The evolution, demise, and restoration of the native fishes of the lower Colorado River

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ABSTRACT

Throughout the last century, the Colorado River's natural flow regime was drastically altered by the infrastructure of water regulation. The once dramatic seasonal and annual variations in water flows, which shaped the life histories and unique morphologies of its native fishes, have been subdued by the many impoundments throughout the river. Bluehead sucker, flannelmouth sucker, speckled dace, bonytail, Colorado pikeminnnow, humpback chub and razorback sucker are fish native to the Colorado River Basin, the latter four being critically endangered endemics. The native fish face two major threats: (1) habitat degradation, caused by cold, sediment-starved, and relatively flat-lined water releases, and (2) nonnative fishes, introduced since the late 1800s. Both of these threats work together in precluding the recruitment of the natives. The cold, clear, hypolimnetic releases degrade the natives' backwater rearing habitat and cause near-zero growth rates in their young-of-year offspring, while the introduced fishes predate upon the young-of-year and juveniles. The current and proposed management strategies for restoring and/or perpetuating the fish native to the mainstem of the lower Colorado River include experimental flows, mimicking the natural flow regime, tailwater warming, nonnative fish control, and artificially-maintained populations. A holistic, ecosystem-based approach, using a combination of these management options, will likely be needed if the sustainable recovery of the lower Colorado River's native fishes is ever to be achieved.

INTRODUCTION

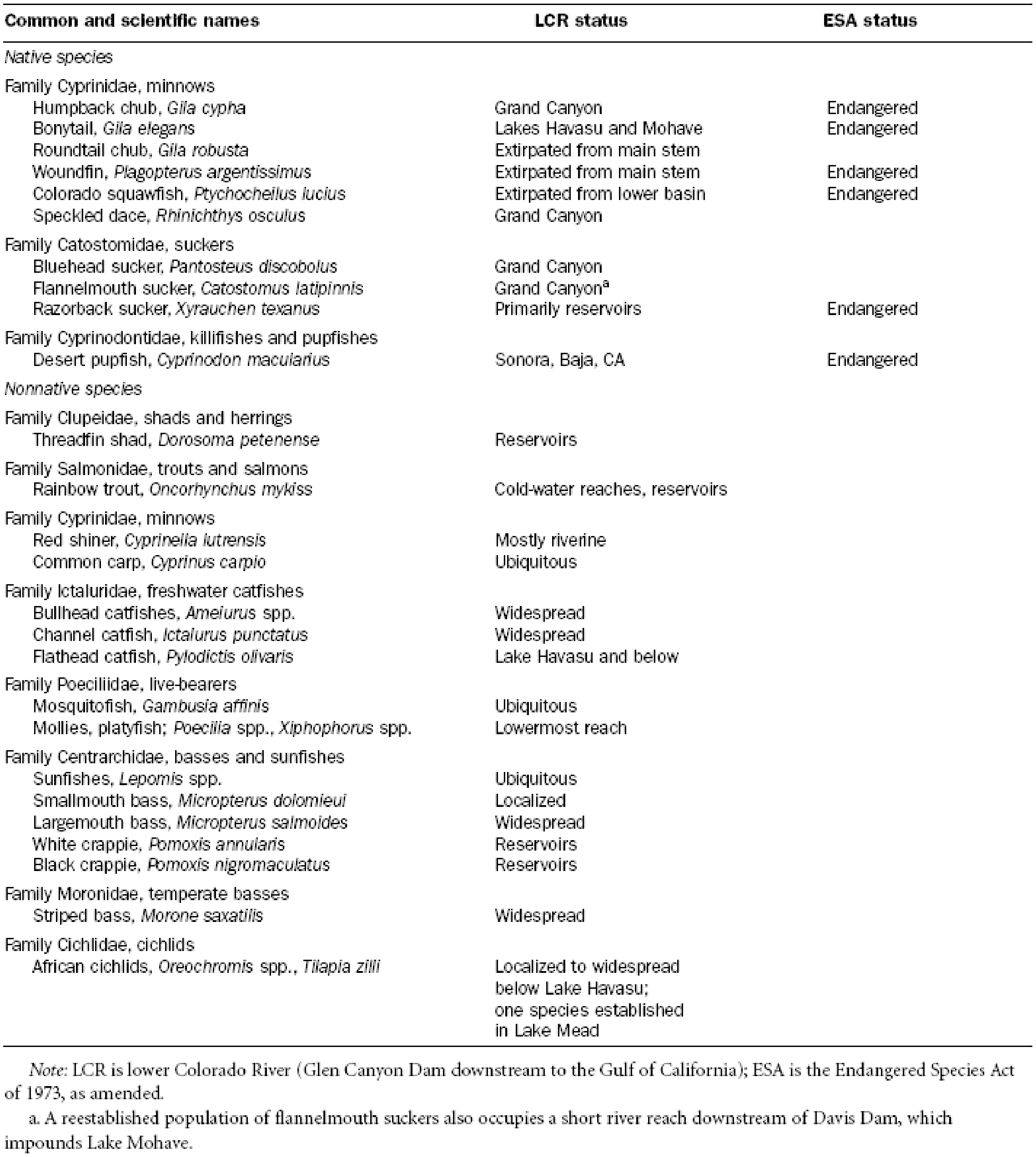
The many dams impeding the natural flow of water on the Colorado River and its tributaries make the Colorado River Basin one of the most altered watersheds in the world (Fradkin 1981). The effects of water development – damming rivers, creating impoundments and cold tailwaters, degrading habitats and desiccating long reaches – and the introduction and establishment of a suite of exotic species, together, have synergistically decimated the integrity of native fish populations of the Colorado River (Minckley 2003). The native fish fauna of the region has suffered catastrophic losses, with extant species ranges' now 45% of their historical distributions (Fagan et al. unpublished). The mainstem of the lower Colorado River, delineated from the upper Colorado River near Glen Canyon Dam, was previously home to ten native freshwater fishes (Table 1). Three of these native fishes – woundfin (*Platopterus argentissimus*), roundtail chub (*Gila robusta*), and Colorado pikeminnow (*Ptychocheilus lucius*) – have been extirpated from the lower Colorado River mainstem. Six of the natives – humpback chub (*Gila cypha*), bonytail (*Gila elegans*), razorback sucker (*Xyrauchen texanus*), desert pupfish (*Cyprinodon macularius*), Colorado pikeminnow and woundfin – are federally endangered. Bluehead sucker (*Catostomus disobolus*), flannelmouth sucker (*Catostomus latipinnis*) and speckled dace (*Rhinichthys osculus*) still persist in relative abundance in the Grand Canyon and the latter two downstream (Table 1).

The plight of these native fishes in the last century is just one of the many reasons the U.S. Bureau of Reclamation's (USBR) Glen Canyon Environmental Studies (GCES) and Glen Canyon Dam Adaptive Management Program (GCDAMP) were spawned. The purpose of the GCDAMP is to help the Secretary of the Interior find a dam operating procedure that balances economic and private interests with protection of the downstream ecosystem, in compliance with the Law of the River, the Endangered Species Act of 1973 and the Grand Canyon Environmental Protection Act of 1992 (GCDAMP Final Strategic Plan). This paper will: (1) briefly review the history of native fish management of the Colorado River, (2) give a synopsis of the life histories of the main-stem lower Colorado's native fish, and (3) analyze the effectiveness of current and proposed management strategies in restoring and/or perpetuating the fishes native to the mainstem of the lower Colorado River.

SHIFTING TO NATIVE FISH MANAGEMENT

The demise of the native fish fauna began just after 1900, as interest in harnessing the river for the agricultural development first arose (Minckley 1991). The decimation started in the southern end of the Colorado River basin and moved northward, in the same sequence the river was regulated. Prior to the 1960s, very few people were alarmed by mankind's detrimental effects on the aquatic habitats and fishes in the West (Holden 1991). The tangible benefits of dams – flood control, water supply, hydroelectric power and valuable recreational assets – overshadowed the unseen ecological losses that were evident only to a few.

Holden (1991) describes the events precluding the construction of Flaming Gorge dam in 1963, arguing that this could have been *the* turning point in the shift to native fish management.



Common and scientific names	**LCR status**	**ESA status**
Native species		
Family Cyprinidae, minnows		
Humpback chub, *Gila cypha*	Grand Canyon	Endangered
Bonytail, *Gila elegans*	Lakes Havasu and Mohave	Endangered
Roundtail chub, *Gila robusta*	Extirpated from main stem	
Woundfin, *Plagopterus argentissimus*	Extirpated from main stem	Endangered
Colorado squawfish, *Ptychocheilus lucius*	Extirpated from lower basin	Endangered
Speckled dace, *Rhinichthys osculus*	Grand Canyon	
Family Catostomidae, suckers		
Bluehead sucker, *Pantosteus discobolus*	Grand Canyon	
Flannelmouth sucker, *Catostomus latipinnis*	Grand Canyon[a]	
Razorback sucker, *Xyrauchen texanus*	Primarily reservoirs	Endangered
Family Cyprinodontidae, killifishes and pupfishes		
Desert pupfish, *Cyprinodon macularius*	Sonora, Baja, CA	Endangered
Nonnative species		
Family Clupeidae, shads and herrings		
Threadfin shad, *Dorosoma petenense*	Reservoirs	
Family Salmonidae, trouts and salmons		
Rainbow trout, *Oncorhynchus mykiss*	Cold-water reaches, reservoirs	
Family Cyprinidae, minnows		
Red shiner, *Cyprinella lutrensis*	Mostly riverine	
Common carp, *Cyprinus carpio*	Ubiquitous	
Family Ictaluridae, freshwater catfishes		
Bullhead catfishes, *Ameiurus* spp.	Widespread	
Channel catfish, *Ictalurus punctatus*	Widespread	
Flathead catfish, *Pylodictis olivaris*	Lake Havasu and below	
Family Poeciliidae, live-bearers		
Mosquitofish, *Gambusia affinis*	Ubiquitous	
Mollies, platyfish; *Poecilia* spp., *Xiphophorus* spp.	Lowermost reach	
Family Centrarchidae, basses and sunfishes		
Sunfishes, *Lepomis* spp.	Ubiquitous	
Smallmouth bass, *Micropterus dolomieui*	Localized	
Largemouth bass, *Micropterus salmoides*	Widespread	
White crappie, *Pomoxis annularis*	Reservoirs	
Black crappie, *Pomoxis nigromaculatus*	Reservoirs	
Family Moronidae, temperate basses		
Striped bass, *Morone saxatilis*	Widespread	
Family Cichlidae, cichlids		
African cichlids, *Oreochromis* spp., *Tilapia zilli*	Localized to widespread below Lake Havasu; one species established in Lake Mead	

Note: LCR is lower Colorado River (Glen Canyon Dam downstream to the Gulf of California); ESA is the Endangered Species Act of 1973, as amended.

a. A reestablished population of flannelmouth suckers also occupies a short river reach downstream of Davis Dam, which impounds Lake Mohave.

Table 1. Status of native and nonnative freshwater fishes of the lower Colorado River mainstem, southwestern United States. (from Minckley et al. 2003)

Despite outcries from a small public opposition, in 1962, just prior to the erection of Flaming Gorge Dam, a large stretch of the Green River was treated with rotenone (a naturally occurring chemical with insecticidal, acaricidal, and piscidal properties). The purpose of the poisoning was to cleanse the river of 'trash' fishes (i.e. native fishes) in order to provide a clean slate from which the managers could build a recreational coldwater fishery in the new reservoir. The dosage of detoxification agent was underestimated and the rotenone made its way down the river into Dinosaur Park National Monument, resulting in the unplanned killing of native fish in a public land set aside for the preservation of the natural beauty and fauna of the region. The issue received national attention.

Originally stimulated by the poisoning of the Green River, the U.S. Fish and Wildlife Service (USFWS) inherited a study program to monitor the native fishes (1963-1980), which led to the Colorado River Fishery Project Act (1979-1987), which was then converted in 1987 to a 15-year, $60 million Recovery Implementation Program (RIP; Minckley et al. 2003). Also, in 1967, the Colorado pikeminnow and humpback chub were listed under the Endangered Species Preservation Act of 1966, indicating substantial evidence of the changing ethics and growing concerns for the Colorado River's native fauna. The federal Endangered Species Act, one of the strongest environmental laws ever written (Orians 1993), was passed in 1973. This legislation constitutes a large proportion of the steering force behind management's actions on the Colorado River today. Unfortunately, no one fish listed under the ESA has been sufficiently recovered that it has been delisted (Tyus and Saunders 2000). Extinction, however, *has* led to the delisting of endangered fish.

THE PRE-DAM CONDITION AND FAUNAL EVOLUTION

Upstream from Grand Canyon, the Colorado River drains approximately 242,086 mi^2 (627,000 km^2). The pre-dam flow regime was extremely variable (Webb et al. 1999). Before the completion of Glen Canyon Dam, seasonal peak snowmelt discharges occurred between May and July. Peak discharge ranged between ca. 25,425 cfs (720 m^3/s) and 300,000 cfs (8500 m^3/s) from 1884 to 1963. The river typically fell to less than 7060 cfs (200 m^3/s) during the fall and winter. Pre-dam, two-year and ten-year floods were 76,230 cfs (2160 m^3/s) and 139,493 cfs (3950 m^3/s), respectively. The river was also extremely turbid by the time it reached the lower basin, with tributaries that drain the semi-arid regions of the subbasin contributing the bulk of the sediment inputs (Webb et al. 1999). At the Grand Canyon gauging station, sediment yield often exceeded $177*10^6$ metric tons/year. Pre-dam water temperatures varied seasonally from 0 to 29°C through the Grand Canyon (Webb et al. 1999).

Interestingly, all of the native fishes in the Colorado River watershed are derived from two families, Catostomidae and Cyprinidae, sympatric taxa classified as members of the Order Cypriniformes, under the series Otophysi. Otophysan fishes share a number of unusual features, including the Weberian apparatus and specialized pharyngeal teeth. The Weberian apparatus is a chain of bones that connects the swimbladder to the inner ear, providing the fishes with a sensitive sound reception system (Moyle and Cech 2004). This acute sense of hearing would be useful in the very turbid water of the Colorado River where vision is severely limited. Their pharyngeal teeth allow for the separation of grabbing and chewing functions, simultaneously allowing for the further specialization and adaptability of feeding habits. Members of Catostomidae and Cyprinidae are also generally quick maturing, highly fecund and long-lived; life history characteristics allowing them to persist through drought conditions and flood their environments with young when conditions are favorable.

The harsh conditions presented by the natural flow regime shaped the fishes of the Colorado River and their adaptations and morphologies reflect it. The native fish fauna has about a 75% level of species endemism (Minckley 1991), probably owing to the pre-dam conditions of seasonally low light penetration, low primary production, and pool-rapid hydraulics, coupled with long geological isolation (Webb et al. 1999). Many of the larger fish possess special features that allow them to cope with the seasonally high flows and turbid water. Body shapes of the mainstem fishes are fusiform and streamlined, with small depressed skulls and pencil thin caudal peduncles, large, often falcate fins and forked tails (Minckley 1991), quite reminiscent of the most efficient swimmers of the oceans: the tunas. Their skins are thick and leathery and their scales are reduced and often embedded to reduce friction (Minckley 1991).

However, these fishes evolved to cope not only with the natural flow regime of the Colorado River, but also with each other. A curious attribute in humpback chub and razorback sucker is the presence of a large post-cranial hump. Several authors have suggested the humps confer a hydrodynamic advantage to life in fast flow, but Portz and Tyus (2004) found high energetic costs of locomotion and position-holding with a large hump, and deduced an additional metabolic expense of forming large humps. Instead, they hypothesized that these large humps represent an evolutionary arms race to limit predation by the Colorado pikeminnow, a jaw-toothless, gape-limited piscivore.

LIFE HISTORIES

The following species accounts of bonytail, Colorado pikeminnow, humpback chub, and razorback sucker are a synopsis of material adopted from the species' respective USFWS Recovery Plans (2002a, 2002b, 2002c, 2002d), unless otherwise noted. The other species accounts – flannelmouth sucker, bluehead sucker and speckled dace– are a synopsis of information presented by Minckley (1991), unless otherwise noted.

Bluehead Sucker

(picture by The Native Fish Conservancy)

This catostomid is found in many high-gradient streams of western North America. In large rivers bluehead suckers attain a maximum of about 50 cm total length (TL) and 20 or more years of life. Blueheads have broad disc-shaped lips and short cartilaginous sheaths on the jaws, specialized for scraping algae and other organisms from hard substrates. They are bottom dwellers, flattened ventrally and rounded dorsally, with broad flat fins, small, embedded scales, and tiny eyes. Caudal peduncles vary in morphology from short and stout to thin and elongate. Adults are bluish gray or olivaceous in color, with white bellies. An exquisite color pattern develops during the spawn: a blue patch appears on the head and infuses to the opercula in breeding adult males, hence the name; the lower fins become yellow to orange, and red or rosy pigments show over the lateral bands.

In clear water, deep pools and eddies are the preferred habitat for adults in the daytime. They exploit shallower water at night. In highly turbid environments, adult blueheads are found shallow throughout the diel cycle. Blueheads appear to be most common at the upper ends of valleys or in the shallows of whitewater canyons.

Like most natives, blueheads enter tributaries in spring to spawn, and remain through autumn. Spawning typically occurs in April to May in swift, flatwater reaches of 16 to 20°C, over mixed gravel sand or gravel-cobble bottoms. Young appear in May to June, seeking areas downstream of riffles and shoreline flatwaters. Rapid growth rates occur for the first few years of life, but stops abruptly when sexual maturity is attained at about 30+ cm TL.

Common food items taken are immature stages of dipterans and amphipods, along with a substantial amount of diatoms and organic debris mixed in.

Bonytail


(picture from USFWS 2002a)

The bonytail is characterized by a small, flattened head, a slender body (relative to other *Gila* spp. on the Colorado River) with a small post-cranial fleshy hump, and a pencil-thin caudal peduncle. The mouth is slightly subterminal. It reaches a maximum size of about 55 cm (TL) and 1.1 kg in weight. Examination of otoliths indicated maximum ages of 49 years. Coloration is dark gray dorsally, blending into white ventrally, with yellow pigment at the base of the paired fins. While breeding, tubercles protrude from the head and fins.

Bonytail were once widespread in the large rivers of the Colorado River Basin. Starting in about 1950, the species experienced a dramatic decline, following construction of mainstem dams, introduction of nonnative fishes, poor land-use practices, and degraded water quality. Today, the species occupies Mohave and Havasu Reservoirs in the lower basin and Lake Powell and some of the major river confluences in the upper watershed.

Little is known about the specific habitat requirements of bonytail because the species was extirpated from most of its historic range prior to extensive fish surveys. The bonytail is considered adapted to mainstem rivers where it has been observed in pools and eddies. Early empirical studies observed no difference in habitat selection from roundtail chub, which are generally found in pools and eddies in the absence of, although occasionally adjacent to, strong current and at varying depths generally over silt and silt-boulder substrates.

Similar to other closely related *Gila* spp., bonytail in rivers probably spawn in spring over rocky substrates; spawning in reservoirs has been observed over rocky shoals and shorelines. Natural reproduction of bonytail was last documented in the Green River in Dinosaur National Monument where ripe spawning fish were captured from mid-June to early July at a water temperature of 18°C. Under hatchery conditions, adult female bonytails (49-56 cm TL) yield an average of 25,090 eggs. It is hypothesized that flooded bottomland habitats are important growth and conditioning areas for bonytail, particularly as nursery habitats for young.

The exact diet of bonytails remains elusive. One study found they were largely omnivorous with a diet of terrestrial insects, plant matter, and fish. Several bonytail have been observed feeding on floating mats of debris, terrestrial insects (mostly adult beetles and grasshoppers), leaves, stems, and other woody fragments.

Colorado Pikeminnow

(picture from USFWS 2002b)

The Colorado pikeminnow is the largest cyprinid in North America and endemic to the Colorado River Basin. The largest confirmed fish weighed in at 15.5 kg and just under 100 cm (TL). Historic accounts estimated a maximum total length of about 180 cm and weight of 36 kg. Colorado pikeminnow are characterized by a long, slender, cylindrical body with silvery sides, a greenish back, and creamy-white belly. Spawning adults are tinged with light rosy-red on the head and body, with tubercles on the head and paired fins. A triangular black patch sits at the base of the caudal fin, distal to a thick caudal peduncle. They possess a large head with a terminal mouth with thickened lips and a large jaw that lacks teeth and extends past the middle of the eye. The pharyngeal arch supports long and knife-like teeth. Scales are small, cycloid, and silvery. Hatchery-reared males became sexually mature at four years of age and females at five years. Fecundity for nine-year old females averages ca. 66,500 eggs/kg.

Once widespread and abundant in warmwater rivers and tributaries, Colorado pikeminnow numbers in the lower basin declined in the 1930s with the last specimens reported in the mid-1970s. Wild populations are found only in the upper basin, currently occupying only about 25% of its historic range basin-wide (Table 1). Where they still exist, adult Colorado pikeminnow utilize relatively deep, low-velocity eddies, pools, and runs that occur in nearshore areas of main river channels. River reaches of high habitat complexity appear to be preferred. In spring, however, adults utilize floodplain habitats, flooded tributary mouths, flooded side canyons, and eddies that are available only during high flows.

The Colorado pikeminnow is a long-distance migrator; adults are hypothesized to have moved hundreds of kilometers to and from spawning areas, requiring long sections of river with unimpeded passage. Adults move to spawning areas shortly after runoff in early summer, and return to home ranges in August and September. Natural reproduction of Colorado pikeminnow is currently known from the Green, Yampa, upper Colorado, Gunnison, and San Juan rivers in canyon-bound and meandering, alluvial reaches. The Colorado pikeminnow is an obligate warm-water species that requires relatively warm temperatures for spawning, egg incubation, and survival of young. Spawning activity begins after the peak of spring runoff during June–August at water temperatures typically between 18 and 23°C. Colorado pikeminnow are broadcast spawners, scattering adhesive eggs over cobble substrate which incubate in interstitial spaces. After hatching and emerging from spawning substrate, larvae drift downstream to nursery backwaters in sandy, alluvial regions. Young Colorado pikeminnow remain near nursery areas for the first two to four years of life, then move upstream to recruit to adult populations and establish home ranges.

Cladocerans, copepods, and midge larvae are the principal diet constituents of Colorado pikeminnow, up to five cm (TL), in nursery backwaters. Insects become important for fish up to 10 cm (TL), after which fish are the main food item. Adult Colorado pikeminnow are the main native piscivorous predator of the Colorado River Basin.

Flannelmouth Sucker

(picture by The Native Fish Conservancy)

Another member of the family Catostomidae, and endemic to the Colorado River watershed, this species is doing well in the upper reaches, but has been extirpated below Lake Mead. Their bodies are thick toward the anterior, but slim gradually to a thin caudal peduncle. The anterior scales are small and embedded in thick skin. Some adults exceed 60 cm (TL) and 30 years of age. Adult fish are light gray to tan dorsally, showing white ventrally. Breeders are dark, with orange pigments on the fins and weekly on the lateral band.

Quiet tributary mouths are often the habitat of choice for adult flannelmouths. In the Marble and Grand Canyon regions, spawning occurs in larger, low gradient tributary mouths, in March to April, in waters of 17 to 23°C. They spawn on the upstream ends of cobble bars in the Yampa River, in April to early June. Some adults remain in spawning tributaries throughout the summer. Young use the tributaries, and shoreline flatwaters of the mainstem.

Flannelmouths commonly feed on aquatic invertebrates (dipterans and crustaceans), organic debris, and algae.

Humpback Chub

(picture from USFWS 2002c)

The humpback chub is a long-lived, big-river cyprinid, attaining a maximum size of about 48 cm (TL) and 1.15 kg, and maximum age of about 25 years. Its body is laterally compressed and relatively fusiform. Distal to its narrow, flattened head – equipped with small eyes, a protruding snout and an inferior, subterminal mouth – is a large fleshy hump that develops as the fish matures. A narrow caudal peduncle supports a deeply forked caudal fin. Subadults have an olivaceous back and silvery sides that fade into a creamy white belly. Adults are light olivaceous to slate-gray dorsally and laterally and have a white belly highlighted with light orange and yellow. Spawning adults are tinged with rosy-red gill coverings, paired fins, and belly, with tubercles on the head and paired fins.

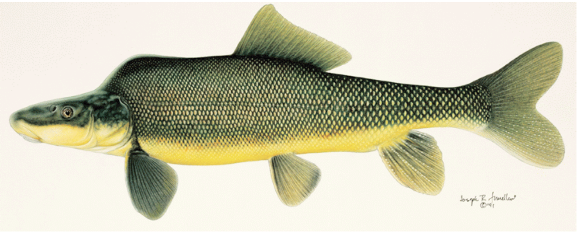
The historic abundance of humpback chub is unknown. It currently occupies about 68% of its historic habitat of about 756 km of river. Today, six humpback chub populations have been identified: (1) Black Rocks, Colorado; (2) Westwater Canyon, Utah; (3) Little Colorado and Colorado Rivers in Grand Canyon, Arizona; (4) Yampa Canyon, Colorado; (5) Desolation/Gray Canyons, Utah; and (6) Cataract Canyon, Utah. Each population consists of a discrete group of fish, geographically separated from the other populations; however, some exchange of individuals occurs.

The humpback chub evolved in seasonally warm and turbid water and is highly adapted to the unpredictable hydrologic conditions that occurred in the pristine Colorado River system. Humpback chub live and complete their entire life cycle in canyon-bound reaches of the Colorado River mainstem and larger tributaries. These reaches are characterized by deep water, swift currents, and rocky substrates. Subadults use shallow, sheltered shoreline habitats, whereas adults use primarily offshore habitats (primarily eddies) of greater depths.

The humpback chub is an obligate warmwater breeder, requiring relatively warm temperatures for spawning, egg incubation, and survival of larvae. Spawning occurs primarily on the descending limb of the spring hydrograph, which is March to May in the Little Colorado River and April to June in the upper basin, in waters of 16 to 22°C. In the Yampa River, humpbacks occupy and spawn in or near shoreline eddy habitats. Humpbacks are broadcast spawners with a relatively low fecundity rate, compared to cyprinids of similar size. Females average of 2,523 eggs in hatcheries and about 4,831 eggs in the Little Colorado River. Young require low-velocity shoreline habitats, including eddies and backwaters. Unlike larvae of other Colorado River fishes larval humpback chub show no evidence of long-distance drift; rather, they tend to remain close to spawning sites.

Opportunistic in their feeding habits, humpbacks utilize food sources as they become available. For young-of-year and juveniles from the Green and upper Colorado Rivers, Ephemeroptera and Diptera were important food items. Adult humpback chub are typically omnivores with a diet consisting of insects, crustaceans, plants, seeds, and occasionally small fish and reptiles.

Razorback Sucker



(picture from USFWS 2002d)

The razorback sucker is a full-bodied, long-lived river catostomid reaching a maximum size of about 100 cm (TL) and five to six kilograms and 44 years of age. Adults are elongated and slightly compressed laterally, with a bony, sharp-edged dorsal keel immediately posterior to the head. The head is elongated with a flattened dorsal surface, and the mouth is prominent and located slightly subterminally. In adults, the upper body is dark brown to olivaceous, with the lower ventro-lateral surfaces ranging from white to yellow. The lateral band varies between yellowish, orange, reddish to reddish brown or even violet. Breeding males display very dark dorsal surfaces and bright yellow to orange ventro-lateral surfaces. Tubercles develop on surfaces of the anal and caudal fins, caudal peduncle, and posterior sides of breeding adults.

Historically, the razorback sucker occupied the mainstem Colorado River and many of its tributaries throughout the entire Colorado River basin, with abundance declining with distance upstream. Distribution and abundance of razorback sucker declined throughout the 20th century over all of its historic range, and the species now exists naturally only in a few small, discontiguous populations or as dispersed individuals. These fish have exhibited little natural recruitment in the last 40–50 years, and wild populations are composed primarily of aging adults, with steep declines in numbers.

Adult razorbacks are found in rivers require deep eddies, backwaters, and flooded off-channel environments in spring; runs and pools often in shallow water associated with submerged sandbars in summer; and low-velocity runs, pools, and eddies in winter.

Spring migrations of adult razorback sucker, some of very long distance, were associated with spawning in historic accounts. Razorback suckers breed in spring on the ascending limb of the hydrograph, mid-April through June in the upper Colorado River. Broadcast spawning of adhesive eggs occurs in rivers occurs over bars of cobble, gravel, and sand substrates during spring runoff at widely ranging flows and water temperatures typically greater than 14°C. In reservoirs, razorbacks spawn over rocky shoals and shorelines. Razorbacks sucker have high reproductive potential with average fecundities ranging from 46,740 to 103,000 eggs/fish. Young require nursery environments with quiet, warm, shallow water such as tributary mouths, backwaters, or inundated floodplain habitats in rivers, and coves or shorelines in reservoirs. Young razorback suckers seek shallow, warm, low-velocity habitats in littoral zones, backwaters, and inundated floodplains and tributary mouths downstream of spawning bars. Young-of-year appear to stay in these sheltered habitats for several weeks after hatching, and then disperse to deeper water.

All life stages of razorback sucker consume insects, zooplankton, phytoplankton, algae, and detritus; however, diet varies by age and habitat. Razorback sucker larvae feed on plankton until their mouth moves to a sub-terminal position and feed on benthos as well. Chironomids are among the most common benthic invertebrates in riverine nursery habitats of the upper basin. The diet of riverine adult razorback sucker consists mostly of benthic organisms (immature Ephemeroptera, Trichoptera, and Chironomidae) and lesser amounts of algae, detritus, and inorganic material.

Speckled Dace

(picture from The Native Fish Conservancy)

This small cyprinid has a far-reaching distribution and is the most widespread freshwater fish west of the Rocky Mountains. Some suggest that this could be a species complex because many of the populations are quite diverse in their morphology. In the Grand Canyon Region, tributary and mainstem brethren are quite different. The mainstem fish has a slightly tapered, cylindrical body, with longer, larger fins, a sharper snout, and longer head, than the tributary forms. Depending on the population, fish have dark longitudinal stripes and a uniform tan dorsum with a white belly or are densely specked with an underlying olive hue dorsally, and white below. All breeding males show crimson red pigmentation on the lower head, bases of the fins, belly and lateral body surfaces. Speckled dace mature in a year or less, live two to three years, and rarely exceed 10 cm.

This species remains common in lacustrine creek mouths and along riverine sand bars. Mainstem fishes enter tributaries in March and spawn in April and May. It is thought that reproduction is constrained to waters of 17 to 23°C. Both young-of-years and adults remain in lower parts of the tributaries through autumn. Common food items in both mainstream and tributary habitats are benthic invertebrates and organic debris.

CAUSES OF THE DEMISE OF THE NATIVE FAUNA

The native fish of the lower Colorado are facing two major threats, both brought about by the encroachment of human settlers to the southwest: habitat degradation and nonnative fishes. Dams have drastically altered the river’s natural flow regime through the Grand Canyon. The annual hydrograph of the lower Colorado River has been flat-lined compared to pre-dam conditions. The historical massive spring snowmelt floods are almost nonexistent. Their energy and volume is stolen by the series of dams upstream from the Grand Canyon. Late summer, fall and early winter flows – times of the year when water would have been a limiting factor in the pre-dam condition – are also near identical to the rest of the year. On the scale of days, however, the hydrograph has only become more heterogenous, with daily fluctuations as high as 15,000 cfs common in many parts of the year. The lack of strong floods to wash away fine particulates, coupled with the increased erosion of sandbars by daily fluctuating low flows, has led to the severe agradation of debris fans (Webb et al 1999). These debris fans are central to maintaining the fan-eddy complexes that create eddy environments used by the native fishes (Webb et al. 1999).

Glen Canyon Dam releases typically fluctuate close to 8°C year round. Mainstem spawning of native fishes is precluded by these cold, hypolimnetic releases (Minckley et al. 2003, Webb et al. 1999), thus, increasing dependence on the warm tributaries for successful reproduction by decreasing available mainstem spawning habitat (Webb et al. 1999). The cold water also presents a lack of rearing areas for the warmwater obligate natives that require relatively warm water for successful rearing. Near-zero growth rates and severe coldwater-related stress ensue when native young-of-year larval fishes drift or migrate from the warm tributaries into the cold Colorado River (Robinson and Childs 2001, Clarkson and Childs 2000); thus increasing the risk of temperature dependent mortality via a prolonged risk of predation and size dependent competition.

The altered flow regime has also provided conditions suitable for the proliferation of more than 15 introduced fishes in the lower Colorado River. Minckley et al. (2003) consider nonnative fishes the fundamental cause to the demise of the native fauna, arguing that if nonnative fishes vanished, the natives would still persist in today's modified habitats. The primary problem with nonnative fish is that they preclude the recruitment of natives by devouring native eggs, larvae and juveniles. Most nonnatives are ecological generalists, widespread and competitive within their natural ranges, and predatory or omnivorous (Minckley et al. 2003). In essence, the exotic fish have out-competed the native fauna and overtaken the now unfulfilled niches in the altered river. Carp consume fish eggs and larvae particularly in small tributaries. Channel catfish, an otophysan fish well equipped to compete with the native otophysans, consume large numbers of native young in conditions the young natives use as cover: night and high turbidity. Nonnative salmonids consume large numbers of juvenile fishes descending from natal streams. Fathead minnows, red shiners, and many other of the introduced otophysan fishes consume newly-hatched larvae in shallow nursery habitats such as backwaters (Webb et al. 1999). A much more detailed account about the interactions between natives and nonnatives on the Colorado River is provided by Wilson (2005) in this volume.

NATIVE FISH CONSERVATION AND MANAGEMENT

Many ideas have been suggested for the conservation of the lower Colorado's native fishes. This section covers currently implemented and proposed management options. Those management plans that have been implemented have not shown much promise, though some do.

An act of immense proportions in terms of time, money, scale, and public will, will be needed if headway in the conservation of the lower Colorado's endangered fishes is to be made.

Experimental Flows

The Modified Low Fluctuating Flow Alternative (MLFFA) was the preferred flow regime of the Record of Decision (ROD) after the Glen Canyon Dam Environmental Impact Statement, and has been in place since the early 1990s. Current dam operations also include five types of experimental releases, in addition to ROD operational flows. The five types of releases are: (1) 8,000 cfs steady flows, (2) 6,500-9,000 cfs fluctuating flows, (3) 5,000-20,000 cfs fluctuating nonnative fish fluctuating flows, (4) 31,000-33,000 cfs habitat maintenance flows, (5) 42,000-45,000 cfs habitat-building high flows. The order in which the releases occur depends on the amount of sediment inputs from the tributaries downstream of Glen Canyon Dam.

Two habitat-building experimental floods have been released from Glen Canyon Dam. The first test flood occurred over a seven day span in March of 1996 and peaked at 45,000 cfs. The second test flood, in November of 2004, was of a shorter duration and magnitude, lasting only five days and peaking at 42,000 cfs. From the results presented by Schmidt et al. (2001) and Valdez et al. (2001), it appears as if the 1996 test flood was a temporary success, but a long-term failure. Results from the 2004 test flood are still being analyzed.

The number and area of return-current channel backwaters increased greatly after the 1996 flood, but the area of these formed backwaters decreased quickly after the flood, to levels *even lower* than the pre-flood condition (Schmidt et al. 2001; Figure 1). Also, created-backwater abundance was spatially variable and did not increase in reaches that are of most concern for native fish (Schmidt et al. 2001).

The 1996 experimental flood had little effect on native fishes and only short-term effects on some native species (Valdez et al. 2001). Young trout were displaced 100 to 209 km downstream by the flood, but the researchers concluded that the flood did not significantly affect the rainbow trout population. The release was of insignificant magnitude to completely displace nonnative fathead minnow and plains killifish, but their populations were initially reduced after the flood. Because of incomplete displacement and reintroductions from tributary populations, these species rebounded to pre-flood levels in eight months. In essence, the flood magnitude and sediment supply were too small to yield a long term significant beneficial impact on the Grand

Canyon ecosystem. Overall, the results from the 1996 experimental flood indicate that properly designed and timed floods can benefit native fishes by temporarily reducing numbers of predaceous and competitive nonnative fishes.

The Glen Canyon Adaptive Management Workgroup (AMW) recently wrote, “we can say with confidence that MLFFA was not effective at reversing the decline [of the Humpback Chub population] or at providing sufficiently good habitat conditions in the CR mainstem to allow enough recruitment for the population to be sustained” (USBR 2004). However, the AMW recognizes that “there is a good chance that juveniles dispersing into the mainstem in summer and fall would be able to grow, survive, and return to the LCR for extended rearing if they were to encounter (1) reduced predation by exotic trout due to mechanical removal treatments, and (2) relatively warm spatial refuges in nearshore locations, as would be created by steady flow conditions in late summer and fall.” In a “Low Summer Steady Flow (LSSF), [the GCAMP] demonstrated that such lateral warming of backwater areas can be quite dramatic.” Thus, the

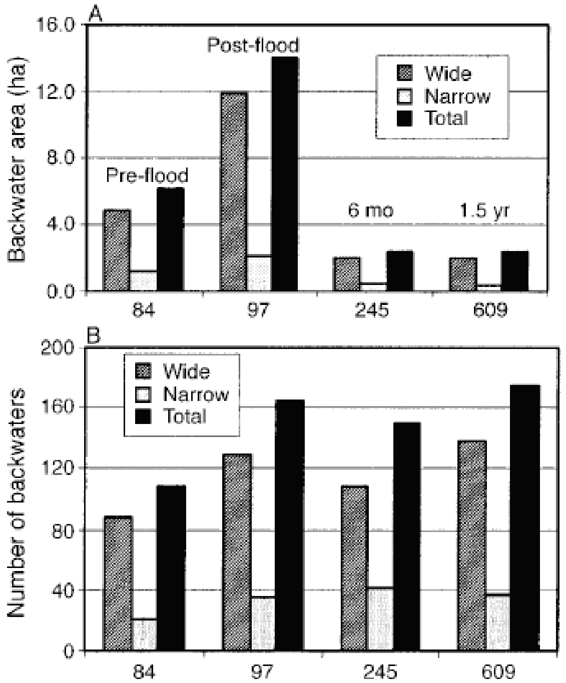


Figure 1. (A) Backwater area and (B) number of backwaters before and after the 1996 flood in the Colorado River corridor between Glen Canyon Dam and Separation Canyon (river kilometer 386), on 24 March, 6 April, and 1 September 1996, and 31 August 1997, measured using Map Image Processing Software (MIPS) from aerial videographic images (from Schmidt et al. 2001).

AWG proposed a Summer-Fall Steady Flow (SFSF) experiment that would "maintain conditions for backwater warming from the time of the first summer freshet that disperses juveniles into the mainstem, until around November 1 when the equilibrium temperature in standing backwaters decreases (due to nighttime cooling) to about the same as the mainstem temperature."

Mimicking the Natural Flow Regime

Others suggest water should be released to closely mimic the natural flow regime, thus enhancing the habitats and native fishes (Minckley 1991). Putah Creek, a regulated waterway in Northern California, is a case study that supports the concept that restoration of natural flow regimes, in company with other restoration measures, is necessary if the continued downward decline of native fish populations in the western United States is to be reversed (Marchetti and Moyle 2001). In Putah Creek, the researchers found that numbers of nonnative fish were negatively correlated, and numbers of natives positively correlated, with the increased streamflows reminiscent of the natural flow regime. On the lower Colorado River, manually induced springtime floods that mimic the natural hydrograph may improve the habitat of native fishes by increasing turbidity, restoring backwater habitat and productivity, redistributing nutrients, and importing a large mass of terrestrial and benthic organisms and debris used as food (Webb et al. 1999). Thieme et al. (2001) found a strong correlation between pool formation at the mouth of the Paria River and survival of YOY flannelmouth suckers when high spring flows were released from Glen Canyon Dam.

Tailwater Warming

The USBR is considering retrofitting Glen Canyon dam with temperature control devices (TCDs) to allow manipulation of downstream water temperatures (USBR 2005). Warming the water in spring would give a chance for the reestablishment of bonytail and Colorado pikeminnow and would benefit other natives as well (Minckley 1991), primarily by increasing the survival of young that require warm water to rear successfully (Robinson and Childs 2001). If TCDs are to be implemented, Robinson and Childs (2001) recommend an adaptive management scheme where: 1) temperature related interactions among native and nonnative fishes is assessed before, during and after implementation of warmwater releases; 2) a coldwater flood is released in spring to reduce nonnative fish populations, if they benefit from the warm water; 3) coldwater releases could be re-implemented if deleterious effects to the native fish populations are observed. Because of the species-specific relationships between temperature and growth rates and the timing of larval drift (Robinson et al. 1998), results would differ among species, with increased benefits attained with heightened temperatures and greater durations of heating (Robinson and Childs 2001). Another benefit of water warming is a possible decreased dependence on backwater rearing habitat in Grand Canyon. It is thought that the one of the main reason that native fishes use the backwaters is for thermal refugia from the cold releases (Webb et al 1999); the other primary reasons being foraging and refuge during high flows. However, water warming could also provide conditions tolerable for establishment of new exotics (i.e. striped bass; Valdez and Leibfried 1999) and/or could augment current exotic populations, thus increasing the exotics' native fish predation and competition with native fishes (Robinson and Childs 2001). These outcomes depend on the degree to which the water is warmed and the duration of warming.

The AMW also recently proposed the use of a TCD to enhance the thermal conditions of backwaters in their SFSF proposal (USBR 2005). Their reasoning was that a TCD alone could likely not achieve a 4-5°C increase in the mainstem near the LCR in late summer, which would be needed for juvenile humpback chub to exhibit normal first-year growth, especially if that TCD were also planned to avoid GCD release temperatures high enough to cause negative impacts on the Lees Ferry trout population.

Nonnative Fish Control

Minckley (1991) argued that the control of nonnative, warmwater species is the single most important requirement for achieving the persistence of native fishes. Recovery efforts have recognized this need for developing nonnative fish control strategies, but no solutions have emerged (Tyus and Saunders 2000). For more information on nonnative fish control in the Grand Canyon, see Epstein (2005; for trout control) and Wilson (2005; for other nonnatives' control) in this volume.

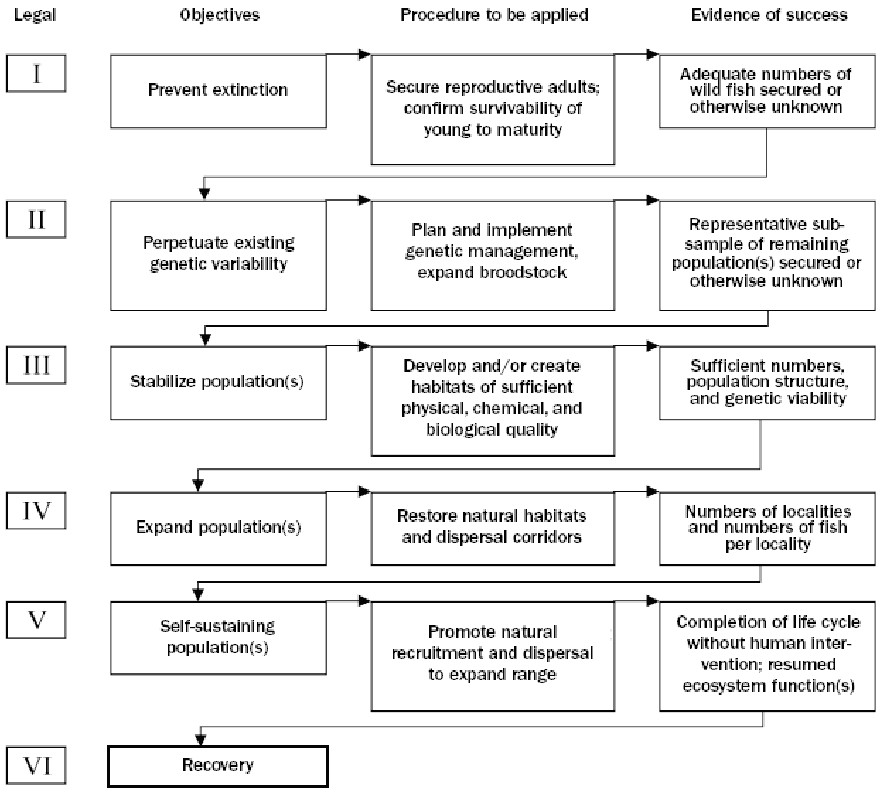


Figure 2. US Fish and Wildlife Service conceptual plan for managing native fishes of the lower Colorado River basin (USFWS 1996) (from Minckley et al. 2003).

Artificially-Maintained Populations

In 1996 the USFWS created a conceptual framework from which to manage the lower Colorado's mainstem and endangered big-river fish: bonytail, Colorado pikeminnow, humpback chub and razorback sucker (Figure 2). Working with this framework and the updated recovery plans of the four species, Minckley et al. (2003) created an innovative conservation plan in their recommendation to the US Fish and Wildlife Service for a strategy to aid the recovery of the endangered big-river fishes in the lower Colorado River. The authors stress the need to maintain a large effective population size to conserve the remaining genetic diversity of the imperiled populations. In their program, the native species would breed, and their progeny grow, in isolated, protected, naturalistic, off-channel habitats in the absence of nonnative fishes (Figure 3). Panmictic adult populations would reside in the main channel and connected waters, from which reproductive adults would be exchanged with repatriated subadults in the populations occupying the created isolated habitats. The immense amount of land needed

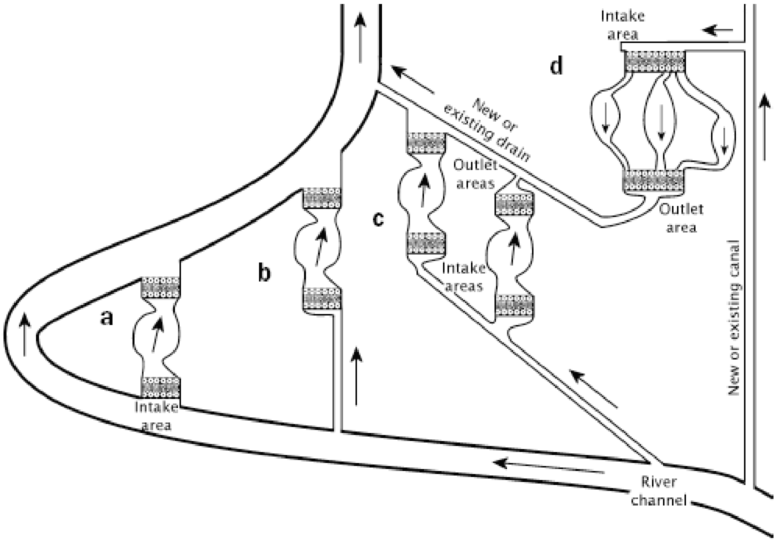


Figure 3. Some potential arrangements for hypothetical lower Colorado River off-channel habitats (from Minckley et al. 2003).

to support the needed effective population sizes refutes the possibility of using hatcheries due to spatial constraints (Minckley et al. 2003).

Maintaining fish in captivity for refugium purposes poses no genetic risks to the wild population; however, the release of captive-reared individuals into the wild does pose numerous genetic and biological risks that need to be seriously evaluated (Van Haverbeke and Simmonds 2004). These risks include introgression, inbreeding depression, domestication, potential to decrease the genetic effective population size of the wild population, a lack of anti-predator responses, and a lack of ability to feed efficiently (Van Haverbeke and Simmonds 2004). According to USFWS and NOAA policy, releasing captive propagated individuals should not be considered as a management strategy unless all other conservation measures fail (Van Haverbeke and Simmonds 2004). Also, part of this policy requires that captive broodstock activities are based on the specific recommendations of recovery strategies identified in recovery plans whenever practical; a feature for which the current Recovery Goals for the species make no provision (Van Haverbeke and Simmonds 2004). However, if properly performed, there appears to pose no serious biological risks to the wild population (Van Haverbeke and Simmonds 2004).

CONCLUSION

The drastic alterations to the Colorado River's natural flow regime, coupled with the introduction of a suite of exotic fishes, has put many of the lower Colorado River's native and endemic fishes in line for extinction. Current management programs on the lower Colorado River focus on individual species and are largely without benefit to the overall plan (Minckley et al. 2003). A holistic, ecosystem-wide approach is needed to restore the many imperiled native fishes of the Colorado River (Tyus and Suanders 2000). However, the complete restoration of native fish populations is improbable owing to the permanent state of the water-development infrastructure in place.

With a large panmictic population, a naturalized environment, and a significant amount of land area, coupled with funding adequate to maintain an efficient, watchful crew, the Minckley et al. (2003) proposal has presented a viable option for the conservation of the lower Colorado's mainstem endangered natives, without posing genetic or biological risks to the wild native stocks still present. However, their planned facilities would face many logistical problems and one ultimate problem. Logistically, the restocking of repatriates into the entirety of the river seems unlikely. How would you get all those fish evenly distributed throughout the entire lower Colorado? The Grand Canyon poses a problem in this respect. In order to restock the Grand Canyon with repatriates, the most viable options would be Lee's Ferry and Lake Mead's newly formed delta. Yet, there are so many relatively inaccessible river miles in between that would be depending solely on migration of the repatriates (which is not entirely impossible).

Ultimately, the Mickley et al. plan *would not* promote a self-sustaining population, a feature required in the recovery criteria for the species. Thus, some form of habitat restoration must be implemented. Their approach could be coupled with yearly to twice-yearly floods of a magnitude greater than 45,000 cfs (when that amount of water is physically available) to continually keep the nonnative fishes in low abundance and constantly rebuild critical native fish habitat. TCDs would likely be necessary to create a habitat in which naturally occurring recruitment of the endangered native fish was possible; however, if implemented, an adaptive management scheme like the one outlined by Robinson and Childs (2001) would be absolutely necessary. Yet, the most essential piece of this restoration dilemma, but perhaps the most difficult to obtain, is the funding and political will to tackle this growing crisis.

I believe Minckley et al. (2003) provide the best plan for conserving the lower Colorado River's endangered fish fauna. Implementation of such a management plan should be enacted in the very near future to preserve what demographic and genetic diversity of the lower Colorado's endangered fishes is left. At the very least, this will be buying us time for new technologies and ideas to evolve, and better solutions to arise.

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