A Conservation Plan for Native Fishes of the Lower Colorado River

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The native fish fauna of the lower Colorado River, in the western United States, includes four "big-river" fishes that are federally listed as endangered. Existing recovery implementation plans are inadequate for these critically imperiled species. We describe a realistic, proactive management program founded on demographic and genetic principles and crafted to avoid potential conflicts with nonnative sport fisheries. In this program, native species would breed and their progeny grow in isolated, protected, off-channel habitats in the absence of nonnative fishes. Panmictic adult populations would reside in the main channel and connected waters, exchanging reproductive adults and repatriated subadults with populations occupying isolated habitats. Implementation of the plan would greatly enhance recovery potential of the four listed fishes.

Keywords: conservation, management, genetics, endangered fishes

Among the native fishes of the Colorado River are four "big-river" species: humpback chub *(Gila cypha)*, bonytail *(Gila elegans)*, Colorado squawfish *(Ptychocheilus lucius)*, and razorback sucker *(Xyrauchen texanus)*. Once generally widespread and abundant (Minckley 1973), these species are now critically imperiled. Water development—damming rivers, creating impoundments and cold tailwaters, degrading habitats, and desiccating long reaches—and the introduction and establishment of a suite of nonnative species have adversely affected the native fishes. Severely reduced in abundance and range and under continuing threats, the four big-river species are now federally listed as endangered (USFWS 2002a, 2002b, 2002c, 2002d).

The Colorado River drains a part of the American West renowned for its natural beauty, open space, and biodiversity. The whole region is arid, and water is critically limiting. Tens of millions of people rely on the river for water and electrical power, and as a result it is one of the most controlled rivers on Earth (Fradkin 1981). In addition to its direct importance to human well-being, the Colorado River is critical to continental biodiversity. Its path through some of the driest, hottest North American deserts forms a mesic, north–south corridor for innumerable organisms. Further, the Colorado River system supports a unique biota of its own. Historical species-level endemism for fishes is approximately 75% for the ancient, long-isolated watershed (Carlson and Muth 1989). The lower Colorado River main stem, defined as the reach downstream from Glen Canyon Dam (figure 1), is the geopolitical focus of this article.

Biotic elements of concern

Thirteen fishes, including 10 freshwater species (table 1), constituted the original fish fauna of the lower Colorado River main stem. Three largely marine taxa from Mexico's Sea of Cortez (machete, striped mullet, and spotted sleeper) and woundfin were extirpated from the lower river main stem before 1900; roundtail chub and Colorado squawfish are also gone. Humpback chub, speckled dace, flannelmouth sucker, and bluehead sucker persist in the Grand Canyon; bonytail, razorback sucker, flannelmouth sucker, and desert pupfish still live downstream, largely because of management action on their behalf. The four big-river fishes—bonytail, humpback chub, Colorado squawfish, and razorback sucker—are the biological subjects of this article.

Over the past century, the original fish fauna of the lower Colorado River has largely been replaced by nonnative species (table 1), especially downstream from Hoover (formerly Boulder) Dam. Rainbow trout live in the cold water below dams; threadfin shad, largemouth bass, black and white

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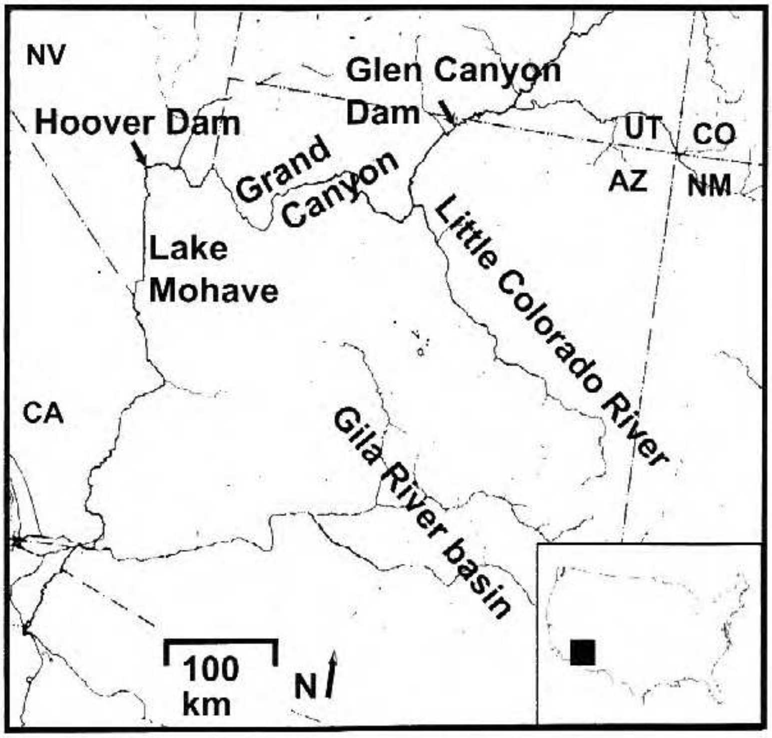

Figure 1. Sketch map of the lower Colorado River basin.

crappies, sunfishes, and striped bass dominate in reservoirs. Common carp; red shiner; channel, bullhead, and flathead catfishes; live-bearers (mosquitofish and mollies); and African cichlids are in most river channels, backwaters, and reservoirs. Other species, such as smallmouth bass, are more localized. Most nonnatives are ecological generalists, widespread and competitive within their natural ranges, and predatory or omnivorous (Marsh and Pacey 2003).

Historical perspectives on Colorado River management

Efforts to control the Colorado River began soon after the arrival of western Europeans. Levees, diversions, and other structures were built to reduce the impact of the flood and drought that plagued development. The river resisted until 1935, when Hoover Dam was closed to form Lake Mead, a reservoir large enough to hold 2 years' average flow. Other dams followed; the total capacity of today's reservoirs is sufficient to store more than 4 years' flow.

Only a few people were alarmed by these early changes (e.g., Miller 1946). Serious controversy did not arise until the 1960s, first over the effects of channel dredging on wildlife and sport fish, then over concern for the native biota (Miller 1961, Minckley and Deacon 1968). Early researchers concluded that development had dramatically altered the system, and public pressure to prevent species' losses was growing. The Endangered Species Act (ESA) of 1973, together with other environmental legislation, inspired the evolution of a "conservation industry"—state and federal biologists, consultants, and academic contractors—funded by the development community in response to the new rules.

In principle, ESA decisions are based on the best biological information, but many issues relating to species' conservation are largely socioeconomic or political. Thus, factors other than biology influence most plans and projects, reducing benefits to the species of concern. The US Fish and Wildlife Service (USFWS), charged with enforcing ESA and promoting sport fishing, has difficulty balancing these conflicting demands. State agencies face the same dilemma. Moreover, state and federal conservation agencies are placed in a position of challenging the responsibilities of other agencies that deal with resources such as water and power—agencies that are better funded and have more political clout. Accommodating the political, socioeconomic, and biological concerns of opposing constituencies and such powerful adversaries is challenging at best.

As recovery efforts have expanded, confrontations have increased: conservationists versus developers, sport fish managers versus native fish proponents, and special interest groups versus protected natural resources. Agency intransigence or failure to comply with legislative requirements has been met by litigation, especially by nongovernmental organizations (NGOs). Legislative relief has been sought and granted, for example, in the form of less than fully protected experimental populations, "reasonable and prudent alternatives" (RPA) to jeopardy opinions, and other exemptions that have amended the ESA. (A jeopardy opinion by USFWS is a determination that a federally funded project will adversely affect a listed species or its critical habitat. RPAs are mitigation actions intended to offset project impacts.) Provisions for habitat management plans (HMP) have appeared, under which nonfederal entities can develop and operate projects with a "take" of listed taxa permitted so long as species' existence is not jeopardized. The conservation industry has answered site-specific questions quickly in response to time constraints. But these data have not been analyzed to any considerable degree; the reports based on them have benefited neither from peer review nor from the scrutiny afforded by publication in the open literature; and public availability of these reports has been short-term or nonexistent. The consequence is that major decisions are based on local and sometimes hastily collected information, often broadly applied.

The lead agency for all four big-river fishes is USFWS Region 6, which has jurisdiction only upstream of Glen Canyon Dam. That office inherited a study program (1963–1980) originally stimulated by the poisoning of the Green River in Wyoming and Utah (Holden 1991), which led to the Colorado River Fishery Project (1979–1987), which was converted in 1987 to a 15-year, \$60 million Recovery Implementation Program (RIP; USFWS 1987). The RIP was designed to allow continued water development and use while simultaneously pursuing recovery of endangered fishes (Wydoski and Hamill

Table 1. Status of native and nonnative freshwater fishes of the lower Colorado River main stem, southwestern United States.

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.

1991). Progress toward recovery was defined by a series of "reasonable and prudent alternatives" in lieu of jeopardy opinions under section 7 of the ESA (Lochhead 1996). Examples of such alternatives include provision of research funds and purchase of land on which occupied habitat could be developed. Recent examination of the success of the RIP's consensus-based approach suggests that conservation goals have been compromised by a process that relies on funding from water development interests and is focused on achieving bureaucratic procedural goals (Brower et al. 2001). This long-term, multimillion-dollar program has established massive administrative and research infrastructures, but according to some informed observers it has accomplished little to improve the status of the listed fishes.

Concentrating efforts in the upper basin de-emphasized the lower Colorado River basin (USFWS Region 2), where important humpback chub and razorback sucker populations existed along with the last wild bonytail (Marsh and Minckley 1992, Valdez and Carothers 1998). Independent workers nonetheless proceeded with research and management funded by diverse sources. But native fishes and their habitats continued to decline. "Nonessential" endangered fishes were stocked, and litigation was considered. Today a major HMP involving state agencies, water supply and irrigation districts, Native American tribes, NGOs, and other groups is being developed for the lower Colorado River. A few NGOs, however, plan to litigate if dissatisfied.

In 1999, USFWS Region 2 asked several of the authors to formulate a plan to perpetuate fishes native to the lower basin. We accepted the assignment with trepidation, since a "common solution [for seemingly intractable situations] is to replace...uncertainty of resource issues with...certainty of a process, whether that process is a legal vehicle—such as a new policy, regulation, or lawsuit—or a new institution *such as a technical oversight committee or science advisory committee*" (Gunderson 1999; bracketed material and italics ours). In this instance, the committee was *ad hoc* and largely undirected, consisting of academic scientists advised by agency biologists. In the meantime, new definitions of recovery goals (USFWS 2002a, 2002b, 2002c, 2002d) for the four big-river fishes became an issue, which in part redirected the group's efforts.

This article presents our recommendations for a science-based recovery strategy that could aid the recovery of the big-river fishes in the lower Colorado River. The recommendations are not new. They are based on our collective knowledge, published papers, and unpublished plans. We believe they offer important new perspectives that should be incorporated into criteria used by the RIP (USFWS 2002a, 2002b, 2002c, 2002d) to determine when a listed big-river species has "recovered."

Rationale and approach

Some workers dealing with the lower Colorado River advocate a return to conditions before the arrival of western Europeans, after which the ecosystem would be allowed to change without management. Others deem the river already so highly altered that it should be written off to save conservation dollars. Many view the first recommendation as too idealistic and unrealistic and the second as defeatist. Instead we choose to take the middle ground by advocating aggressive, ongoing management, because the lower Colorado River is one of only a few places in the American Southwest where surface water will persist into the foreseeable future.

We expect management practices to evolve in concert with changing sociopolitical practices and cultural values. Until now, varying emphases have been placed on flood control, power generation, irrigation, recreation, municipal supply, and other uses. Today's trends include a shift from rural to urban water uses and increasing emphasis on promoting maintenance of biodiversity. Native fish management in the lower Colorado River has become an increasing responsibility for federal and state agencies over the past three decades. That responsibility is likely to continue increasing, as is evident in the Lower Colorado River Multi-Species Conservation Program planning process currently under way. Herein lies an opportunity to perpetuate native fishes. The key to success is to embed secure, exclusive native fish habitats and effective native fish management as part of daily river operations.

We recognize that the Colorado River as now regulated differs substantially from what it was, and we accept that it will not be the same again. We also recognize that regulation of discharge and flow patterns is not per se the principal threat to the persistence of the four species considered here. The fundamental problem is that abundant, nonnative predatory species preclude recruitment of natives. We have no doubt that if nonnative species vanished, the big-river fishes would persist in today's modified habitats. But although all native species tested thus far reproduce to sustain themselves in predator-free habitats, few have succeeded in waters shared with nonnative species (Marsh and Pacey 2003). Nonnatives prey on the larvae and juveniles of native species. All nonnative species are actual or potential predators or competitors, and where they occur we believe reestablishing an original fauna is impossible. We recognize that nonnatives cannot be eradicated everywhere, but at least we can provide local habitats from which nonnatives are excluded. If an original fauna is to persist, continuing management will be required.

Our proposal deals with the concepts of, rationale for, and uncertainties about the numbers of individuals necessary to satisfy the goal of species maintenance. The need to maintain large effective population sizes makes it necessary to use space in the main stem, off-channel floodplain, and distributaries (*effective size* is a term that relates a population in nature to an idealized population with certain genetic characteristics). The proposed solution involves translocation of native species between predator-free, off-channel habitats and the main channel, backwaters, and reservoirs (hereafter channel plus connectives). Reproduction and recruitment take place off-channel, and large, wide-ranging, and panmictic populations of adults maintain both population size and genetic variation there and in the channel plus connectives. The plan briefly addresses habitats that are needed to accomplish such goals and anticipated problems in developing such habitats; it also suggests ways that the native fishes can be managed successfully over the long term.

Dwindling populations. The last wild Colorado squawfish was caught in 1975 in the lower Colorado River (Minckley 1991). Bonytail persist only in Lake Mohave (in Arizona and Nevada) and perhaps in Lake Havasu (in Arizona and California) as a few wild fish that are augmented by hatchery reintroductions. Humpback chub are represented by one viable population in the Little Colorado River–Grand Canyon complex. Cold water from Glen Canyon Dam precludes humpback chub reproduction downstream in the Colorado River main stem, and most humpback chub live and spawn in the Little Colorado. Some young move into the main stem, mature, and reenter the tributary to spawn. The Little Colorado population hovered near 10,000 adults into the early 1990s but recently is thought to have declined substantially. Perhaps 10% as many humpback chub occupy the adjacent Colorado River main stem (Valdez and Ryel 1995).

Among native fishes in the lower Colorado River, the razorback sucker has received the most attention since the 1970s (Minckley 1983). Although annual spawning occurs, the population consists mostly of large, old adults, and there is no evidence of recruitment (Minckley et al. 1991). A large population apparently formed when Lake Mohave filled in the early 1950s, and the catch-per-unit effort indicated exceptional population stability through the late 1980s (Marsh and Minckley 1992, Marsh 1994). An estimated population of 73,500 wild adults in the period 1980–1993 dropped to 18,248 by 1992–1999. Annual estimates have consistently declined, from 40,093 in 1992 to 9086 in 1999 (table 2). Our success, and that of others, at rearing razorback suckers in isolated backwaters to sizes sufficient to avoid predators (Minckley et al. 1991) led to a program to collect wild larvae from Lake Mohave and rear them in isolation for repatriation as subadults (Mueller 1995). The first repatriates joined breeding aggregations in 1993, and by 1999 they accounted for 12% of the population (figure 2). As noted above, the wild fish population was by then reduced to approximately 9000 individuals, to which Pacey and Marsh (2003) added an estimated 3000 surviving adult repatriates for an estimated total of approximately 12,000 adults.

Table 2. Population estimates[a] for wild adult razorback suckers in Lake Mohave using Schumacher and Eshemeyer's multiple census (left) and Schnabel's annual census methods (center and right).

Period	Estimate	Year	Estimate	Year	Estimate
1980–1993	73,500[b]	1992	40,093	1993	23,118
1988–1993	59,500[b]	1994	21,292	1995	21,913
1991–1993	23,300[b]	1996	15,187	1997	11,122
1992–1999	18,248	1998	12,614	1999	9,086

a. Ricker (1975).
b. From Marsh (1994).

Prognosis. Our central argument is that quantitative recovery goals for the four big-river fishes (USFWS 2002a, 2002b, 2002c, 2002d) are grossly inadequate. An earlier, conceptual plan for managing lower Colorado basin native fishes (figure 3) included six levels of accomplishment, starting with preventing extinction (level I) and ascending to ultimate recovery (level VI, delisting, is removal from ESA protections and represents political recovery; USFWS 1996). In our view, the damage already suffered, coupled with predictable future demands on the lower river, makes achieving level IV (expansion to sustainability in natural habitats) or higher unlikely under present conditions. It is reasonable, however, to predict success to level III (stabilization), thereby contributing significantly to species' perpetuation and, in concert with other efforts (e.g., USFWS 2002a, 2002b, 2002c, 2002d), perhaps to downlisting (from endangered to threatened) and delisting. Native fishes can survive so long as appropriate habitat and management are provided and they are afforded commitments comparable to those for sport fish and wildlife.

We define level III (stabilization), the goal of species maintenance, not in terms of numbers of individuals but rather in terms of the genetic variability that existed a century ago in native big-river fish populations. This is the level of variability produced by the evolutionary process. If recovery plan amendments (USFWS 2002a, 2002b, 2002c, 2002d) are implemented, they will significantly erode this variability. Those plans may maintain some of the products of evolution for a time but will severely curtail the process. As Rolston (1991) convincingly argued, "It is not form (species) as mere morphology, but the formative (speciating) process that humans ought to preserve, although the process cannot be preserved without its products" (p. 103). Our recommendations delineate conditions under which these fishes may retain characteristics essential to the continuation of this formative process.

Rationale for population goals

No quantitative data, historic or otherwise, exist on original numbers of any native fish in any habitat of the Colorado basin. It is thus impossible to specify numbers required for downlisting or delisting that are based on restoration of historical population sizes. Estimates might be made using methods such as population viability analysis, but demographic data are too sparse for accuracy or reliability. We therefore used three approaches to estimate the numbers of reproducing adults that are sufficient to sustain the four species: (1) qualitative observations, (2) genetic information,

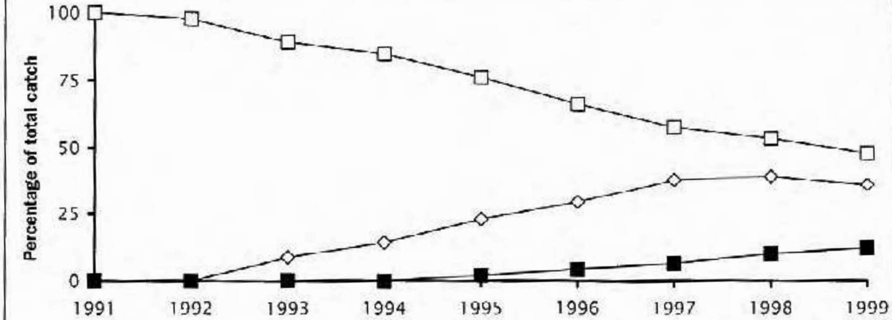

Figure 2. Untagged wild adults (open squares), tagged (recaptured) wild adults (open diamonds), and repatriated (recaptured) razorback suckers (filled squares) as a percentage of total catch in the springtime "razorback roundups" in Lake Mohave, Arizona and Nevada, 1991–1999. From Pacey and Marsh (2003).

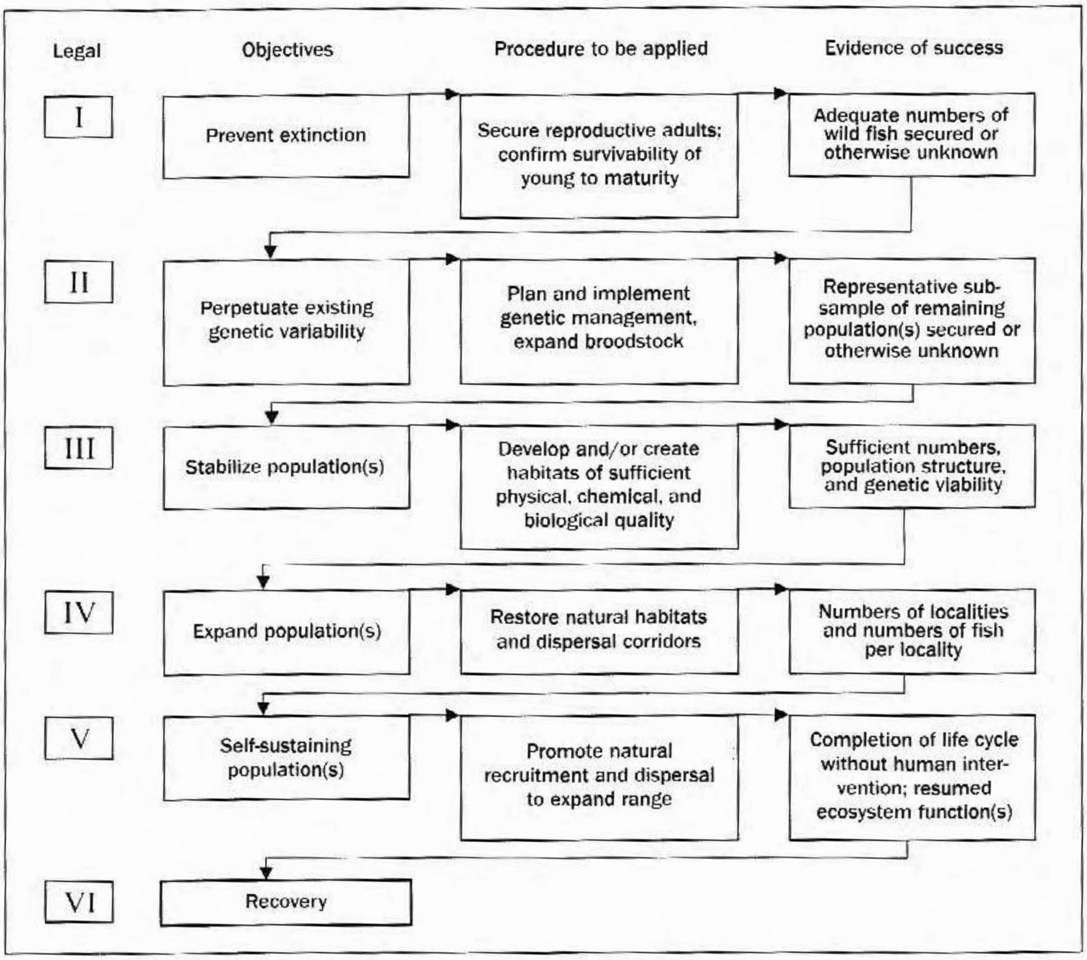

Figure 3. US Fish and Wildlife Service conceptual plan for managing native fishes of the lower Colorado River basin (USFWS 1996).

and (3) empirical data on survivorship, standing crops, growth, and other population statistics.

Qualitative observations. We suggest that it may be justifiable to use data for nonnatives as a surrogate for population sizes of native fishes (large versus small), on the assumption that today's food supplies in many places are quantitatively, if not qualitatively, comparable with those of the past. For example, adult Colorado squawfish and nonnative flathead catfish are large-bodied, ambush piscivores, so past numbers of Colorado squawfish and present-day flathead populations may be similar. The giant native minnow originally occupied the entire lower Colorado basin, including the delta and Gila River drainage. Adults moved upstream to spawn in numbers sufficient to harvest as human and livestock food (Miller 1961, Minckley 1973, 1991). Flatheads now usurp the minnow's whole former range in the lower Colorado River, where surface water remains.

Numbers of Colorado squawfish in approximately 550 kilometers (km) of the Green River flowing through Colorado and Utah, where the largest wild population persists, were estimated in six ways by Tyus (1991). The number of adults longer than 40 centimeters (cm) total length (TL, the distance from the snout to the tip of the depressed tail fin) varied from 1.4 to 80 fish per km (averaging approximately 17). This must be a minimum estimate of original abundance, since squawfish now must contend with factors that presumably reduce their abundance. These factors include naturally cooler waters, which probably result in lowered productivity (Kaeding and Osmundson 1988); new dams and river regulation; and competition with shoreline competitors not historically present (e.g., northern pike *Esox lucius*, for space at least). Comparable estimates for adult flatheads are 156 to 259 fish per km in the Colorado River main stem near Yuma, Arizona (Young and Marsh 1990), and an average of approximately 70 fish per km in the Gila River (Marsh and Brooks 1989). This means that approximately 4 to 15 times more flatheads live in lower-basin streams than Colorado squawfish in the Green River. Thus, if past and present ecological situations indeed are comparable, even by an order of magnitude, large numbers of Colorado squawfish occupied lower-basin streams in the past. Ample literature exists on standing stocks of prey needed to support predatory fishes, and forage is clearly adequate for flatheads. Pristine rivers must have supported numbers of other native fishes adequate to feed Colorado squawfish as well.

Genetics. Conserving genetic variation has been a major focus of recovery efforts for many endangered species, including Colorado River fishes (Wydoski 1994). It is important to retain the variation that will permit adaptation to environmental change, particularly because many imperiled taxa are in recently altered habitats and thus exposed to new biological threats, including nonnative predators, competitors, and parasites. In general, the amount of genetic variation within a population results from a balance between mutation, which introduces new variation, and genetic drift, which reduces it. Also, selection may reduce the frequency of detrimental variants or increase the frequency of advantageous alleles.

Franklin (1980) suggested that for neutral variants, if the effect of new mutations is about a thousandth of the environmental variance in fitness per generation, then loss of genetic variation in a finite population is balanced when effective population size (N_e; see Hedrick 2000) is 500. N_e can be thought of as the size of a theoretical, randomly breeding population with the same rate of genetic drift as the population in question. This was the basis for Franklin's very general choice of $N_e = 500$ for maintaining genetic variation. However, N_e equals the adult breeding number only if, from generation to generation, individuals at the same life stage are produced at random, that is, if all parents are equally likely to contribute gametes. For most organisms, there typically is higher variance in contribution than predicted from random breeding because of unequal sex ratio, high variance in mating success, fecundity or progeny survival over individuals, and other factors. Further, N_e over time (i.e., generations) depends on the harmonic mean of the number of individuals for each generation, which may be far lower than the arithmetic mean (Hedrick 2000). Lande (1995) suggested up to 90% of the increase in genetic variance by mutation over time may be caused by changes that unconditionally reduce fitness, so most new variation is unavailable for adaptive change. Thus, he thought that $N_e = 5000$ may be required to maintain potentially adaptive genetic variation. Franklin and Frankham (1998) suggested that this number may be too high, largely because heritability may be lower than Franklin (1980) and Lande (1995) assumed. Lynch and Lande (1998) noted that the mutation rate for some traits (e.g., genes that may confer disease resistance) may be 1000-fold lower than for quantitative traits, making the numbers needed to maintain their variation 1000-fold higher.

Caution should be used in discussing N_e because important parameters—mutation rates, selection on new mutants, and N_e itself—are poorly understood in general and are unknown for Colorado River fishes. Also, the actual N_e may be a fraction of the total adult population. Frankham (1995) reviewed published estimates and suggested that N_e is only about 10% of the adult population size. Within-generation estimates of the ratio of N_e to adult numbers often appear higher than 0.10 (Vucetich et al. 1997), but for long-term maintenance of genetic variation, temporal variance in N_e should be included. In other words, to maintain genetic variation in a population with N_e of 500 would require a census population (N_c) size of approximately 5000 adults per generation. With N_e of 1000 (e.g., USFWS 2002a, 2002b, 2002c, 2002d), an adult N_c of approximately 10,000 would be required.

Large populations of the four endangered fishes were present in the lower Colorado River as late as the mid-20th century. Because generation time is long (4 to 8 years or more) and the age span of reproduction is large in all four species, there probably have been few recruitment failures where genetic variation could be lost to the succeeding generation. Thus, we expected extensive variation to remain in today's wild adults. One way to examine this is to explore the amounts of variation for molecular variants. An estimate of long-term N_e can be derived from mitochondrial DNA (mtDNA) sequence data (Garrigan et al. 2002), using a maximum likelihood approach. This method assumes, as above, that new sequence variants appear by mutation and are eliminated by genetic drift. For a given mutation rate and N_e, a sample of mtDNA sequences thus should exhibit an appropriate pattern of pairwise differences. However, these long-term estimates of the effective population size for a species throughout a substantial portion of its evolutionary history do not necessarily reflect the historical or recent effective population size. Other approaches can be used to estimate contemporary effective population size (Hedrick 2000), a topic we do not consider here.

Examination of mtDNA sequence variation in bonytail, humpback chub, and razorback sucker showed substantial variation (Garrigan et al. 2002): 5, 3, and 10 haplotypes were found in samples of 16, 18, and 49 individuals, respectively (table 3). In a sample of 16 bonytail, 4, 7, and 5 individuals exhibited three haplotypes: Zx, Zz, and Yy, respectively (figure 4b). Humpback chub and razorback sucker genealogies are similar in that rare haplotypes are most divergent and common haplotypes are closely related. Humpback chub and razorback sucker showed similar divergence over all sequences of about 1.5 nucleotides between all pairwise comparisons, while bonytail averaged 2.8 nucleotide differences.

Assuming a mutation rate of 2×10^{-8} per nucleotide, we can estimate the long-term female effective population size from these data (table 3). If population size is constant over evolutionary time, estimates are 97,500, 89,500, and 669,000 for humpback chub, bonytail, and razorback sucker, respectively. Overall effective population size should be about twice this value if sex ratios are equal. Taking population growth into account, estimates suggest bonytail has been declining and razorback sucker expanding in numbers over evolutionary time (table 3). Overall, this analysis suggests the three species historically existed in large numbers.

Although there is less genetic variation for bonytail, and estimates of effective population size are smallest for it, the

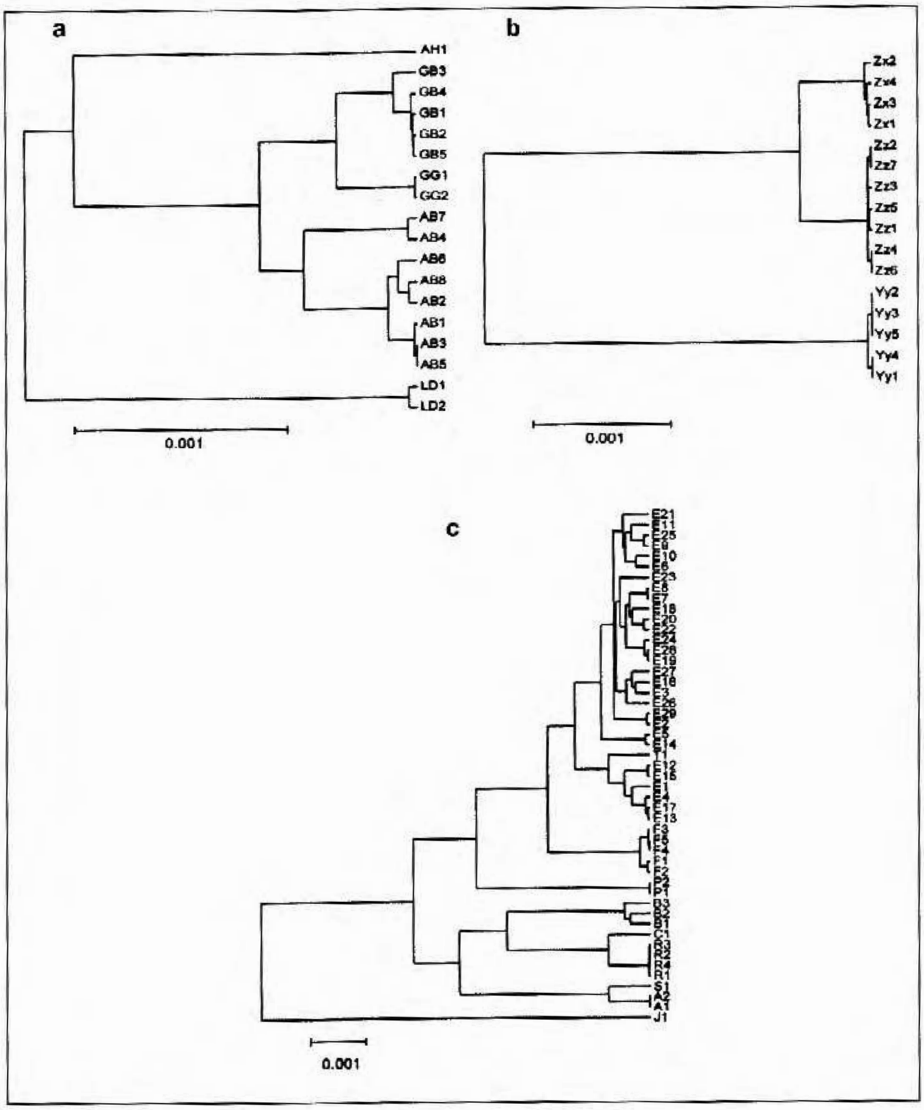

Figure 4. Coalescent genealogies that maximize the likelihood of the mitochondrial DNA data for (a) humpback chub, (b) bonytail, and (c) razorback sucker (from Garrigan et al. 2002). Branch lengths are scaled in terms of the number of substitutions per site. The letters on the tree branches represent the names of the haplotype, and numbers represent individuals with those sequences. The distance between identical sequences represents the time, in generations, since a common ancestor.

three remaining haplotypes are quite divergent; this suggests that present genetic variation still reflects a high degree of ancestral variation. Variation in the other three species remains even more intact. However, this variation will decay quickly if population sizes that define recovery are small and, more critically, if the population is founded or maintained by small numbers of brood fish. The Fish and Wildlife Service (USFWS 2002a, 2002b, 2002c, 2002d) proposed recovery goals of N_e = 700–5800 wild fish per species or river reach for big-river fishes in the upper Colorado basin. Recovery goals for downlisting and delisting include minimum census population sizes of 2100 adult humpback chub in each of 3 populations, 4400 bonytail in each of 4 populations, 5800 razorback sucker in each of 4 populations, and 700 (upper Colorado River) or 800 (San Juan River) plus 2600 (Green River) Colorado squawfish (USFWS 2002a, 2002b, 2002c, 2002d).

Brood stocks for razorback sucker, on which future stocking toward recovery is to be based, have been developed from as few as 5 and up to 25 paired matings using 5 males and 5 females (Minckley et al. 1991). Such low initial stocks are utterly inadequate and cannot be supported by any contemporary science. The goals proposed by USFWS are lower than any historical estimate of population size for bonytail, the species with the smallest estimated long-term N_e. These low numbers are especially disconcerting for the other taxa because far larger numbers, and thus far more genetic variability, can be readily maintained.

We strongly recommend circumventing the pitfalls of hatchery culture (Ryman et al. 1993, Hindar 1994, Dowling et al. 1996a), as this has already severely restricted the genetic variability of hatchery stocks and their progeny of bonytail (Hedrick et al. 2000) and razorback sucker (Dowling et al. 1996a). However, we recognize there are differences of opinion relative to the role of artificial propagation and growth from larvae into larger (juvenile or adult) life stages. Regardless of the mating strategy applied, the only genetic variation that can be passed to the future from a hatchery setting is that of the original brood fish. Despite uninformed protestations to the contrary, all possible combinations of 5 males and 5 females still provide the genetic variation of only 10 fish and are wholly inadequate for the recovery of lower Colorado River native fishes. If N_e is reduced, either naturally or through improper management, genetic variation is diminished and less new variation generated, potentially reducing fitness because of fixation of detrimental alleles. Such reductions in fitness when N_e declines appear to be a particularly severe problem in species with large ancestral populations and high historical genetic loads (Hedrick and Kalinowski 2000).

A far higher target for N_e must be set so all four endangered fishes may continue to evolve in a way resembling that of the past. Since substantial genetic variation remains, it is prudent to perpetuate it, and with a sufficiently large N_e (the larger the better) generation of novel variation will continue. Management should be under the most natural condition possible, emphasizing achievement and maintenance of species' carrying capacities in diverse habitats. The result will be increased opportunities for emergence of novel variation, thus maximizing adaptive potential.

Table 3. Estimates of mitochondrial DNA (mtDNA) variation in three Colorado River fishes, with maximum likelihood estimates of long-term effective female population size, N_e, if the population is assumed constant over evolutionary time. Also given is the estimate of N_e if the population is allowed to grow or contract over evolutionary time and the direction of that change (used with permission from Garrigan et al. 2002).

	Species		
Data and estimates	Humpback chub, Little Colorado	Bonytail, Lake Mohave	Razorback sucker, Lake Mohave
Data			
mtDNA gene	ND2	ND2	cytb
Number of nucleotides	790	763	311
Sample size	18	16	49
Number of haplotypes	5	3	10
Estimates			
N_e (constant size)	97,500	89,500	669,000
N_e (growth)	149,000	61,900	940,300
Growth	Stable	Declining	Expanding

Demographics. Because of their great reproductive potential, conservation of large-bodied, long-lived fishes differs fundamentally from conservation of large-bodied, long-lived terrestrial vertebrates. Unlike most dry land vertebrates, almost all fishes produce great numbers of gametes—10^4 to 10^6 ova per female are not unusual. Survival from egg to adult is, however, highly variable and typically low. Natural recruitment can be 0.01% or less. For razorback suckers living in communities with predatory nonnative fishes, recruitment failed for approximately 40 to 50 years because of the near-total loss of juveniles.

Thus, a declining fish fauna commonly remains individual-rich while becoming species-poor. This paradox, absent in most terrestrial vertebrates, presents a great advantage for the manager who can devise ways to exploit the high reproductive rate while still maintaining genetic variability. Each female razorback sucker bears an average of 1700 ova per cm standard length (SL), and average SL in Lake Mohave was approximately 50 cm in 1983–1984 (i.e., 85,000 ova per female; Minckley et al. 1991). A manager can consider this at two extremes, one from a simple view of production and the other incorporating genetic concerns. If they all survived, the progeny of a single large female would more than replace the entire population of approximately 73,500 adults estimated for Lake Mohave in the period 1980–1993. They would, however, all be siblings (or half siblings if more than a single male was involved), reducing genetic variation in a single event from high (Dowling et al. 1996b) to dangerously low. Alternatively, 0.005% survival (two young per female) of offspring produced by approximately 36,750 females (half the 1980–1993 N_c of adults in Lake Mohave) would also replace the whole population, at the same time preserving the existing genetic variation.

Natural conditions obviously fall between these extremes. Long-lived species frequently reproduce in alternate years or even less frequently, so numbers contributing each year to a next generation may be only a fraction of N_c (see above). However, even if relatively few fish spawn each year, asynchronous spawning across years means that, over a reproductive life of more than 35 years, most if not all adults may well contribute to future generations. To most closely mimic such natural reproductive processes, and thereby retain existing and promote novel genetic variation, management must aim for the largest possible panmictic population, perpetuated by the highest possible N_c.

How can such a large, genetically diverse population be achieved for endangered species inhabiting a highly modified river? Hatcheries are a poor choice because spatial constraints may excessively restrict genetic diversity within managed populations (e.g., Hedrick et al. 2000). Perpetuating these fishes requires exploiting both the reproductive potentials of the fishes themselves and the continuing strict regulation of the Colorado River. Below we outline a plan that is grounded in biology, hydrology, and engineering and involves relatively modest funding.

Off-channel habitats for conservation

Part of our proposal's rationale is to avoid competition with sport fishermen. Traditional off-channel angling areas such as backwaters and ponds behind levees cannot realistically be expropriated, so new habitats—exclusively for native species—must be provided. Costs are also a concern, so these habitats should be secure, simple, and low maintenance, and they should exclude nonnative predators while providing adequate physicochemical and other conditions for life history requirements of natives. We envision a series of excavated habitats (figure 5) resembling the pristine lower Colorado River floodplain—isolated oxbow lakes and backwaters—as primary components of dedicated off-channel complexes. A successful prototype has been developed on the USFWS Havasu National Wildlife Refuge at Beal Lake, Arizona.

Nonnative fishes can be excluded by passing water through size-graded gravel at inlets and outlets of excavated habitats. Proximity to the river will allow easy construction and maintenance access, shorten travel distances, and allow exploitation of gravity flow and high water tables. An elevation difference (head) between inflow and outflow is critical to promote current, to minimize water quality problems by exchanging water, and to avoid the cost and unreliability of pumps. A river bend would be ideal, shortened by dredging or other means and served by surface inflows and outflows in addition to groundwater (figure 5a, 5b). Other options include using more distant intakes (figure 5b, 5c), positioning habitats between canals, or integrating them with river-drain or canal-drain features (figure 5c, 5d). Single inlets and outlets for multiple habitats reduce construction costs.

Floodplain position is critical. A complex behind a levee is as well protected from invasion by nonnatives during floods as the structures and uses the levee was originally designed to protect are. If inside the floodplain, however, a complex must at least be protected from high flows. Multiple complexes need to be spaced along the river and other protection implemented to ensure against loss of all the complexes from a single catastrophe. Severe, uncontrolled flooding may destroy both protected and unprotected complexes, but the presence of adults in the river channel plus connectives precludes loss of whole species. Indeed, big-river fishes of the Colorado persisted through millennia that featured floods of greater volume than the controlled river can produce today.

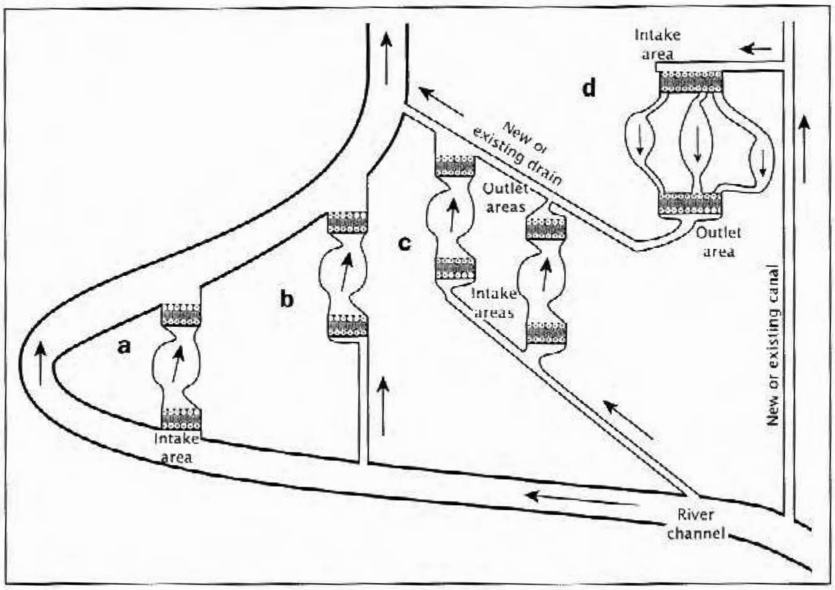

Figure 5. Some potential arrangements for hypothetical lower Colorado River off-channel habitats.

Drying of off-channel habitats during low flow or water outage is a concern that can be circumvented by ensuring that the bottom is below the water table. Arranging complexes from upstream to downstream will also benefit management by reducing transport distances and assuring a diversity of habitats for adult fish.

Land ownership and topography (fewer sites exist in canyons) also control placement, number of habitats per complex (e.g., figure 5), and number of complexes. Areas already reserved for state and federal use, either undeveloped or within existing wildlife refuges, are obvious choices. Deeded and Native American property may also be leased or purchased.

Because large numbers of fish are required, we recommend a habitat configuration avoiding as many problems in harvest as possible. Decisions must be made a priori on methods, extent, and season of harvest; access, holding, and transport of fish; and agency responsibility, gear limitations, and manpower. Other major questions include how much area per habitat, how many habitats per complex, and how many complexes are needed.

Habitat size should be a function of ease of control of nonnatives, which are certain to appear. Thus a complex would be better if it had a number of small units rather than a single large one. We recommend no fixed size, but 1 to 2 hectares (ha), or 2.5 to 5 acres, per habitat seems optimal. We judge that less than a hectare would be too small to provide the diversity and productivity that is required to simultaneously accommodate adults, larvae, and fast-growing juveniles of one species, or all life stages of multispecies populations, if such are developed. Habitats tens of hectares in size or larger are too large to harvest and too large for efficient water exchange (local conditions become lentic and thus more susceptible to problems of high temperature, oxygen depletion, and other physicochemical extremes) or for manipulations such as complete renovation (fish removal). We favor elongate, narrow shapes to promote uniform water passage, and a depth that inhibits rooted aquatic plants. Habitat heterogeneity (e.g., lotic [near intakes, outlets, or both] to lentic; shallow to deep; gravel to silt or sand [natural] substrate) may be spatially or temporally manipulated as desired. Ten complexes seem a reasonable goal. The number of off-channel habitats per complex depends on availability of land, security, and other factors and can vary from one to many. Answering the question of how many are needed depends on the numbers of fish desired.

Population goals

We do not quantify the numbers of fishes required to satisfy level III or above of the conceptual plan for managing lower Colorado basin native fishes (i.e., population stabilization, expansion, and recovery; figure 3, USFWS 1996), but we provide examples to support our proposal. We are convinced that large populations and high genetic diversity are the only sound biological options for all four species, and these are feasible and sustainable through dedicated management. Even a modest effort using off-channel habitats will yield populations far exceeding the meager 700 to 5800 individuals proposed by USFWS (2002a, 2002b, 2002c, 2002d). We advocate and describe means of producing and rearing recruits in isolated habitats for introduction en masse into the channel plus connectives to establish and maintain a large, genetically diverse, panmictic population that closes the circle by supplying brood fish for ongoing production in isolation (figure 6).

When recovery efforts were begun, the abundance of predatory, nonnative species in the lower river made realizing these goals seem highly unlikely. Recruitment failure was poorly understood, so millions of larval razorback suckers per year were cultured in hatcheries for stocking in southern Arizona (Inslee 1982, Hamman 1987), with essentially no success (Minckley et al. 1991, Hendrickson 1993). Stocking juvenile, hatchery-reared razorback suckers at somewhat larger sizes yielded the same result (Langhorst 1989, Marsh and Brooks 1989). Data for bonytail were similar. Each year, Lake Mohave brood fish produced bonytail progeny in 0.04-hectare (0.1 acre) hatchery ponds, but approximately 200,000 fish that were repatriated between 1981 and 1990 essentially disappeared. Survival, although detected, was low (< 0.001%); the total length of these fish at the time they were stocked rarely exceeded 10 cm.

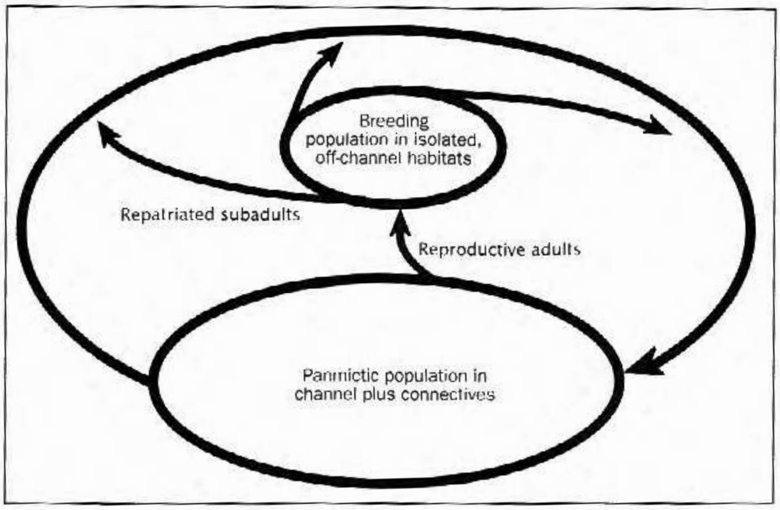

Figure 6. Schematic interrelations between lower Colorado River off-channel habitats and channel plus connectives.

When predation on larvae and juveniles was identified as the limiting factor (Minckley 1983, 1991), effort was shifted to circumventing its impacts (Minckley et al. 1991, Pacey and Marsh 2003). Few problems existed with adults. Large individuals of all four taxa persisted under diverse conditions where nonnatives were common, and all but humpback chub were known to successfully reproduce in farm ponds, under hatchery conditions, and elsewhere (Marsh and Pacey 2003). To speed the process for the razorback sucker, by then beginning its decline, we captured wild larvae directly from Lake Mohave, reared them in isolation from predators, and repatriated subadults back to the reservoir. In 1993–1995, stocking razorback sucker in small (0.05 to 0.17 ha, averaging 0.13 ha), predator-free habitats resulted in an average survival rate of 22% (0% to 81%) from larva to subadult. As noted before, repatriates entered the breeding population 2 years after the program was begun, and in 1999 they constituted approximately 12% of the reproductive adults. Hatchery-cultured larval and juvenile bonytail were added, grew well, and were also repatriated (table 4) with lesser success.

On the basis of a model created in part from these observations, managing 100 ha with 50 females per ha yielding 10 young per female provides 50,000 subadults per year for transfer to the channel plus connectives. If 5% survived the first year after repatriation and 80% survived each succeeding year of freedom, and if the same production–transfer rates continued, approximately 54,500 adults would theoretically be present in the channel plus connectives after 5 years. N_c would stabilize at approximately 60,000 adults in about 20 years (in our model, adults are programmed to die at 35 years of age). In a second example, if a goal was 5% of the N_e estimated to produce today's genetic legacy for razorback sucker (about 1,000,000 females; table 3), 50 females per ha, an average of 10 progeny per female per year, and 250 off-channel hectares might approach that figure. Under the last scenario, 125,000 juveniles would be available annually for transfer, and at survival of 5% the first year and 80% thereafter, a N_c of approximately 139,000 adults would exist in the channel plus connectives at the end of 5 years; N_c would stabilize at approximately 20 years with close to 150,000 fish (approximately 50% female).

Unknowns. We have insufficient data to quantify the relationship of N_c and N_e, and because each female produces a vast surplus of ova, gross production of progeny may be only indirectly related. Demographic data from radiotelemetry studies and genetic data from an experiment examining production of razorback sucker progeny using mtDNA analysis independently suggest that individual razorback sucker females may not spawn every year.

However, available survival estimates include only part of the life cycle and do not include most of the survival components for breeding adults. To properly measure N_e from

Table 4. Numbers of bonytail repatriated to Lake Mohave from natural reproduction in ponds at US Fish and Wildlife Service Dexter National Fish Hatchery, New Mexico, 1981–1997.

Years	Number of fish	Total length (millimeters)		
		Average	Maximum	Minimum
1981	26,817	102[a]	—	—
1981–1982	14,700	102	—	—
1985	12,618	102	—	—
1987–1988	34,011	140	—	—
1988–1989	15,540	102	—	—
1989–1990	44,678	90	—	—
1990–1991	9,283	102	—	—
1991–1992	6,617	72	—	—
1992–1993	17	167	259	95
1993–1994	7	243	265	227
1994–1995	12,507	105	322	101
1995–1996	131	308	368	154
1996–1997	784	279	420	225

a. 102 mm = "fingerling" size; other data are actual measurements.

generation to generation, one needs information at the same life stage (e.g., adult breeders) to encompass all factors that influence it. Nonetheless, if 33% of female razorback suckers contribute progeny each year, N_c of the 150,000 fish would very likely exceed the stated goal of 5% (50,000) of the ancestral 1,000,000 fish. The annual yield of 10 progeny per female in our model may be too conservative, but it was held at that level because of the uncertainties regarding N_p and concerns about production and harvest discussed below.

We address these unknowns directly by promoting large, panmictic populations in the channel plus connectives, from which brood fish may be drawn. Doubling the number of hectares, females, or young per female in our model results in an order-of-magnitude change in estimated production. However, unlike these parameters (some of which, such as area dedicated for off-channel habitat, can be costly), altered survivorship results in logarithmic adjustments in population size. An increase from 5% to 15% in first-year survival of repatriates, for example, results in an estimated 40% increase in N_c in the channel plus connectives, from approximately 54,000 to 85,000 and 150,000 to 210,000 at 5 and 20 years, respectively, in the examples given above. Increased survivorship, with a reduction in investment in the number of isolated habitats, brood fish, and other necessities, is thus the way to succeed.

Completing the cycle. Step-like relationships exist between body size of repatriates at the time of release and their survival in both rivers and reservoirs (figure 7). Thus, the young should be nurtured toward the largest possible body size before they are transferred to the river. Given the major role of size-dependent predation in limiting reestablishment of Colorado River fishes, transferring a few large (i.e., > 35 cm TL) individuals is far more productive than repatriating many smaller fish that would be devoured by predatory nonnative fishes.

At moderate densities in lower-basin waters, young razorback suckers can reach more than 30 cm and bonytail more than 25 cm TL in the first year of life. By their second year, they commonly reach 45 cm and 30 or more cm TL, respectively. These growth rates allow for annual or biannual harvesting. Growth rates of repatriates in Lake Mohave are similar, and substantial growth continues with increasing age (figure 8). As demonstrated by survival of repatriates (figures 7 and 9), and in view of undetectable adult mortality inferred from long-term catch-per-unit efforts in Lake Mohave between the 1970s and the onset of population collapse in the late 1980s (Pacey and Marsh 2003), razorback sucker of approximately 30 cm TL and longer are essentially immune to existing predators. First-year survival of approximately 5% for repatriates in the wild increases to approximately 80% in subsequent years (figure 7, top graph), corresponding roughly to increases in average TL from 30 to 35 cm at repatriation to 45 cm 2 to 3 years later (figure 9). These trends should apply as well for Colorado squawfish, although that species has a slower growth rate than razorback sucker

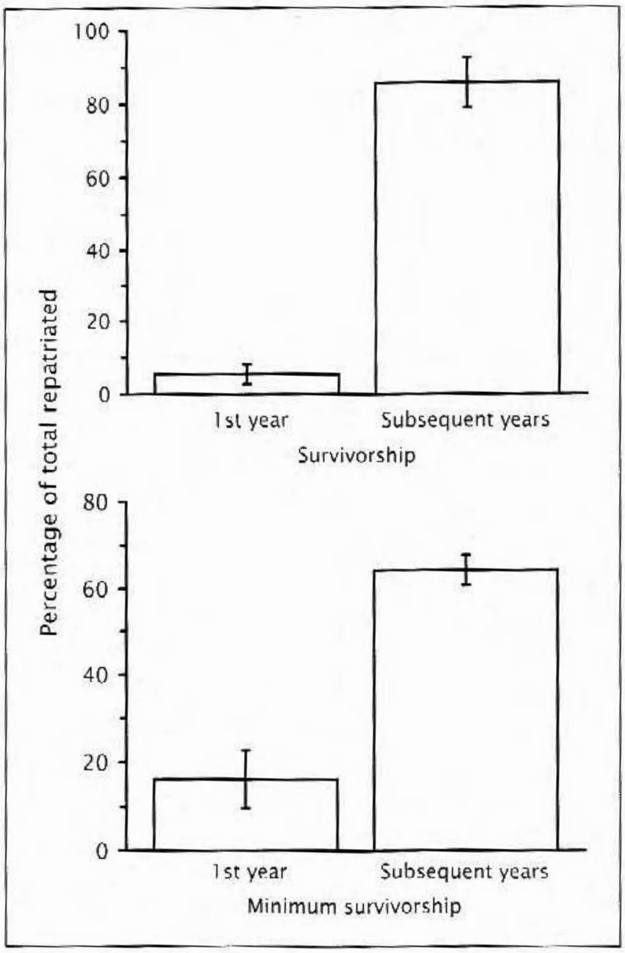

Figure 7. Estimated survival of repatriated subadult razorback suckers in Lake Mohave (Arizona and Nevada) and San Juan River (New Mexico and Utah) that is based only on fish greater than 29 centimeters total length at time of stocking. The top graph is based on raw data, with no assumptions applied. The bottom graph is based on the assumption that no individual is recaptured twice; as a result, all fish captured once are theoretically lost from the population.

(Minckley et al. 1991, Osmundson et al. 1997). Chub, which more rarely exceed 35 to 40 cm TL as adults, may or may not be more vulnerable to such size-structured predation. Whatever the case, young should be nurtured toward harvest and repatriation at the largest possible body size.

In practice, time of transfer from off-channel habitats is controlled by growth, which is partially a function of population size, which in turn is related to recruitment. Harvest and transfer should be balanced with production of appropriate-sized fish, but care must be exercised not to allow off-channel populations (brood fish plus progeny) to exceed carrying capacity, which would cause stunting. Potential deleterious impacts on off-channel populations, such as parasitism, can be avoided by maintaining relatively low-density, highly productive stocks by appropriate harvest and translocation to the channel plus connectives. Monitoring for parasites, other pathogens, and heavy metals or other contaminants may be incorporated into management protocols as part of the harvest–transfer protocol. If a problem is detected, harvest should be increased, though transferring small fish to the channel plus connectives should not be expected to do much more than provide supplemental rations for nonnative predators.

To maintain high turnover in parentage, sexually mature repatriates should regularly be transferred back into off-channel habitats. Males reach maturity in 2 to 3 years and females in 3 to 4 years (Minckley et al. 1991). Replacing 10% of breeding female razorback suckers in off-channel habitats each year results essentially in a complete turnover each decade, which is slightly longer than an estimated generation time of ± 7 years.

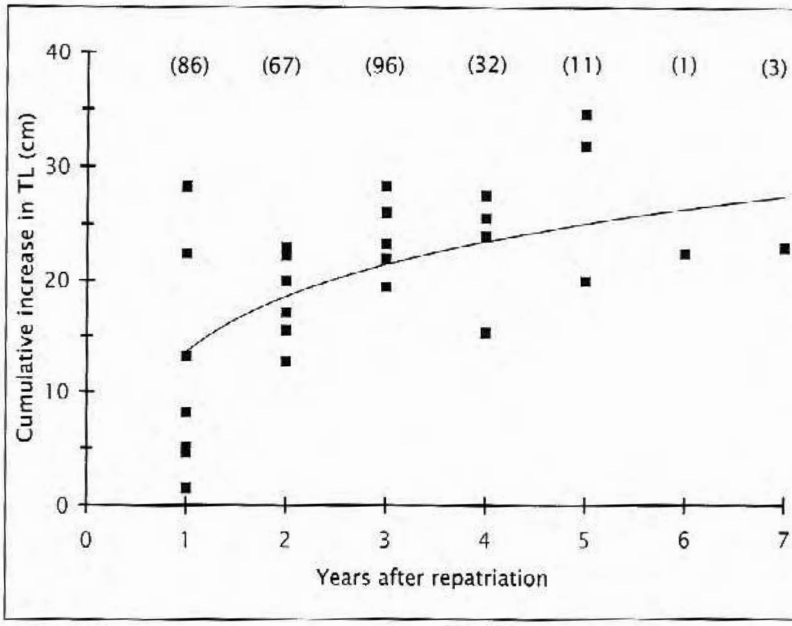

Figure 8. Growth of cohorts in centimeters (cm) total length (TL) of repatriated razorback suckers in Lake Mohave, Arizona and Nevada, based on recaptures of individual fish. Total numbers of fishes in all cohorts for a given year are in parentheses.

Accommodations for harvest. Other practical problems center on physical capture and transfer of fish from isolated backwaters for repatriation and of new brood fish from the channel plus connectives back into off-channel habitats to turn over the parental pool. It would be gratifying to produce, for example, 25,000 or 100,000 fish of appropriate size in isolated backwaters for repatriation, or 40,500 or 162,000 adults in the channel plus connectives after 10 years, but such goals have the potential to be a logistic nightmare involving harvest and transfer. On the other hand, complexities of fish capture, transport, and handling are all surmountable. If serious management is built into water-use infrastructure, a full-time crew with appropriate equipment, training, and incentives can move large numbers of fish, as proved by successful commercial fisheries of the past. All four native big-river species in the lower basin are vulnerable to capture, recapture, or other manipulations, in part because of existing knowledge from studies of these species' movements, their habitat use, and other aspects of their biology.

Some harvest priorities, such as habitat morphology, may compete with biological requirements. Such conflicts can be resolved using a cost–benefit perspective. Whatever resolution is reached, harvest methods should stress mass collection. Thus, large, smooth-bottomed areas with no obstructions, relative shallowness, and appropriate landing areas should be designed for seining. Both razorback sucker and bonytail may show extensive seasonal movement, so movable traps or fixed weirs can be deployed effectively. Electrofishing is especially efficient for subadult and adult Colorado squawfish (Tyus 1991), as are entanglement devices such as gill and trammel nets when used by trained personnel. Summer air and water temperatures and chemical conditions can result in elevated mortality, so harvesting should be concentrated in cooler seasons.

Conflict resolution. Adult native fishes in the channel plus connectives are not likely to affect nonnative sport fisheries. The magnitude of ecological saturation by nonnative species in the river channel plus connectives is, however, unknown. If the channel plus connectives are at carrying capacity, food and other resources may be in short supply, and survival of adult natives may suffer. It may thus be necessary to limit the numbers of nonnative fishes to maintain natives at desired densities. Increased public angling pressure might be encouraged, locally at least, to reduce population sizes of nonnatives, as is being explored in the upper basin (Tyus and Saunders 1996).

The success of such efforts can be enhanced by education and by liberalizing angling regulations to ensure sufficient provisions for natives. Options should be kept open for other action, including direct control of nonnatives, especially as future system modifications for water use reduce the quantity and quality of main channel plus connective habitat. For example, if water intakes for Las Vegas and coastal California cities were moved upriver, the reduced discharge below Lake Mead would alter downstream conditions dramatically.

Because of actual or perceived liability under the ESA, we expect reluctance on the part of water purveyors to accept the presence of large numbers of listed fishes associated with their commodities or facilities developed for water distribution and use. Sport-fish managers will also resist changes that reduce the catch. Further, and from the other side of the issue, strict adherence to ESA's "take" stipulations for listed fishes in the channel plus connectives may, in fact, need relaxation to apply, assess, and adjust management strategies to ensure their success.

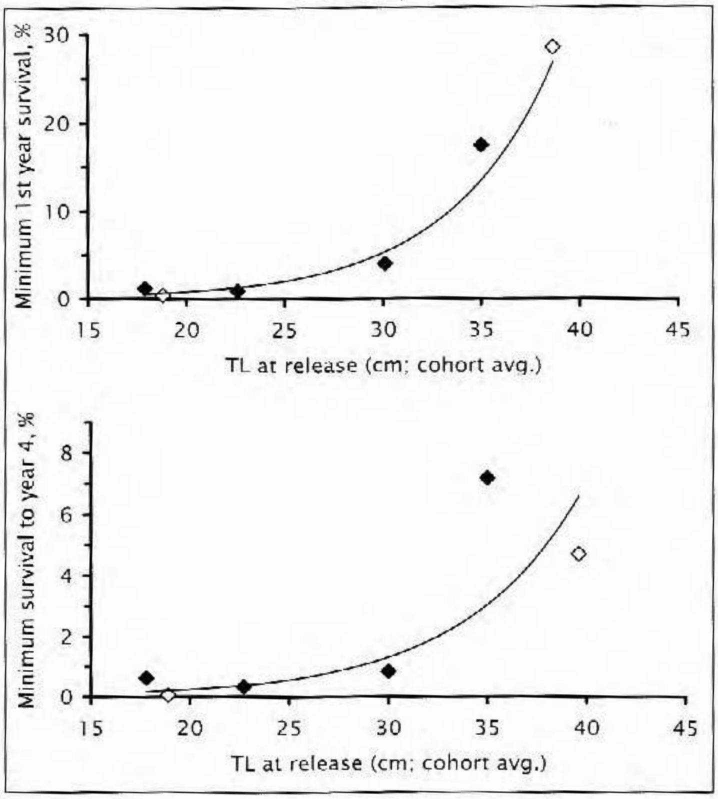

Figure 9. Relationships between the average cohort total length (TL) at repatriation (release) and recapture (survival) of subadult razorback suckers in Lake Mohave, Arizona and Nevada (darkened diamonds), and the San Juan River, New Mexico and Utah (open diamonds), based on cohorts of more than 100 individuals. The top graph displays the minimum first-year survival; the bottom graph, the minimum survival to the fourth year after release.

Benefits to native fishes must be a specified target in any future endeavors on the lower Colorado River; otherwise the fishes will disappear. System upkeep and repair, sport-fish management, alterations that may influence listed fishes and their habitats, and other manipulations are the concerns of the various agencies already involved. Enforcement of closures for security, questions of beneficial use of water, legal concerns over water apportionment, concern for evaporation from new water surfaces, and other issues will also need consideration.

Our greatest concern is that nonnatives may become established in places dedicated to native fish production. It is unreasonable to expect off-channel, isolated habitats to entirely avoid vandalism or inadvertent addition of nonnatives. Education and information programs for boaters, anglers, and others will be essential. Nonetheless, contamination will predictably occur, necessitating renovation and reestablishment of native populations. This might be achieved by regularly destroying and reconstructing habitat, introducing a surrogate for natural processes of channel realignment, aggradation (oxbow filling), and degradation (scour).

Conclusion

Ongoing programs to manage native fishes in the lower Colorado River focus on individual species and are largely without benefit of an overall plan. Their ultimate contributions to recovery are unknown. At best, fulfillment of the major commitment to native fishes envisioned by developers of a lower river recovery implementation program waits in the distant future. Nonetheless, genetic and demographic conditions of the native resources are inarguably worse today than a decade or two ago, and certainly they are worse than at the time of target species' respective listings as endangered. Further deterioration seems inevitable unless innovative management scenarios are developed and implemented in the near term.

We offer a practical plan for management of lower Colorado River native fishes that is biologically sound, fiscally responsible, and considerate of potentially conflicting resource uses. The plan incorporates state-of-the-art information from conservation genetics and population dynamics arenas and offers a realistic mechanism by which to ensure the continued presence of healthy populations of native fishes in the lower river ecosystem. Proactive decisions and fund allocations by bureaucrats, coupled with aggressive implementation by fisheries managers, are all that is required to realize the full benefits of the plan. What may well be missing is the political will to carry it out.

Acknowledgments

The US Fish and Wildlife Service, Region 2, convened a scientific work group (SWG) in 1999 to draft a plan for management of endangered fishes in the lower Colorado River. This article is one outcome of that process. The members, technical advisors, and support group of the SWG included the following people, in addition to the authors: from the US Bureau of Reclamation, Thomas Burke and Glen Gould; from the Nevada Department of Wildlife, Jon Sjoberg, Mark Warren, and Gene Weller; from the US Fish and Wildlife Service, Chester Figiel, Lesley Fitzpatrick, Owen Gorman, Stuart Leon, Cynthia Martinez, C. O. Minckley, Sam Spiller, Pete Stine, Manual Ulibarri, and Robert Williams; from the California Fish and Game Department, Chris Hayes; from the Arizona Game and Fish Department, Rob Bettaso, Tom Liles, and Kirk Young; and from the New Mexico Department of Game and Fish, David Propst.

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