided that federal water project planning must consider impacts on wildlife
1944	Mexican Water Treaty signed	Assured Mexico of 1.85 $km^3 \cdot yr^{-1}$ of Colorado R.

B. Dams, diversions, and other structural modifications

Year	Action	Rationale/effect
1892	Grand Ditch (Colorado R. to eastern slope, CO) completed	First diversion of water from Colorado basin
1901	Imperial Canal completed (Colorado R. near Yuma, AZ, to Imperial Valley, CA)	Irrigation of Imperial Valley
1909	Laguna Diversion Dam (Colorado R., CA/AZ) completed	Irrigation of Yuma Valley, AZ/CA
1911	Roosevelt Dam and Power Plant completed (Salt R., AZ)	First high dam (multipurpose) in basin[b]
1913	Strawberry Dam (Strawberry R., UT) completed	Water storage for Provo, UT, area (Great Basin)
1915	First Imperial Irrigation District temporary diversion dam completed	Ensuring minimum flows to imperial Valley
1935	Hoover Dam completed (Colorado R., NV/AZ)	Multipurpose (water storage, flood control, and power generation)
1938	Imperial Dam (Colorado R., AZ/CA) and Parker Dam (Colorado R., CA/AZ) completed	Desilting of irrigation water to AZ and CA; water storage for southern CA and central AZ; flood control
1940	All-American Canal (Imperial Reservoir to Imperial Valley) opened	Irrigation of Imperial Valley
1941	Colorado River Aqueduct (L.	Municipal water for Los Angeles and

TABLE 3. *(Continued)*

A. Laws, compacts, treaties and other decisions

Year	Action	Rationale/effect
		water[a]; authorized Davis Dam
1948	Upper Colorado River Basin Compact signed	Apportioned upper basin water to upper basin states and AZ[a]
1956	Colorado River Storage Project Act passed	Authorized Flaming Gorge, Glen Canyon, Navaho and Curecanti projects in upper basin
1964	*Arizona* v. *California* Supreme Court decision issued; Canyonlands National Park established	Apportioned lower basin water between AZ, CA and NV[a]
1968	Colorado River Basin Project Act passed	Authorized Central Arizona Project and five upper basin projects
1969	National Environmental Policy Act passed	Required Bureau of Reclamation to work under provisions of acts and consult with wildlife authorities
1973	Endangered Species Act passed	—
1974	Colorado River Basin Salinity Control Act passed	Controlled salinity of Colorado R. water
1982	Reclamation Act amended	Raised limitation on land owned by Bureau of Reclamation water users

B. Dams, diversions, and other structural modifications

Year	Action	Rationale/effect
	Havasu to Southern CA)	environs
1943	Gila Project (Imperial Res. to lands along Colorado and Gila rivers) opened	Irrigation of lower Gila and Colorado Valleys
1946	Headgate Rock Diversion Dam (Colorado R., CA/AZ) completed	Irrigation of Indian lands along Colorado R.
1950	Morelos Dam (Colorado R., Mexico) completed	Storage for irrigation of Mexicali Valley, Mexico
1953	Davis Dam (Colorado R., AZ/NV) completed	Regulation of water delivery to Mexico; flood control
1963	Flaming Gorge Dam (Green R., UT) and Navaho Dam (San Juan R., CO) completed	Multipurpose
1964	Glen Canyon Dam (Colorado R., AZ) and Fontenelle Dam (Green R., WY) completed	Multipurpose
1977	Bypass drain (Colorado R. to Gulf of California) opened	Diverting brackish water from Colorado R.
1978	Crystal Reservoir (Gunnison R., CO); Curecanti Unit (name changed to Wayne Aspinall Storage Unit 1980) completed	Storage
—	Under construction Yuma Desalting Plant; central Arizona Project (L. Havasu to Pheonix)	Desalting water; supplying water to central AZ and to central NV and UT.

[a]See Graf (1985) for legal water entitlements to basins, states and Mexico.
[b]See Graf (1985) for heights and storage capacities of major high dams in the Colorado system.

The U.S. Bureau of Reclamation, created by legislative action in 1902 (Table 3A), is responsible for construction and operation of projects that support economic development, primarily irrigation agriculture and industrial water uses (Graf 1985). Fradkin (1981) referred to five phases of the Bureau's "conquest" of the Colorado River. First, it constructed several small, non-controversial projects and followed these with the larger Strawberry Valley Project, Utah; Gunnison Tunnel, Colorado; Roosevelt Dam, Arizona; and Laguna Dam on the lower Colorado (Table 3B). Plans to enhance irrigation of the Imperial Valley by building a new canal (within the borders of the United States) and large reservoirs on the river to store water, control floods, and produce power led to fears in upper-basin states that the lower basin would claim rights to all water in the river under the doctrine of prior appropriation. Discussions culminated in the Colorado River Compact, which divided waters between the upper and lower basins (above and below Lee Ferry, respectively) on the basis of estimated virgin flows at Lee Ferry from 1896 to 1921. Negotiators based allocations on an annual flow of at least 22.20 km^3 (Hundley 1966). Average annual virgin flow at Lee Ferry is now estimated at 20.72 km^3 for the pre-Compact period and 17.52 km^3 since 1922 (Upper Colorado River Commission 1984). The Colorado's waters were overcommitted by this first attempt at apportionment.

After a period of stagnation through the 1920's, the Bureau of Reclamation launched its major dam-building era (the second phase of its conquest of the river) with passage of the Boulder Canyon Project Act in 1929 (Fradkin 1981). That law and the Upper Colorado River Basin Compact apportioned waters among states in the lower and upper basins, respectively, and Mexico was guaranteed water from the Colorado River by the Mexican Water Treaty (Graf 1985). High dams in the upper basin were authorized by the Colorado River Storage Project Act of 1956. Plans to construct dams at Echo Park in Dinosaur National Monument and at Bridge and Marble canyons in Grand Canyon were scuttled when public opinion stimulated by Wilderness Society and Sierra Club advertising reached U.S. congressmen (Watkins 1969; Nash 1970; Coats 1984). Welsh (1985) described the prolonged controversy over the Central Arizona Project and withdrawal of funding for Orme Dam.

The Bureau entered its third phase of conquest, construction of large aqueducts to deliver water to local areas, with passage of the Colorado River Basin Project Act of 1968. Fradkin's (1981) fourth phase, designed to "clean up the mess" caused by preceding phases, was launched by passage of the Colorado River Basin Salinity Control Act in 1974. The final phase will involve increasing the amount of water in the Colorado River Basin by imports from other basins or augmenting runoff through weather modification, strategies which will require additional study and negotiation (Pillsbury 1981; Harris 1983).

Since closure of Hoover Dam, the Colorado River System has become one of the most intensively controlled in the United States (Petts 1984). Although high dams provide security and profit for humans in the southwestern United States (Graf 1985), they have also transformed most of the streams in the Colorado basin into man-made rivers (Petts 1984).

Modifications documented in Table 3 B represent only the "tip of the iceberg" of man-induced changes in the Colorado River System. Bishop and Porcella (1980) reported some 117 reservoirs with individual storage capacities over 0.001 km^3 in the upper basin alone and about 40 trans-mountain canals and tunnels exporting water from that region. Water from the Colorado River Basin has long been diverted to and used in the Arkansas, Platte, and Rio Grande river basins and the Great Basin. On the lower Colorado, channels have been shortened by excavation, banks rip-rapped, and channels deepened by dredging (Minckley 1979). Lowering of water tables due to groundwater pumping, diversion and modification of spring runs, channelization, and impoundments have reduced fish habitats in desert portions of the Colorado basin (Pister 1981; Meffe et al. 1983; Williams et al. 1985).

Reservoir construction and diversion of water (often in open canals) from streams in the Colorado River Basin have enormously increased evaporative water loss from the system (Welsh 1985). Twelve percent of the Colorado's annual flow evaporated from reservoirs by the 1970's, and another 3 % was diverted from the basin (Graf 1985). Weatherford and Brown (1986) noted that 6.16 km^3 of water are exported from the basin annually. These phenomena team with crop irrigation and effects of municipal and industrial water uses to exacerbate natural downstream salinity increases (Carlson and Carlson 1982). High salinity, the river's most serious water quality problem, increases costs of water use and adversely affects agricultural productivity (Graf 1985).

By 1974, salt concentrations in the lower river had reached maximum levels recommended for agriculture and human consumption, and basin states agreed upon a program to maintain salinity at or below levels measured near lower-basin mainstream dams in 1972. The Colorado River Basin Salinity Control Act restricted salinity of water delivered to Mexico at Morelos Dam (Pillsbury 1981). A canal was constructed to divert highly saline water from the Welton-Mohawk Irrigation District to the Gulf of California, and the Bureau of Reclamation is building a desalting plant at Yuma, Arizona, to ensure delivery of required flows and salinities to Mexico. Such projects are expected to reduce TDS by 130 $mg \cdot L^{-1}$ at Imperial Dam (Paulson and Baker 1983).

Increased use of Colorado River water has also caused local problems associated with high heavy metals concentrations, radioactive materials, acid mine drainage, and oxygen levels near waste-treatment facilities (Bishop and Porcella 1980; Graf 1985). Additional energy development in the upper basin will increase impacts related to mining and rapid urbanization (Spofford et al. 1980; Jacobsen 1982; Adams and Lamarra 1983), and acid deposition may become a serious problem.

Watkins (1969) and Carothers and Johnson (1983) recognized the conflict between increasing visitation to National Park System areas in the Colorado River Basin and preservation of natural qualities of such lands. The National Park Service, Forest Service, and Bureau of Land Management now impose quotas on river rafters (Coats 1984) and enforce strict regulations on camping areas, use of fires, and waste management on lands they administer (Graf 1985). Nash (1986) emphasized the need to protect the Colorado's remaining wilderness.

The Colorado River Today

The Colorado River Basin is largely an area of very low human population density. It has few large cities but is highly urbanized; only 20 % of its population is rural (Graf 1985). Most of the land in the basin is administered by the United States government, primarily as Indian reservations, National Park System lands, national forests, and Bureau of Land Management (BLM) areas. The basin includes nine national parks, four recreation areas, 25 national monuments, and huge tracts of national forest and BLM-administered grazing or mineral-bearing lands (Graf 1985).

The present-day Colorado River supplies more water for consumptive use than any other river in the United States (Pillsbury 1981) despite having the lowest unit-area discharge (28 575 $m^3 \cdot km^{-2}$) of any United States river basin (Bishop and Porcella 1980). Stanford and Ward (1986a) referred to the basin as one of the driest in the world.

The long-term (1896-1984) estimated annual average virgin flow of the Colorado River at Lee Ferry was 18.26 km^3, but 1983 and 1984 levels were 29.60 and 30.22 km^3, respectively (Upper Colorado River Commission 1984). Stream regulation in the basin has reduced high spring flows and resulted in relatively high summer flows; drastic daily variation is common (Graf 1985). The Colorado River below Glen Canyon Dam may rise as much as 1.8 m in a few minutes, but potential for ecological damage in the Grand Canyon has no bearing on the dam's operating criteria (Coats 1984). Less than one percent of the river's virgin flow now reaches its mouth (Petts 1984).

Dams have also changed the capacity of streams in the Colorado River System to transport sediments. Sediments previously moved by streams are deposited in reservoirs, and space intended for water storage is gradually reduced as they accumulate (Graf 1985). Flows released from dams are relatively clear as well as seasonally constant; an excellent example is provided by data collected before and after closure of Glen Canyon Dam (Table 4).

Studies at several mainstream Colorado River dams (Petts 1984) have demonstrated that rapid degradation of channels may extend for many kilometres downstream from dams releasing frequent and prolonged outflows of clear water. Regulated flows have, thereby, changed channel forms and armoured stream bottoms in tailwaters (Graf 1985; Stanford and Ward 1986a). Numbers and sizes of mid-channel bars or islands and channelside bars or beaches have also been reduced below dams (Graf 1985). By limiting ability of streams to move coarse material, flow regulation has led to stabilized rapids downstream from dams (Graf 1985; Stanford and Ward 1983) and accumulation of sediments discharged from tributaries to mainstream channels (Dolan et al. 1974; Howard and Dolan 1981). Reductions in peak flow and channel and bank modifications have reduced the extent of backwaters and marshes.

Regulation has lowered mainstream water temperatures 10–15°C and resulted in cooler summer and warmer winter water temperatures below dams (Stanford and Ward 1986a). Lowered summer temperatures have adversely affected native fishes below Flaming Gorge and Glen Canyon dams (Kaeding and Zimmerman 1983).

By 1957, natural salt levels (about 250 mg•L^{-1}) at Lee Ferry had doubled (Graf 1985). Welsh (1985) reported a salt concentration of 600 mg•L^{-1} below Lake Powell and noted that the Central Arizona Project will extract water with 750 mg•L^{-1} from below Lake Mead. Paulson and Baker (1983) reported salinity of 825 mg•L^{-1} at Imperial Dam. Sulfate constitutes nearly half of the TDS in the Colorado River but has little effect on agriculture or municipal water uses.

Paulson (1983) discussed means of reducing TDS in and evaporation from Lake Mead by regulating releases from Lake Powell at Glen Canyon Dam. Lake Powell construction and regulation have affected a marked reduction in phosphorus transport to and productivity in Lake Mead 450 km downstream (Evans and Paulson 1983; Prentki and Paulson 1983; Stanford and Ward 1986b). A decline in the fishery of Lake Mead has been partly attributed to the reservoir's diminished fertility (Baker and Paulson 1983). Production in Colorado River reservoirs is strongly influenced by physicochemistry of river inflows (Stanford and Ward 1986b).

More uniform water temperatures and reduction in backwater and marsh habitat can be expected to diminish the frequency and severity of oxygen depletions in the Colorado River System. However, river regulation has introduced potential for downstream release from reservoirs of waters supersaturated with air gases; these could have detrimental effects on aquatic life (Holden 1979).

Aquatic flora and invertebrate fauna of few mainstream reaches of the Colorado River have been studied. Ward et al. (1986) stated that the filamentous green alga, *Cladophora glomerata*, is common on solid surfaces for several kilometers below dams in the basin. The cooler and less turbid waters in the Grand Canyon are now characterized by dense bottom mats of this alga, which is little used by most invertebrates but provides food for introduced fishes (Carothers and Minckley 1981; Carothers and Dolan 1982). The alga provides habitat and food for diatoms and the non-native *Gammarus lacustris*, a common mainstream invertebrate. Benthic invertebrate productivity and diversity in the Grand Canyon are low, and the main river lacks many common invertebrate groups found in tributaries.

Ward et al. (1986) reviewed studies of lotic zoobenthos in the mainstem Colorado River and at 34 tributary loca-

TABLE 4. Hydrological and sediment transport characteristics of the Colorado River below Glen Canyon Dam (modified from Dolan et al. 1974 and Petts 1984).

	Lee Ferry (24 km downstream)		Grand Canyon (165 km downstream)	
	Pre-dam	Post-dam	Pre-dam	Post-dam
Daily average flow equalled or exceeded 95 % of the time (m^3•s^{-1})	102	156	113	167
Median discharge (m^3•s^{-1})	209	345	232	362
Mean annual flood (m^3•s^{-1})	2 434	764	2 434	792
10 year's flood (m^3•s^{-1})	3 481	849	3 453	1 132
Annual maximum stage (m):				
Mean	5.04	3.56	6.89	4.79
Standard deviation	0.96	0.17	0.35	0.15
Annual minimum stage (m):				
Mean	1.76	1.46	0.46	0.70
Standard deviation	1.40	0.23	0.85	0.45
Mean sediment concentration (mg•L^{-1})	1 500	7	1 250	350
Sediment concentration equalled or exceeded 1 % of the time (mg•L^{-1})	21 000	700	28 000	15 000

tions. Chironomids, baetid mayflies, amphipods, planarians, oligochaetes, and snails tend to be predominant in tailwaters below deep-release dams. Common benthic invertebrates in potamon reaches in the upper basin and lower river are oligochaetes, chironomids, gastropods, leeches, turbellarians, sphaeriid clams, odonates, beetles, simuliids, net-spinning caddisflies, and baetid mayflies. Introduced freshwater shrimp and crayfishes are locally abundant in the lower river, and the introduced Asiatic clam, *Corbicula fluminea*, occurs as far upstream as Lake Mead. The Colorado River System appears unique in that unionacean clams are virtually absent from its waters and isopods are usually absent from lotic sites.

The fish fauna of the Colorado River Basin bears little resemblance to its original state. Approximately 100 species are now present; some 67 non-native fish species in 16 families have been introduced since the turn of the century and are now predominant in most fish communities (Miller and Lowe 1964; Minckley 1973, 1979; Moyle 1976; Carothers and Minckley 1981; Tyus et al. 1982). In terms of numbers of species, cyprinids, centrarchids, salmonids, catostomids, and ictalurids head the list of introduced fishes. Of the 54 natives listed in Table 2, 17 are either threatened, endangered, or extinct, and most have experienced drastic abundance and range reductions (Miller 1972; Minckley 1973, 1979; Joseph et al. 1977; Behnke and Benson 1983). Two species (Pahranagat spinedace and Las Vegas dace) are extinct, and the woundfin is almost gone. The cutthroat trout is threatened in the upper basin (Behnke 1979), and most stream- and spring-inhabiting fishes of the middle and lowermost Colorado River drainage are legally protected or of special concern (Johnson 1987). All of the "big-river" fishes are in jeopardy (Minckley 1973, 1983; Carothers and Minckley 1981; Tyus et al. 1982; Behnke and Benson 1983; Hickman 1983). Wild Colorado squawfish are gone from the lower basin, and the flannelmouth sucker is extirpated from the Gila River drainage (Williams et al. 1985). Tyus (1987) considered razorback sucker one of the rarest fishes in the Colorado River Basin. The humpback chub persists tenuously in the Little Colorado River and Grand Canyon (Kaeding and Zimmerman 1983) and occupies a few scattered canyon areas in the upper basin (Behnke and Benson 1983). The bonytail, originally widespread and abundant in the basin, is functionally extinct; a few scattered individuals exist in the Green and Upper Mainstem Colorado rivers and in Lake Mohave in the lower basin (Behnke and Benson 1983). Behnke and Benson (1983), said of the bonytail's demise that "If it were not for the stark example provided by the passenger pigeon, such rapid disappearance of a species once so abundant would be almost beyond belief". Several authors (Minckley 1979; Behnke 1980; Hubbard 1980; Molles 1980; Behnke and Benson 1983; Williams et al. 1985; Stanford and Ward 1986c) have attributed decline of native fishes to (1) modification and loss of habitat and (2) introduction of non-native species.

Construction and regulation of dams have had severe impacts on the fish fauna of the Colorado River, and little unaltered habitat remains (Tyus 1984). Coats (1984) described general lack of regard for minimum flow needs of fishes in operating Colorado River dams. Extreme fluctuations and alteration of seasonal flow regimes have been implicated in alleged loss of 1983 and 1984 year classes of the Colorado squawfish in its most productive remaining nursery habitat (Jones and Tyus 1985).

Williams et al. (1985) discussed adverse impacts of introduction of non-native species on native fishes in most of the 15 aquatic ecosystems in North American deserts that they considered. Schoenherr (1981) described behavioral interactions between introduced redbelly tilapia, *Tilapia zillii*, and sailfin molly, *Poecilia latipinna*, leading to replacement of desert pupfish. Schoenherr (1981), Minckley et al. (1977); Meffe et al. (1983), and Meffe (1984, 1985) studied predation by mosquitofish, *Gambusia affinis*, resulting in endangerment of Sonoran topminnow. Behnke and Benson (1983) discussed possible redside shiner, *Richardsonius balteatus*, competition with Colorado squawfish in the upper basin. Colorado squawfish interactions with other non-natives, e.g., "choking" on channel catfish, *Ictalurus punctatus*, (McAda 1983; Pimentel et al. 1985) and competition with northern pike, *Esox lucius*, (Wick et al. 1985) need further research.

Surveys by Moffett (1942, 1943), Dill (1944), and Wallis (1951), stimulated stocking of game fishes, and threadfin shad (*Dorosoma petenense*), and various invertebrates were stocked as forage. Trouts (*Salmo gairdneri, S. clarki,* and *Salvelinus fontinalis*) and Pacific salmon (*Oncorhynchus kisutch* and *O. nerka*) were stocked in reservoirs, and coldwater fisheries developed. Striped bass, *Morone saxatilis*, were introduced in Lake Mead in 1969, and a successful fishery developed in the 1970's. Rainbow trout and threadfin shad populations declined as a result of predation by striped bass (Baker and Paulson 1983).

A number of attempts were made to remove "coarse" fishes to make room for introduced species. In 1962, 700–800 km of the Green River and its tributaries were treated with rotenone to allow Flaming Gorge Reservoir and the streams to realize their full potentials as trout fisheries (Miller 1963; Dexter 1965; Pearson et al. 1968). Downstream detoxification failed, and rare endemic fishes were killed in Dinosaur National Monument. Binns (1967) reported that Colorado squawfish, razorback sucker, and rare mayflies had not reestablished populations in the treated area after 2 yr. Rotenone was also applied in the San Juan River prior to closure of Navaho Reservoir and on the Gila River upstream from San Carlos Reservoir. Impacts of these incidents have never been fully assessed.

Non-native trout fisheries downstream from Colorado River dams (Mullan et al. 1976) have become valuable assets. Flaming Gorge Dam has been modified to improve such a fishery through increase in tailwater temperatures (Holden 1979).

Other fisheries in the Colorado River Basin are dependent on non-native centrarchids and striped bass, but fishing for channel and flathead catfish (*Pylodictis olivaris*), walleye (*Stizostedion vitreum*), and northern pike is popular locally (Behnke et al. 1982; Stanford and Ward 1986c). Threadfin shad are important as food for piscivores in Lake Powell and lower-basin reservoirs (Johnson 1970, 1971; Stanford and Ward 1986c). Martin et al. (1982) estimated the annual economic value of Lake Mead fisheries at $69 million. Mullan et al. (1976), Carothers and Dolan (1982), Persons and Bulkley (1982), Morgenson (1983), and Baker and Paulson (1983) considered fishery management and cited similar studies on the Colorado system.

Studies of fish production in the system are rare. Scarnecchia and Bergersen (1986) estimated production (2.2 and 3.6 g$\cdot$m^{-2} in 1979 and 1980, respectively) of Colorado River cutthroat trout in a headwater tributary of the Colorado River and concluded that biomass and production were dependent on stream-specific physical properties.

The Endangered Species Act of 1973 mandated efforts to maintain rare native fishes and their habitats in the Colorado basin. Listing of fishes stimulated studies of their basic biology. Information on distribution and relative abundance of fishes in the Upper Colorado River System was compiled by Tyus et al. (1982). Behnke et al. (1982) provided supplemental information on fishes of the Green and Upper Mainstem Colorado sub-basins.

Recent reports on fishes of the Colorado River System have concentrated on reproduction (Morgensen 1983; McAda and Wydoski 1983, 1985; Nesler et al. 1988), early life history (Haynes et al. 1984), marking (Muth et al. 1988), life-history strategies (Constantz 1979, 1981), foods and feeding (Barber and Minckley 1983; Marsh 1987), artificial propagation (Hamman 1985a, 1985b, 1986; Berry 1984; Muth et al. 1985), and conserving genetic diversity (Vrijenhoek et al. 1985). Culture efforts have focused on preservation of genetic material of rare fishes, description of early life stages (sensu Snyder 1981), or reintroduction of extirpated fishes within their native ranges (Minckley 1983; Johnson 1985). Migrations of Colorado squawfish to restricted upper-basin spawning grounds have been documented (Tyus and McAda 1984; Tyus 1985; Haynes and Bennett 1986). Other reports relate to responses of native fishes to temperature changes (Bulkley and Pimentel 1983; Ihnat and Bulkley 1984; Black and Bulkley 1985a, 1985b; Marsh 1985) and toxic retorted oil shale (Woodward et al. 1985) associated with dams and energy development, respectively. Amin (1968), Marsh and Rinne (1983), and Haynes and Muth (1985) noted fish spinal deformities which may be associated with altered ecosystems. Much information on upper-basin fishes has resulted from field studies through the Colorado River Fisheries Project (Miller et al. 1982b-d), while emphasis in the lower basin has been on acquisition of habitats and brood stocks, production, and reintroduction (Johnson and Rinne 1982; Johnson 1985).

Recovery of native Colorado River fishes is the responsibility of the U. S. Fish and Wildlife Service. The Recovery Implementation Task Group of the Upper Colorado River Basin Coordinating Committee and an ad hoc recovery team for lower basin fishes spearhead recovery efforts. A Desert Fishes Recovery Team deals with native species of North American deserts within the basin.

Since 1935, riparian vegetation along Colorado basin streams has been modified by water management, grazing of cattle, competitive interactions involving tamarisk, and phreatophyte removal to conserve groundwater (Ohmart et al. 1977; Brown et al. 1977; Graf 1985; Stanford and Ward 1986a). Tamarisk has competed effectively with native riparian plants since its appearance on the Salt River near Phoenix in the 1890s. It has spread northward at an average rate of 20 km$\cdot$yr^{-1} (Graf 1985) and is becoming established on beaches along the lower Yampa River (Haynes and Bennett (1986). It has had greatest impact in the central and lower portions of the basin, where it occurs in dense thickets which have replaced willows and cottonwoods on sandbars and banks. Stream regulation has favored tamarisk expansion along fluctuating reservoir shorelines. Ill-advised efforts to salvage water through phreatophyte control have occurred in the Colorado River Basin, and millions of dollars have been spent on such clearing projects in the southwestern United States over the past 40 yr (Graf 1985).

Ohmart et al. (1977) observed that cottonwood communities along the lower Colorado River have been reduced to a precarious state. Only about 1 130 ha of cottonwood-willow communities remain, and less than 202 ha can be considered pure cottonwood communities.

Regulated outflows from high dams may create more favorable environments for riparian vegetation (Turner and Karpiscak 1980). Below Glen Canyon Dam, woody plants unable to withstand yearly inundation or grow on unstable substrates are colonizing previously inhospitable river banks (Carothers and Johnson 1983). New strips of woody vegetation extending from Glen Canyon Dam to Lake Mead grow on sediments of unknown stability deposited before construction of Glen Canyon Dam; the wildlife they support are an unexpected benefit from regulation (Carothers and Johnson 1983). A post-dam ecological equilibrium has not been achieved along the Colorado River in Grand Canyon, and establishment of a stable riparian community may require decades (Turner and Karpiscak 1980).

Recommendations for the Future

The future for the Colorado River is certain to be replete with conflicts. Coats (1984) observed that basin water is overappropriated, and there are no immediate prospects of importations from other basins. Therefore, new consumptive water uses must take water from existing ones. Conflicts will intensify between wilderness values and instream water uses, agriculture and other uses, and economic efficiency and social equity. Future shocks to the system, such as prolonged drought, energy crisis, establishment of native American water entitlements, or large-scale sales of water across state boundaries could exacerbate conflicts (White 1986). Potential solutions include importation of new water supplies (study is prohibited until 1988 by Central Arizona Project legislation), market pricing of water, managing groundwater and surface water as a single system, implementing water conservation technologies, and renegotiating the Colorado River Compact to remedy mistakes concerning river discharge and disincentives for conservation in the upper basin (Coats 1984; White 1986). Parts of the Colorado River System might be added to the Wild and Scenic River System and responsibilities of the Bureau of Reclamation broadened to include such social goals as water conservation and instream use protection.

We consider conflicts between development and natural ecosystems paramount and find it difficult to be optimistic about the remaining natural elements of the Colorado River. All agencies working toward recovery of rare native fishes of the Colorado River System have established goals and priorities for research and management. There is need for further biological research (emphasizing threatened and endangered fishes) on population dynamics, homing mechanisms, interactions involving native and non-native species, habitat requirements of all life-history stages, responses to potential water-quality modifications, and potential value of management strategies. Monitoring schemes to routinely assess the status of threatened and endangered fishes should be developed for use by basin-wide recovery teams. Research and management in the river system as a whole should be reviewed and coordinated by a single panel, and peer review and publication of results in refereed journals must receive greater emphasis.

Beyond the need for research is that for rehabilitation (sensu Regier et al. 1989). A water budget for the system and consideration of requirements of aquatic organisms in water management are needed. Remediation to benefit big-river fishes of the upper basin should include habitat manipulations and fish passage facilities (Valdez and Wick 1983; Tyus 1984; Tyus et al. 1984; Berry and Pimentel 1985; US Department of the Interior 1986a). The importance of instream flow needs of rare fishes has been recognized, and flow release from Flaming Gorge Dam was managed to improve spawning and survival of endangered fishes in 1986. Introduction of non-native fishes should be curtailed, and stocking of hatchery-reared natives considered only after careful research (Tyus 1984). In the lower basin, preservation of free-flowing riverine areas and protected refugia and management of non-native species are needed to maintain viable populations of native fishes (Williams et al. 1985). Reintroductions of rare native species and attempts to remove non-natives (Meffe 1983) should be handled in a responsible manner. Meffe's (1986) suggestions for genetically sound management of endangered fishes also deserve consideration.

Public education programs on the condition of the river and its unique, jeopardized biota are also needed. Greater cooperation between all political entities and agencies responsible for management of the system will be required if elements of that unique biota are to be preserved.

Conclusion

Research on the biota of the Colorado River System has been largely descriptive. Little is known regarding productivity, yield, and economics of the system's fisheries. Despite calls for consideration and testing of ecological concepts (Carlson et al. 1979; Ward and Stanford 1983), only a few examples of such research exist for the system (Molles 1980; Annear and Neuhold 1983). Ward et al. (1986) concluded that the Colorado system generally lacked the structural and functional integrity of eastern woodland streams on which the river continuum concept is based. Continued research should be supplemented by rehabilitation of the system.

The Colorado River has been drastically altered in less than a century of human activity, and ecological relationships have been changed most significantly in the past 50 yr. Stanford and Ward (1986a) stated that the future of this regulated system depends on whether (1) there will be enough water to maintain desirable ecosystem values and (2) native and non-native fishes can co-exist. Welsh (1985) was convinced that a future water shortage will occur in the basin and that the upper basin states, which have not yet developed their allocations, will play a major role in determining its timing. The basin is expected to experience a surface-water shortage sometime after the year 2000 unless its water supplies can be augmented. Stanford and Ward (1986a) concluded that endangered endemic fishes are incompatible with stream regulation and non-native species and that future water shortages will preclude allocations for them and other ecological concerns. Alternative scenarios might include legal provisions to protect or restore affected aquatic communities as a result of increased citizen awareness of and concern for natural values and species survival. Limits on humans population growth and development in the Southwest may also be imposed by water supply and/or other factors before the biota of the Colorado River system is significantly changed from its current status.

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Hydrological, Morphometrical, and Biological Characteristics of the Connecting Rivers of the International Great Lakes: A Review[1]

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