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ABSTRACT.

The Lower Colorado River was originally one of the most erratic and slit-laden rivers in the world. Seasonal discharge and water quality were enormously variable, and the rigorous environment limited the numbers and kinds of aquatic species to a few specialized types. In less than five decades, the river was completely changed by dam construction and formation of large reservoirs for hydroelectric power and irrigation, and by channelization, meanders of the original stream bed that were cut off by dikes became man-made backwaters, which added to the natural backwaters already present along the river. The Lower Colorado River system now consists of three distinct but interacting major habitat types - reservoirs, inter-reservoir mainstream segments, and natural and man-made back waters.

The specialized endemic biota of the Lower Colorado River and its backwaters has undergone much change since man modified the river environment. Endemic fishes are rare or extinct, and entirely new biotic communities have developed in each of the major habitats. In an attempt to increase the recreational potential of the new system, man has introduced many of the fishes he believes are desirable for sport fishing. Currently, the entire sport fishery of the Lower Colorado River system is supported by introduced species.

INTRODUCTION

The Lower Colorado River system is an important hydrological resource exploited by the rapidly growing human population in the arid American Southwest. According to the U.S. Bureau of Census (Newspaper Enterprise Assoc. 1975), the populations of Arizona and California numbered 1,772,482 and 19,953,134 in 1970; these figures represent increases of 36 percent and 27 percent since the 1960 census. To meet increasing water needs, the U.S. Water and Power Resources Service (formerly the Bureau of Reclamation) has controlled the flow of the Colorado River by constructing several storage reservoirs. The Water and Power Resources Service releases water from the reservoirs primarily to meet requirements for irrigation and for municipal and industrial users (U.S. Dept. of the Interior 1964). Under these operating conditions, water releases cannot always accommodate the ecological needs of fish. In addition to controlling river discharge rates, the Water and Power Resources Service has channelized and stabilized the river to reduce flooding (caused in part by meandering of the stream and deposition of sediment in the main channel) and increase water salvage. This program reduced the value of the mainstream as fish habitat because pools and riffles were eliminated (Beland 1953). Channelization also created faster currents that deepened the main channel and lowered the water table, causing the loss of many backwater fish habitats.

The Lower Colorado River system between Davis Dam and the Arizona-Sonora border (Figure 1) comprises three major types of habitat: large reservoirs, segments of river between

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FIGURE 1. Locations of dams and reservoirs along the Lower Colorado River.

reservoirs, and small backwaters. The environmental conditions in each of these habitats are influenced by man's control and use of the water. This modified system bears little resemblance to its original state.

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THE NATURAL RIVER SYSTEM

Before the construction of dams and channelization, the Lower Colorado River had seasonally fluctuating flows and salinities, and high turbidities. Monthly discharges often varied from less than 200 m³/s during fall and winter to more than 1,500 m³/s in summer (Figure 2); Grinnell (1914) reported a maximum of 2,800 m³/s. Salinities flucuated inversely with discharges, and ranged from less than 350 mg/l in summer to more than 1,250 mg/l in fall and winter (Figure 3). Turbidities typically ranged above 15,000 mg/l and occasionally exceeded 30,000 mg/l (Figure 4).

Under these natural conditions, the only significant aquatic habitats other than the mainstream were backwaters that were distinct entities during low river flow and became part of the mainstream during high flow. Although they resulted from frequent meandering of the mainstream, the backwaters were few and small because of the rates of evaporation and siltation were rapid (Grinnell 1914). Consequently most of these natural backwaters were short-lived; Ohmart et al. (1975) estimated that they lasted for only 50 to 75 years. Many backwaters had recently been part of the river and had water qualities closely resembling those of the mainstream; they differed from the mainstream mostly in having reduced current and decreased turbidities.

The system was characterized by a low biotic diversity, which reflected the fluctuating, harsh environment. Since the floodplain was subject to continual erosion through channel meandering, predominant vegetation consisted of such hydrophytic, rapidly growing species as carrizo cane (*Phragmites communis*), willow (*Salix gooddingii*), cottonwood (*Populus fremontii*), and arrowweed (*Phuchea sericea*). Plants commonly found in marsh soils were cattails (*Typha* spp.), bulrushes (*Scirpus* spp.), and saltgrass (*Distichlis stricta*) (Grinnell 1914). Submergent vegetation was scarce or lacking in the mainstream, presumably because of the high turbidity; backwaters may have supported more submergent plants because they had clearer water.





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The invertebrates in the system of this period are virtually unknown. Small crustacea (cladocerans, copepods, and ostracods) probably occurred because these organisms are ubiquitous. Various aquatic insects also may have been present. According to Grinnell (1914), there were no aquatic molluscs or decapod crustaceans in the Needles-to-Yuma area in 1910.

Few species of fish were present. Minckley (1973) reported that eight freshwater species occurred naturally in the Lower Colorado River system; four cyprinids (bonytail chub, *Gila* elegans; Colorado chub, *G. robusta*; woundfin, *Plagopterus argentissimus*; and Colorado squawfish, *Ptychocheilus lucius*); two catostomids (razorback sucker, *Xyrauchen taxanus*, and flannelmouth sucker, *Catostomus latipinnis*); one cyprinodontid (desert pupfish, *Cyrinodon marularius*); and one poeciliid (Gila topminnow, *Poeciliopsis occidentalis*). Species were generally more numerous in backwaters than in the mainstream (Grinnel 1914).

THE EFFECTS OF DAMS

Dam construction on the Lower Colorado River greatly altered the physiochemical characteristics of the system. Laguna Dam, built in 1909, had only a slight effect on the lower river because of its small size and downstream location (Table 1, Figure 1). Completion of Hoover Dam (about 108 km upstream from the more recently constructed Davis Dam) in 1935 allowed the storage of large quantities of flood water in Lake Mead; regular releases during the dry season made possible a more nearly constant river flow. Fluctuations in salinity concentrations decreased and the water of the lower river cleared (Figure 5). Later, Parker, Imperial, Davis, Headgate, and Palo Verde dams further stabilized discharge rates and increased salinities and transparencies in the downstream river water.

TABLE 1. Major dams and reservoirs along the Lower Colorado River.^a

Reservoir	Dam type ^b	Dam Height (m)	Reservoir Area (ha)	Year Completed
Laguna	ER	3.0		1909
Imperial	SB	14.3	2,957	1938
Palo Verde Diversion	ER	12.5		1958
Havasu (Parker Dam)	VRA	25.9	8,262	1938
Moovalya (Headgate Rock Dam)	E	13.7		1941
Mohave (Davis Dam)	ER	42.1	1,134	1953

^aCompiled from California Dept. of Water Resources (1974), Douglas (1947), & Slawson (1972). ^bE = earth; ER = earth and rock; SB = slab and buttress; VRA = variable radius arch.

The regulated and clarified waters were distinctly different from those of the preimpoundment period. Immediately below dams, the mainstream was clear and currents were swift (Borland and Miller 1960; Dill 1944; Moffett 1942). The currents scoured the river bottom, leaving it rocky and gravelly. Farther downstream from the dam, turbidities were higher and current velocities lower; certain downstream areas had braided and meandering channels and resembled the original river. Diurnal water level fluctuations resulting from irrigation and hydroelectric needs replaced the seasonal fluctuations of the original river.

Static water habitats during the immediate post-impoundment period are poorly described. Backwaters were usually clear and had little or no current. In many respects, the backwaters probably resembled those present before dam construction. One obvious difference was that more of the backwaters were permanent because seasonal floods were eliminated.

Perhaps the greatest single influence of dams on the river system was the creation of large reservoirs that were not present in the original river. The reservoirs had clear water and reduced currents, and some - such as Lake Havasu and Imperial Reservoir - had relatively stable water levels. Because rapid water passage through all of the reservoirs prevented prolonged thermal stratification, dissolved oxygen concentrations remained high from surface to bottom (Beland 1954; Dill 1944; Kimsey 1957; Ponder 1971).

After impoundments were built, the biota in the remaining stretches of mainstream between dams responded to their altered environment in several ways. Some species were able to live and reproduce in the new environment but many less adaptable species became locally extinct. Exotic species entered the mainstream through natural immigration and stocking. In areas with sandy and muddy soils, some carrizo cane, cattails, and bulrushes survived. The paucity of submergent aquatic plants continued except for attached algae in clear, rocky portions of the river (Dill 1944; Moffett 1942). Ditch grass (*Ruppiasp.*) spiny naiad (*Najas marina*), and sago pondweed (*Potamogeton pectinatus*) were common rooted submergent plants, although submergents were not abundant enough to be important to fish, except in a few areas (Dill 1944). Production of invertebrates in the river was low because





submergent vegetation was scarce and much of the river bottom was composed of shifting sand. Many of the invertebrates that colonized the mainstream were probably immigrants from upstream reservoirs and backwaters.

The effects of dam construction on biota in the mainstream are most clearly illustrated by changes in fish populations. Exotic species, some present in small numbers since their initial introduction in the early 1900's (Gilbert and Scofield 1898; Grinnell 1914; Miller 1961), responded favorably to the altered conditions and became abundant. Concurrently, most native fishes declined - some to extinction - in most areas of the lower river. The major probable causes for the decline of native species of fish are competition with exotic fishes (Dill 1944; Miller 1961), predation by exotic fishes (Dill 1944; Miller 1961) and construction of upstream spawning migrations by dams (Miller 1961). Recent data on Colorado squawfish, Colorado chub, and bonytail chub (Vanick and Kramer 1969) indicated that competition may have been of special importance; the foods of squawfish and chubs apparently are similar to those of many introduced centrarchids, but the native species

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have the reproductive disadvantages of lower fecundities, no parental care for eggs and young, and sexual maturation at an older age than centrarchids.

By the early 1940's all major species of fish in the mainstream were exotic (carp, Cyprinus carpio, channel catfish, Ictalurua punctatus; yellow bullhead, I. natalis; mosquitofish, Gambusia affinis; bluegill, Lepomis macrochirus; green sunfish, L. cyanellus; and largemouth bass, Micropterus salmoides). Minor species included black bullhead (Ictalurus melas), brown bullhead (I. nevulosus), black crappie (Pomoxis nigromaculatus), white crappie (P. annularis), razorback sucker, machete (Elops affinia), and striped mullet (Mugil cephalus). Only the razorback sucker, machete, and striped mullet immigrated from the Gulf of California and, according to Miller (1961), probably survived in the river at this time because of the clearer water and the local extinction of predatory squawfish. Although annual yield of the sport fishery was unknown, fishing success was considered satisfactory by Dill (1944).

The status of biota in the backwaters in the early 1940's is poorly known. Favorable limnological conditions probably existed, and biological productivity in most backwaters may have been higher than that in the mainstream. Dill (1944) reported that oligochaetes, gastropods, ephemeropteran nymphs, and chironomid larvae were found in backwaters near Palo Verde, California, and Yuma, Arizona. These waters supported large populations of fish, including carp, channel catfish, yellow bullhead, mosquitofish, bluegill, green sunfish, largemouth bass, black crappie, white crappie, razorback sucker, and striped mullet.

The newly built reservoirs developed limnological conditions conducive to the establishment of emergent and submergent plants and phytoplankton (Kimsey 1957), which provided food and cover for fish-food organisms. Microcrustacea were present in open waters, and various insect larvae, gastropods, and oligochaetes inhabited the bottom sediments and plants (Beland 1954; Dill 1944). Crayfish were not seen at Lake Havasu in 1953 (Beland 1954), although *Procembraus clarki* was established in Imperial Reservoir and the Yuma area by 1942 (Dill 1944). The greater diversity of plants and invertebrates in reservoirs provided a habitat for larger fish populations than those occurring in the remnants of mainstream between the reservoirs. Common reservoir fishes in the early 1950's were largemouth bass, bluegill, green sunfish, black crappie, channel catfish, carp, and mosquitofish. Among the rare species were yellow bullhead and razorback sucker. White crappie, black bullhead, Colorado squawfish, and bonytail chub were reported, but the reports were not confirmed by Beland (1954).

THE EFFECTS OF CHANNELIZATION

Since the dam-building era ended in the 1950's, channelization and dredging of the river have modified the mainstream and caused losses of backwater habitat. Only two portions of the mainstream remain relatively unaltered: a 19 km reach above Lake Havasu and a 63 km reach above Imperial Reservoir (Ponder 1975).

Modifications of the mainstream include reduction of stream length, reduction in width of some reaches, and deepening of the channel. These changes increased the water velocities and lowered the water table. However, water quality in the mainstream was not substantially changed; average monthly discharges (84 to 504 m³/s) remained relatively stable (Figure 6) and daily discharges continued to fluctuate in response to water releases at upstream dams. In the reach adjacent to the Colorado River Indian Reservation near Parker, Arizona, the average and maximum daily river level fluctuations were about 0.2 and 0.5 m during the winter and 0.8 and 1.5 m during the summer (Krummes 1969). Average fluctuations differed in other reaches of the mainstream. Narrow monthly salinity ranges (650 to 1,050 mg/l) were maintained (Figure 7).

Total biotic production in the mainstream may be higher now than at any other previous period. However, much of the biomass is contributed by the recently introduced Asian clam (Corbicula flaminea). Although this clam is eaten by carp and redear sunfish (Lepomis microlophus) (Saiki 1976), a large portion of the clam population consists of individuals too large for the fish to eat. Other invertebrates useful as fish forage are scarce (Federal Water Pollution Control Admin. 1968). Fishes in the mainstream include at least 16 species







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above Palo Verde Diversion Dam and 21 below it (Table 2). Fish production decreased after channelization destroyed the eddies and pools that were important sites for cover and food production (Beland 1965). Fish production was also reduced by the loss of insects and of detrital fish-food caused by the removal of much riparian vegetation.

TABLE 2. Fishes of the Lower Colorado River mainstream, 1974-75.^{a,b}

Family and Species		Above Palo Verde Dam	Below Palo Verde Dam
Contropolidoo			
Warmouth Lanomic autocus	X	X	
Green sunfish I councilius	X	X	
Bluegill, L. macnochimus	X	X	
Redear sunfish L. migrolophus	X	X	
Hybrid, blugill X redear sunfish	X	X	
Smallmouth bass. Micropterus dolomieui	X	X	
Largemouth bass, M. salmoides	X	Х	
Black crappie, Pomoxis migromaculatus	Х	Х	
Mozambiquo tilapia <i>Milania</i> mocoambian		v	
Mozambique citapia, recapia mossambica		Λ	
Clupeidae			
Threadfin shad, Dorosoma petenense	Х	Х	
Cupuinidae			
Coldfich Company with the		v	
Comp Caracteria compile	v	A V	
Caldon chinon Notomicomus amusilauses	A V	Λ	
Red shiner, Notropis Lytrensis	x	Х	
Elopidae			
Machete, <i>Elops affinis</i>		Х	
Ictalunidao			
Vellow bullboad Tetalumus matalia	v	Y	
Channel catfish I municipal	X	A Y	
Flathead catfish <i>Pladiatic alignmic</i>	X	X	
Traineau cairish, Floatetts ortoarts	~	Λ	
Mugilidae			
Striped mullet, Magil cephalus		Х	
Deve is high start de s			
Percientnyidae	v	v	
surped bass, morone saxatilis	Λ.	٨	
Poeciliidae			
Mosquitofish, Gambusia affinis	Х	Х	
Sailfin molly, Poecilia latipinna		Х	
Mexican molly, P. mexicana		Х	
Colmonidos			
Salmonidae	V		
Raindow trout, Salmo gairdneri	Х		
aData compiled from Minckloy (10752, 10756, 1075	c+ 1075d+ 10	750) and uppublic	hod data of
D.J. Kennedy and M.K. Saiki.	c, 1975u, 197		nea aata or

 $b \chi = present.$

Channelization and dredging of the mainstream adversely affected the sport fishery (Beland 1953). It attempts to mitigate these effects, the Water and Power Resources Service deepened many shallow backwaters by dredging them and constructed channels or installed culverts between them and the river. These backwaters now exhibit a wide range of environmental conditions and represent the most diverse habitat along the lower river. The physiochemical and biological conditions in some backwaters nearly duplicatie those in the mainstream, the main difference being the reduced currents in the backwaters (Arizona Cooperative Fishery Research Unit 1975; Marshall 1976; Ponder 1975). Other backwaters resemble stagnant pools, devoid of game fish but harboring biota capable of surviving wide temperature fluctuations, low dissolved oxygen concentrations, and high salinities (Ponder 1975). Most backwaters range between these extremes. In general, biotic standing crops in the backwaters are higher than those in the mainstream (Arizona Cooperative Fishery Research Unit 1975; Saiki 1976). Emergent and submergent aquatic plants are abundant, as are immature forms of aquatic insects. There are substantial populations of bottom organisms such as chironomids and oligochaetes. Zooplankton is abundant only in some of the more lentic types of backwaters. Major game fishes include channel catfish, largemouth bass, bluegill, redear sunfish, and black crappie (Arizona Cooperative Fishery Research Unit 1975; Marshall 1976; Ponder 1975; Saiki 1976). Of the endemic fishes, only razorback sucker is still present in backwaters (Arizona Cooperative Fishery Research Unit 1975; Marshall 1976).

THE FUTURE

Over the next decade, significant further changes in the Lower Colorado River system will probably ensue in response to man's continuing attempts to control and use the hydrological resource. About 1.36 x 10^9 m³/year of water is now withdrawn from Lake Havasu by the Southern California Metropolitan Water District (Valantine 1974). Under this regime of water depletion, the annual discharge below Parker Dam averages 8.63 x 10^9 m³ (calculated from unpublished data of scheduled water releases at Parker Dam by the U.S. Water and Power Resources Service, 1 January 1973 to 31 December 1975). When the Central Arizona Project begins operations in the mid-1980's, about 1.75 x 10^9 m³ of water will be diverted each year from Lake Havasu; concurrently, the Southern California Metropolitan Water District will cut back its use of Colorado River water to about 0.52 x 10^9 m³/year (Valantine 1974). These estimates indicate that a net increase of 1.01 x 10^9 m³/year will be withdrawn from the reservoir by 1990. Assuming that other factors (inflows of the Colorado River into Lake Havasu, evaporative rates, precipitation rates, etc.) remain constant, this increased comsumption rate will reduce the annual discharge below Parker Dam by nearly 12 percent. The decreased rate of flow may reduce average river water levels and lower the surrounding water table. Consequently, some of the backwaters now serving as fish habitat might be greatly reduced in volume or eliminated.

Reductions in the quality of water may also occur because reduced flows in the river below Parker Dam could lead to higher salinities and wider seasonal temperature ranges - conditions that might exceed the tolerance limits of many fishes. Skogerboe and Walker (1975) and Slawson (1972) reported that return flows from agricultural irrigation in the Lower Colorado River basin are highly saline, presumably from the effects of evaporation and soil leaching. These inflows cause the total dissolved solids content of the mainstream to increase. If agricultural activity intensifies in the future, the salinity of the river will also increase. Valantine (1974) predicted that salinities in the mainstream below Parker and Imperial dams will be 880 and 1,080 mg/l, respectively, by 1990; when extrapolated to conditions in backwaters, much higher concentrations are expected. Annual ranges of water temperatures may also increase because the reduced water volume of the system would be subject to rapid equilibrium interactions with seasonal air temperatures. These altered water quality conditions could affect all biota, including fishes, and cause species changes toward organisms tolerant of higher salinities and wider temperatures ranges.

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