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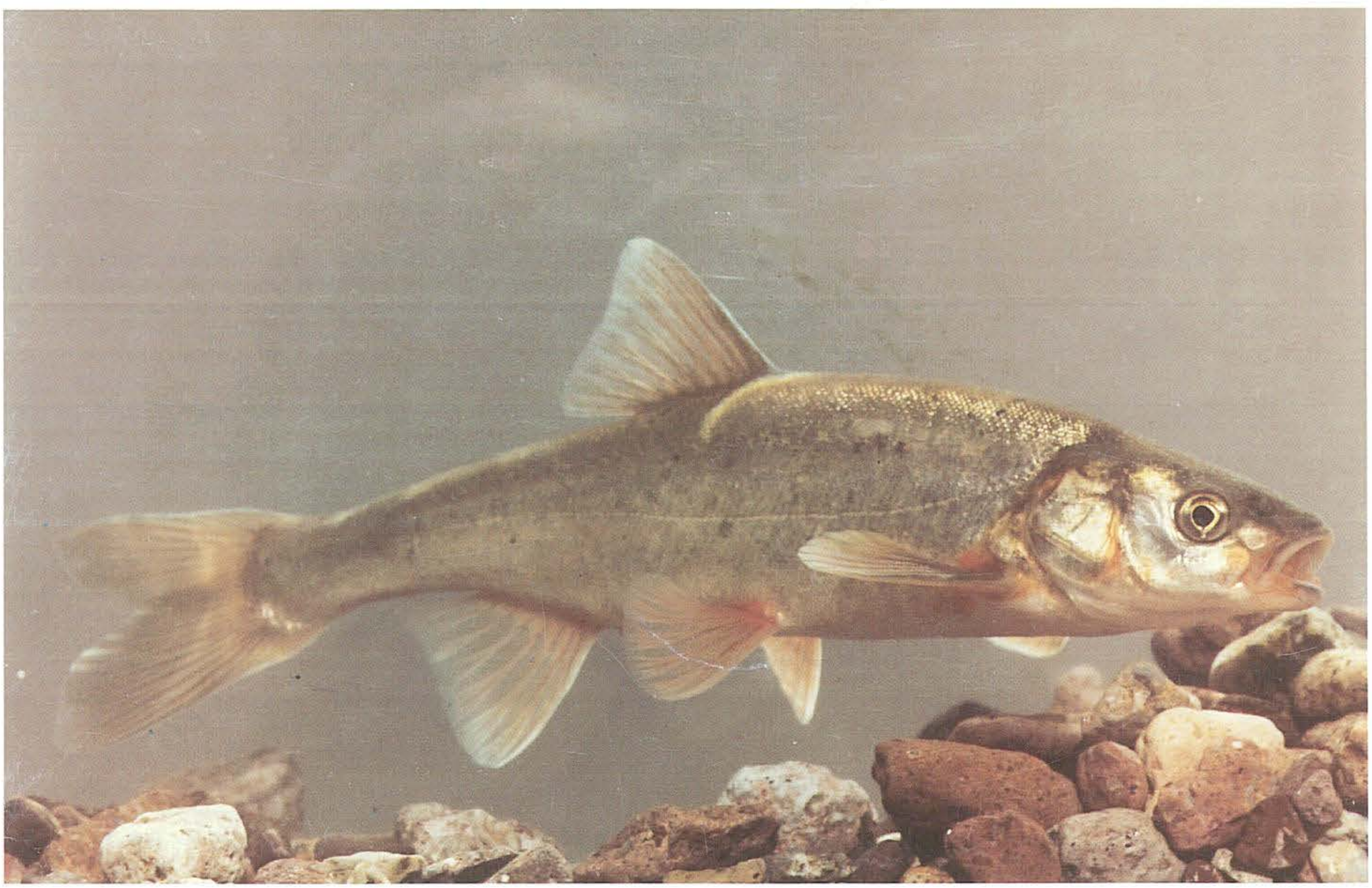
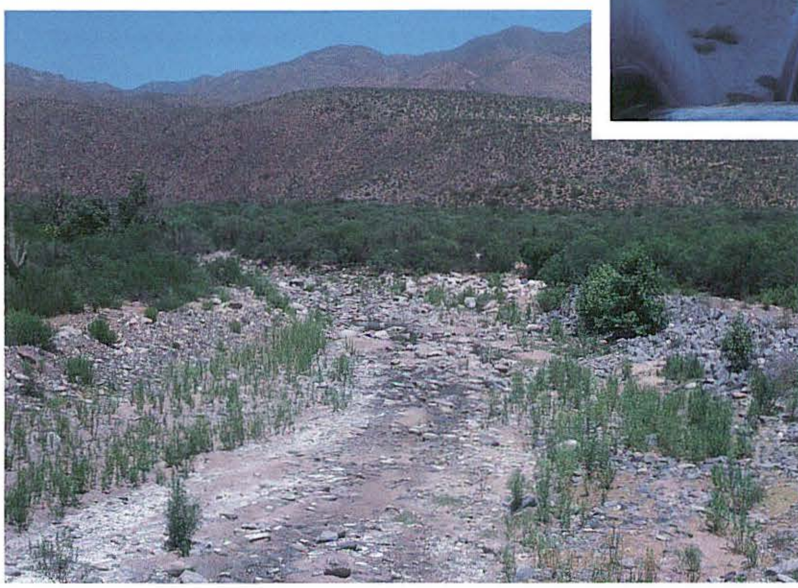
**General Technical
Report RM-206**

Native Fishes of Arid Lands:

A Dwindling Resource of the Desert Southwest





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Includes color photos of 44 species of fishes, many published for the first time. Text describes aquatic systems in the mountains and deserts of the Southwest, the unique fishes they support, and habitats the fishes need.

Front cover: Roundtail chub.

Back cover: Aravaipa Creek, one of the best examples of native fish habitat remaining in Arizona.

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General Technical Report RM-206

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Native Fishes of Arid Lands: A Dwindling Resource of the Desert Southwest

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Preface

Native freshwater fishes of the desert Southwest are disappearing. Fishes obviously require water, scarce in the past in this vast arid zone, and even more so now with burgeoning human populations. As a result, this relatively small, special group of animals has fallen on hard times.

Native freshwater fishes have received little attention from resource managers, or for that matter the public, simply because they tend to be unfamiliar. Most people do not recognize the differences between different species of fishes, or even that different species of certain groups exist. Common names are confusing in fishes, since the term "minnow" means a little fish to almost anyone, and "sucker" is often used in a derogatory sense, referring to a species that feeds on other than "healthy" foods accumulated on the bottom. Actually, both minnows and suckers are each separate families, the Cyprinidae and Catostomidae, that make up a large proportion of the fishes native to western North America. Some minnows get big, and most suckers feed on live foods such as algae and mayflies, just like other stream fishes.

Recognizing the problems of unfamiliarity and difficulties of identification, Rinne began to accumulate photographs of native fishes in the 1970s. Efforts included development of a special chamber where fish could be kept alive and well during photography, and emphasis was on natural colors of living individuals, to illustrate how these animals actually look in nature. Photographs were chosen to illustrate not only their various body shapes, but also their functional features such as breeding color and morphologic variation—some of the more dynamic aspects of their existence. As permitted by other assignments, he traveled to obtain photographs throughout southwestern United States and northwestern Mexico. Acceptable photographs accumulated slowly. Some were published elsewhere to further other research efforts; others appear here for the first time. The present report includes photographs of 46 species of fishes, some of the places in which they live, and of some past and present conditions of regional aquatic habitats.

The text by Minckley draws upon his experience of more than 30 years of research on desert aquatic systems and fishes. It emphasizes historic aspects of rivers and springs in the West—where they are, when they formed, and how they work. Treatments of fishes include comments on life-history traits, species uniqueness, and historic and present values, along with their roles in natural aquatic communities.

The goal is to advertise these unique, threatened and endangered fishes, and try to increase public awareness of their plight. Knowledge of how these animals look and live, along with general information on their status, may contribute to their perpetuation. A list of technical literature on fishes of the region, their basic biology, and the imperiled status of the entire aquatic fauna is provided as Appendix I.

Use of terms that refer to the conservation status of various species follows that of the International Committee on Endangered Species of the American Fisheries Society. "Endangered" fishes are those in danger of extinction throughout all or a significant portion of their ranges. "Threatened" species are likely to be endangered within the foreseeable future. Fishes of "special concern" may become threatened or endangered by minor disturbances, or those which require additional information to determine their status. Scientific names are not included in text or figure captions in an attempt to make the presentation more readable. Both common and scientific names of fishes mentioned in text are provided in Appendix II.

Acknowledgments

Permits for collecting, photographing, and otherwise dealing with native western fishes were granted by the States of Arizona, Nevada, and New Mexico, and for threatened and endangered species, by the U.S. Fish and Wildlife Service. Work in Mexico was under permits issued through the courtesy of the Mexican government. The Defenders of Wildlife and Nature Conservancy were especially helpful in allowing access to the Aravaipa Canyon Preserve. Uncredited photographs were taken specifically for this work. Photographs provided by others—B. D. DeMarais, S. G. Fisher, D. A. and J. R. Hendrickson, B. L. Jensen, J. E. Johnson, W. G. Kepner, G. C. Kobetich, G. Mueller, R. D. Ohmart, R. Todd, and the U.S. Bureau of Reclamation—are credited in the figure captions; Figure 63 is reproduced by permission from Arizona Game and Fish Department. Forest Service personnel who provided able and substantial assistance with the project included Marty Jakle and Scott Belfit. Many others helped, and all are due our thanks.

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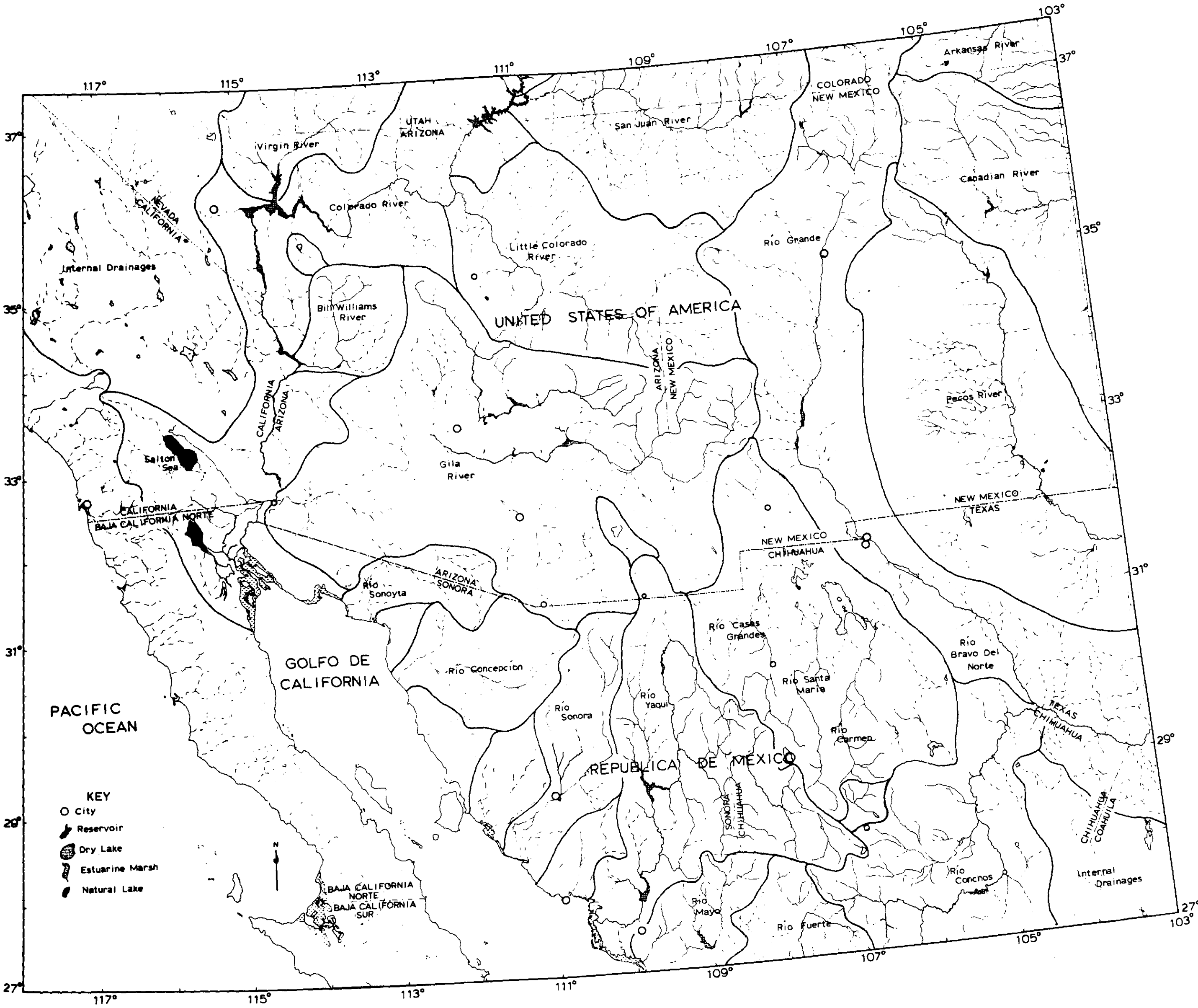


Figure 1. The region termed the American Southwest encompasses parts or all of the Mexican states of Baja California Norte, Baja California Sur, Chihuahua, Coahuila, and Sonora, and Arizona, California, Colorado, Texas, New Mexico, Nevada, and Utah in the United States.

Native Fishes in Arid Lands: A Dwindling Resource of the Desert Southwest

Photographs by John N. Rinne

Text by W. L. Minckley

INTRODUCTION

The American Southwest is usually defined to include all or part of 12 States in western United States and Mexico (Fig. 1), much of which is lowland desert interrupted and diversified by isolated mountains and plateaus. Evaporation exceeds precipitation so greatly that surface water should theoretically not exist. Nonetheless, major rivers such as the Colorado and Yaqui formerly collected sufficient water to flow all the way through the arid lowlands to the sea.

Just a few decades ago, western streams swarmed with fishes that had survived millennia of remarkable geologic and climatic changes. They had adapted to survive the special conditions in canyon-bound rivers that varied from raging torrents in flood to isolated pools in drought. Some had specialized to withstand high summer temperatures and salts concentrated by evaporation in desert lakes and marshes. However, when technological humans moved in droves to the warm, arid region, native fishes began to disappear. Humans need lots of water too, and typically far more than required to support native fishes.

Early diversions for mineral and cattle production and irrigated agriculture were followed by giant mainstream dams that not only stored and controlled runoff, but produced electricity as well. This abundant source of power led to expansion of industry, and to retirement communities, recreation, and more urbanization—the "Sun Belt" enterprises of today. All these demand water for drinking, watering lawns and golf courses, and other uses—as well as for more and more electrical power.

As a result, native fishes are being exterminated. Destruction of aquatic habitats, changes from natural to artificial conditions, and predation and competition by alien species enhanced by artificial conditions, all combine to destroy them. Many are nearing extinction, some are already gone, and neither legislation, nor determined attempts at conservation by agency, academic, and other managers has succeeded in reversing the trend. The only chance seems to lie in an emergence of public opinion that recognizes native fishes as valuable resources and demands their conservation.

THE SETTING

Elevations in the region vary from sea level to more than 3600 m. Precipitation is equally variable, averaging less than 5.0 cm per year in the most severe desert, to more than 128 cm at the higher elevations. Most of the vegetation zones of North America are represented, from patches of tundra on the highest peaks, downhill through extensive conifer forests then woodlands and grasslands, to end with desertscrub on the basin floors.

The region is also hydrologically complex. Most major drainage basins are composites of once-independent systems brought together by crustal movements or volcanic activity. Most of the Sonoran Desert region, emphasized here, is characterized by through-flowing rivers passing from mountains to the sea. Closed basins (Fig. 2), from which water escapes only through evaporation or seepage, are common in the Mohave, Great Basin, and Chihuahuan deserts. Coverage is restricted to watersheds west of the Continental Divide, which ultimately drain to the Pacific Ocean through the Colorado River, Rio Yaqui, and lesser streams between those two major basins (Fig. 1).

Origins of the Desertlands

Desert conditions are new, in geologic time, to much of this area. Studies of fossil plants and animals have convincingly demonstrated that only a few thousand years ago woodlands and prairies flourished where desert now exists. Because trees and grasses require more water than cacti and shrubs, available precipitation and runoff were either greater in amount, far different in distribution throughout the year, or both. Cycles of drying alternating with periods of substantial moisture have progressed toward more and more frequent and severe drought. The region is now more arid than ever before.

Over a longer time scale, complex geologic activity shaped the land surface to help set the stage for development of southwestern deserts. The coastlines of Mexico and California slid northwest along the San Andreas and related faults in response to

Figure 2. Left: The Willcox Playa, Arizona, was flooded to form this broad, shallow lake following extensive rainfall in 1983 (photo by R. Todd). In even wetter times, the closed Willcox basin was occupied by pluvial Lake Cochise. Right: In periods of drought, extensive closed-basin lakes quickly dry into a sea of salt and sand, such as in this playa in Death Valley, California, 1972.

interactions among plates in the earth's crust. Opening of the Gulf of California was part of this tectonic pattern. Inland, east-to-west stretching of the land surface in Miocene (~20 to 5.0 million years ago) fractured an ancient almost-level terrain into northwest-southeast-trending mountains and parallel valleys.

Rivers with large enough watersheds cut deep canyons through rising plateaus and mountain blocks. Others were diverted by uplifting mountain ranges. Huge lakes, represented today by dry playas and a few remnants such as Great Salt Lake, were formed in closed basins. Their waters rose and fell, filling followed by episodic drying, refilling, and spilling over their rims to connect with other lakes, rivers, or the sea. In Pliocene and Pleistocene (5.0 to ~2.0 and after ~2.0 million years ago, respectively), mountain glaciers came and went on the highest peaks, reflecting colder, wetter conditions than today and corresponding with alternating pulses of continental glaciation in the north.

Plio-Pleistocene uplift of the Sierra Nevada and other mountain ranges of California resulted in permanent climatic change when they rose high enough to intercept the eastward flow of Pacific moisture. Water falling on their western slopes ran back to the sea, and only dry air passed downslope to the inland basins and plateaus. Persistent aridity was thus assured. Even drier conditions were induced in the Sonoran Desert by formation of permanent cells of high atmospheric pressure, caused by descent of high-altitude air to the earth's surface. The descending air lacks humidity because of its origin at cold, polar latitudes, so little water is available to condense to precipitation. In addition, as happens to air flowing down a mountain, descent from high altitude results in compressional heating, and the hot dry air removes even more water from land surfaces.

Water, Aquatic Habitats, and the Impacts of Humans

Essentially the only water available to this vast, arid region originates on mountains high above the desert floors. The highlands intercept movement of air masses, forcing them upward to cool and condense their sparse humidities into precipitation. Winter snowpacks accumulate, melt in spring, and seep into shallow soils or form overland rivulets. Seeps and rivulets combine to form brooks which emerge from the mountain fronts. Water in such channels mostly percolates into the coarse-grained valley floors, where protected from evaporation it is stored or continues on a subsurface path to the sea.

Only channels with substantial montane watersheds support perennial streams. The Colorado River itself originates in the Rocky Mountains to flow through Great Basin and Mohave deserts to enter the Gulf of California surrounded by Sonoran Desert. The Gila River, most southern major

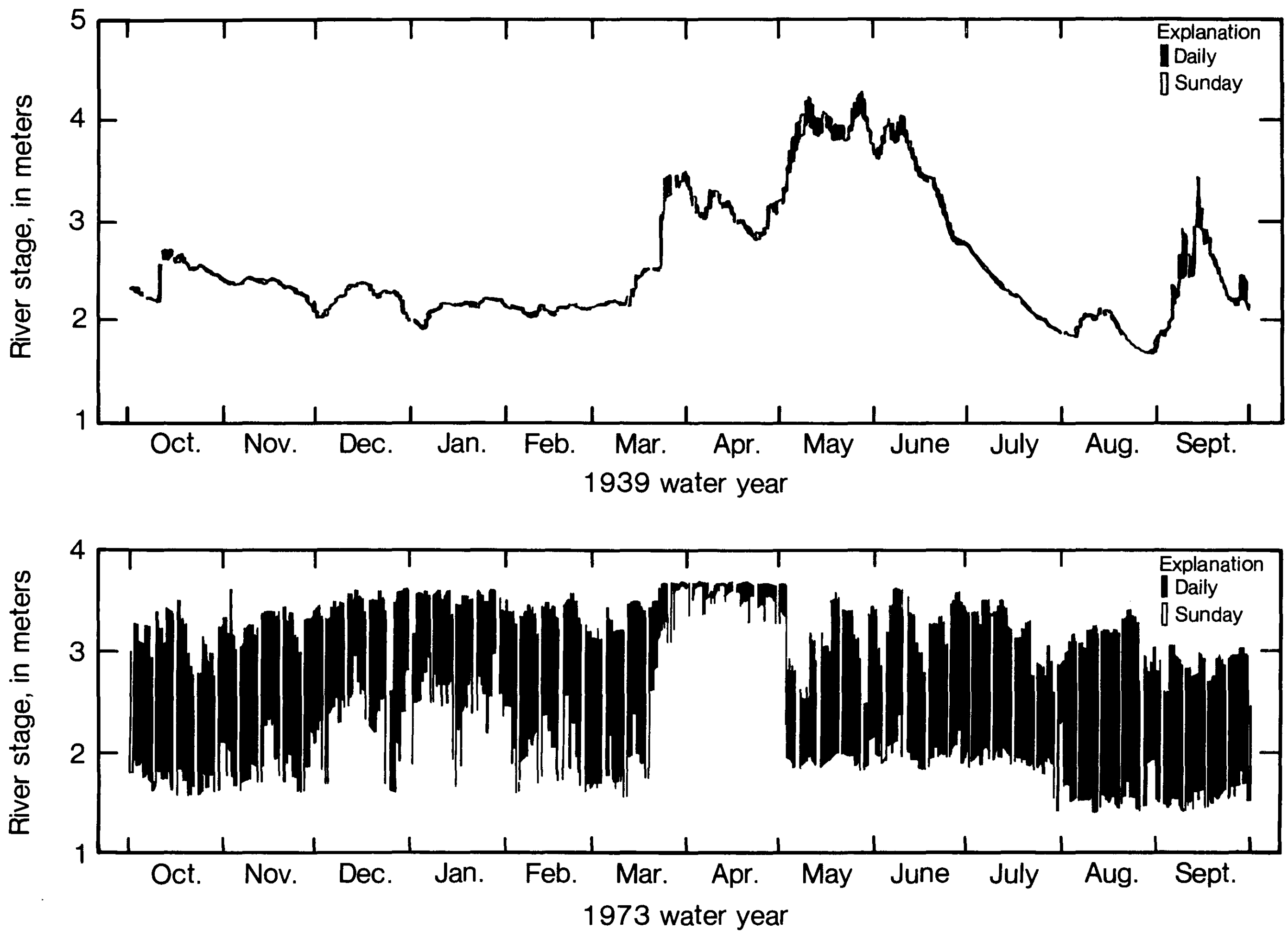


Figure 3. Pre- and post-impoundment patterns of discharge in the Colorado River mainstream in Grand Canyon, downstream from Glen Canyon Dam.

tributary to the Colorado (Fig. 1), originates in highlands of Arizona and New Mexico. The Rio Yaqui in Mexico similarly passes from the northern Sierra Madre Occidental through hot desert lowlands to the sea.

These rivers were characterized by remarkable variation in discharge (Fig. 3). Floods from spring snowmelt in the north and both during regional winter rains and late summer monsoons in the south, are followed by mere trickles under the intense evaporation and minimal precipitation during early summer and autumn droughts. Down-cutting of canyons and transport of tremendous volumes of sediments are the rule. Canyons alternate with reaches flowing through broader floodplains, and diversity is high (Fig. 4). Where floodplains are wide, gallery forests and woodlands of cottonwood, willow, and other trees formerly lined desert watercourses; extensive marshes occupied their backwaters. Water tables were only a few feet beneath the surface in even the driest desert basins, and seepage maintained rivers, or at least filled pools in protected canyons during major droughts.

The situation changed dramatically with intervention of technological humans. Now, floods alternating with intermittency in drought are an exception rather than the rule (Fig. 3). Rivers are dammed before they leave the mountains. Flood waters and sediments are caught in reservoirs, and water is released as needed for irrigation, power generation, and domestic use. Low flow occurs when humans deem it so; dams can be closed and rivers turned off like a kitchen tap.

Far more surface water exists today than before, but it is in quiet reservoirs markedly different from the originally turbulent streams (Fig. 5). Canals instead of streams, lined with concrete and chain-link fence rather than riparian trees, descend from reservoirs to and through the lowlands (Fig. 6). Sediment carried downstream in flood is no longer

Figure 4. Left: Canyon-bound reaches alternating with more open sections in bends characterize most desert rivers (San Juan River, photograph by U.S. Bureau of Reclamation). Right: In wider, valley sections, meandering channels and sandbars are common and riparian woodlands develop on floodplains (Gila River, New Mexico).

Figure 5. Left: Boulder Canyon reach of the Colorado River prior to Hoover Dam, contrasted with; Right: the same reach after the dam was in place to form Lake Mead, Arizona-Nevada (photographs provided by U.S. Bureau of Reclamation).

replaced from above, and unlined channels soon are deeply incised. Arroyo cutting (Fig. 7) due to watershed abuse such as overgrazing stimulates further erosion, draining water tables to decrease stability even more. Groundwater is pumped from beneath the desert floor far faster than it is restored, seepage into channels fails as water tables drop, and streams cease to flow. Riparian vegetation disappears,

Figure 6. Imperial Dam, Arizona-California, a major diversion on the lower Colorado River, from which canals supply agricultural and domestic water for southern California (photograph provided by U.S. Bureau of Reclamation).

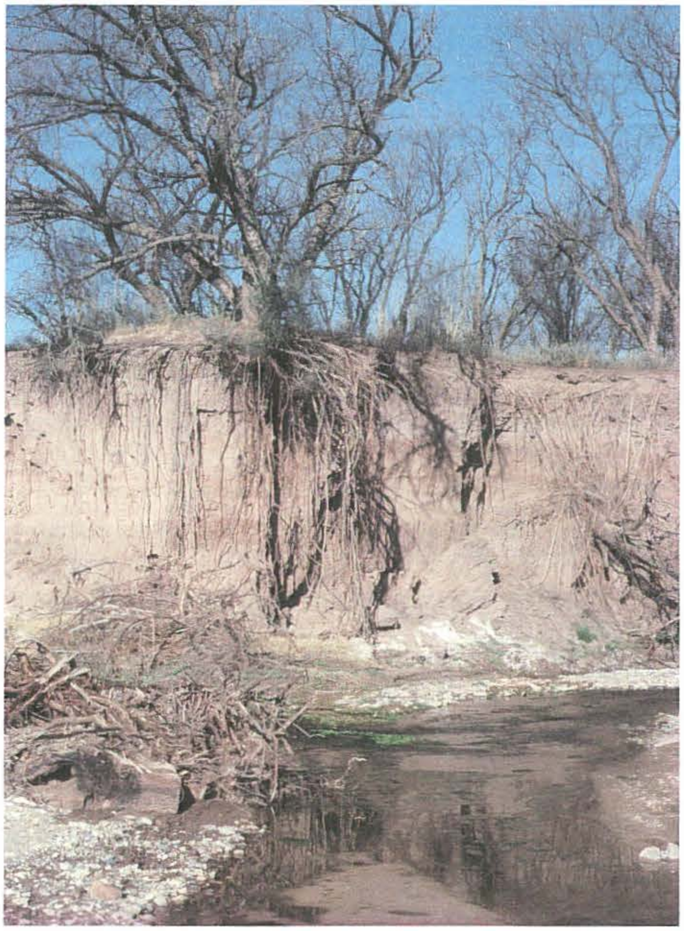


Figure 7. Eroded bank along Cienega Creek, Arizona, 1977. Mesquite, growing on the elevated terrace, forms deep roots in pursuit of a declining water table, quickly replacing cottonwood-willow riparian woodlands after channel incision.

either eroded away or killed by dropping water tables, and soon consists mostly of introduced pests such as saltcedar or Russian olive. Natural riparian communities persist only as isolated remnants, almost as curiosities.

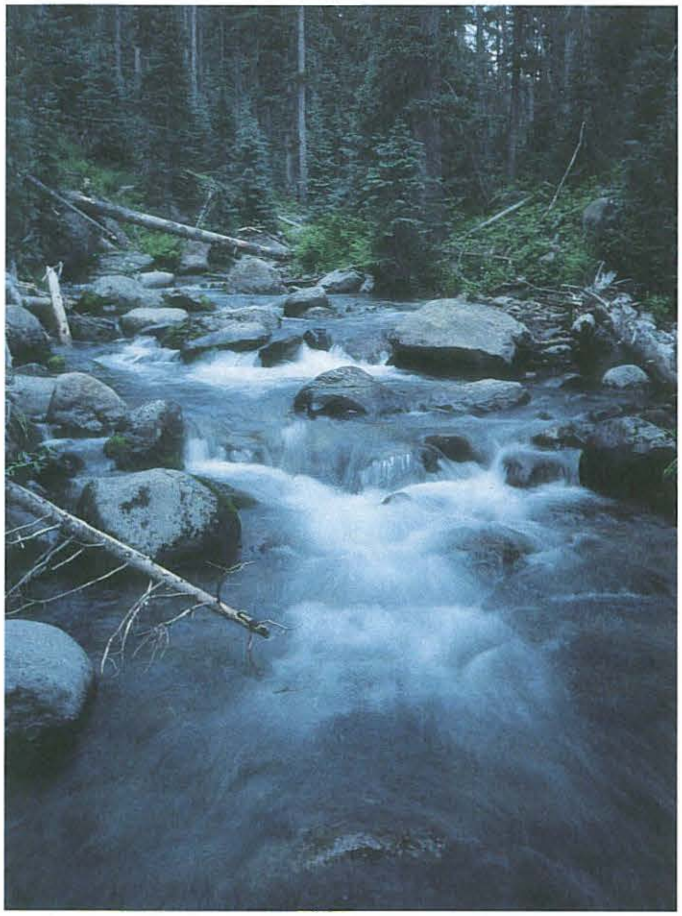
Not everywhere is as bad as just described (Fig. 8). If it were this paper would simply be a history of habitat and species extinction. Some natural systems persist, especially at intermediate elevations where humans judge it less costly to allow the natural streams to deliver water. Native fishes also persist in such places, and therein lies one key to their conservation. Other habitats have been set aside by governmental or private conservation groups.

Figure 8. The stream in Cajon Bonito, Sonora, is one of the most intact, low-desert watercourses in the American Southwest. Photograph by D. A. Hendrickson, 1978.

NATURAL AQUATIC HABITATS AND NATIVE FISHES

Creeks in the Pines

In the United States, streams higher than 1800 m elevation (Fig. 9) generally remain cool enough in summer to support trouts, as well as to exclude other, more temperate fishes like minnows and suckers. Winters are too severe or summer water temperatures do not rise high enough for successful reproduction and recruitment of warmwater species. Winter water temperatures hover near freezing at the highest elevations. Water also remains cold (less than 15.5 ° C) in summer, except where slow-flowing reaches are exposed to sunlight throughout the day. Even there, summer temperatures greater than 21.1 ° C are uncommon.



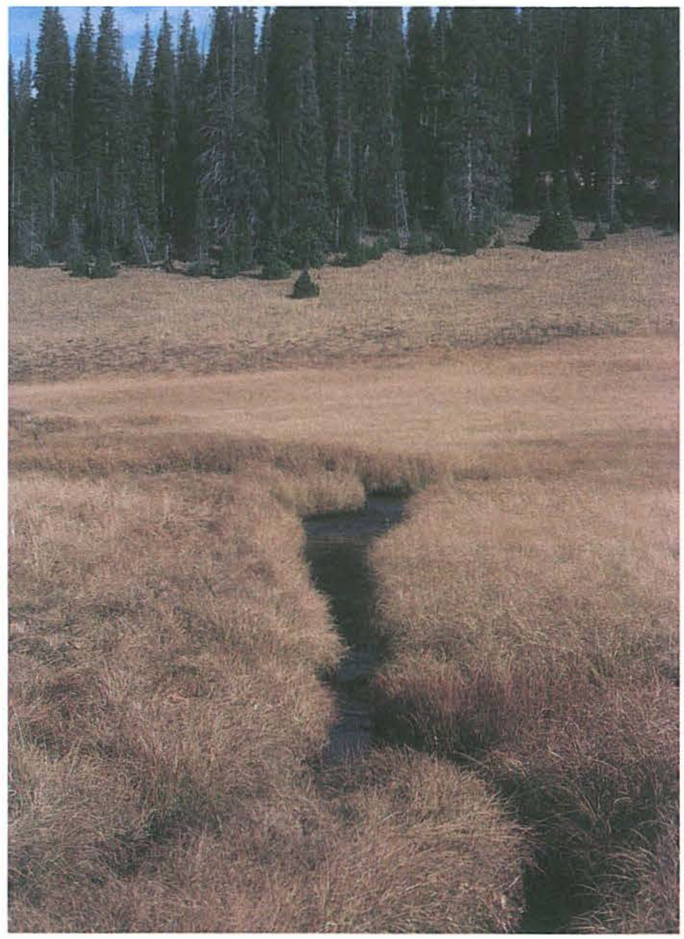


Figure 9. Upper left: East Fork of the White River, Arizona, near the type locality for Apache Trout, 1980. Above: Ord Creek, Arizona, flowing through Bull Cienega, 1979. This stream has been the subject of unsuccessful attempts since 1978 to eradicate non-native brook and brown trouts that have been progressively replacing the native Apache trout. Left: Iron Creek, New Mexico, illustrating an artificial barrier installed to protect a pure population of Gila trout, 1979.

Trouts are of northern derivation, and thus do well in such places. Headwater streams above perhaps 2100 m at lower latitudes in Mexico are also high and cool enough to support trouts, but they are not too high or cold to exclude temperate species. Thus, a far more diversified fauna is present on Mexican mountaintops.

Most high-altitude, perennial southwestern streams depend on ground storage of melted snow for sustained flow during drought. Severe drying can induce intermittency, with pools maintained by underground seepage. Alternatively, scouring floods may occur at snowmelt, especially when warm rains fall on an accumulated snowpack or after violent convectional storms in summer. In their natural state, however, banks of mountain creeks are protected by dense riparian forests. Their channels are choked with downed logs and other organic debris and lined with armouring of cobbles and boulders, so the erosive power of floods is minimized.

In fact, most mountain streams may be so heavily shaded by trees that few aquatic plants can grow. Low light intensity impedes photosynthesis, and colonization by all but specially adapted algae is precluded. Reaches exposed to sunlight in meadows support flourishing aquatic and semiaquatic plant communities, which may fill the channel to form complex marshes. Considerable organic material may be produced in such sections.

Most mountain streams are nonetheless heterotrophic, with organic input coming from the watershed rather than produced within the aquatic system. Pine needles, leaves, and woody debris are attacked by bacteria and fungi to form detritus, which serves as the food base. Invertebrates capable of shredding leaves, others that gather and eat finely divided organic debris, and some that feed on decomposing wood are common. These animals are eaten, in turn, by predatory invertebrates and fishes.

High Mountain Trouts

Native trout of the Southwest can only be relicts of the past that achieved their present distributions either by entering the rivers from a much cooler sea or by the far more difficult process of dispersal over drainage divides. Two endemic species are isolated in highlands of Arizona and New Mexico, one or more undescribed kinds (collectively called *trucha de Yaqui*; Figs. 10, 11) live in the rugged Sierra Madre of Sonora and Chihuahua, the Mexican golden trout/*trucha dorada mexicana* lives in Sinaloa, and a native subspecies of rainbow trout (*trucha de San Pedro Martir*) lives on top of Sierra San Pedro Martir in Baja California Norte. The last two kinds are out of the area of present coverage.

In the United States, the Apache trout (Fig. 12) is native to the White Mountains of Arizona, in headwaters of the Little Colorado, Black, and White rivers. Gila trout (Fig. 13) once lived in tributaries of the Verde River, Arizona, from which natural populations have long been extirpated. It persists naturally only in tributaries of the upper Gila River, New Mexico. Both formerly ranged downslope into larger streams.

Both the Apache and Gila trouts became increasingly restricted in range and numbers as non-native species were introduced to enhance sport fishing. Each progressively disappeared as alien fishes became established and increased in abundance. Rainbow (and likely cutthroat) trout hybridized with them, brown trout ate them, and brook trout

Figure 10. Yaqui trout/*trucha de Yaqui*, 13.5 cm in total length, a yet-to-be-described species from Arroyo Ahumado, Chihuahua.

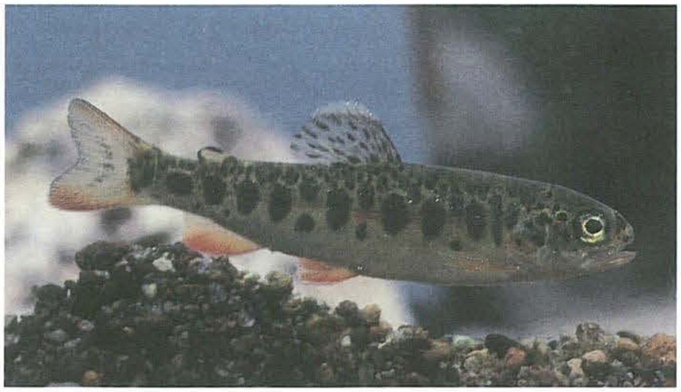


Figure 11. Juvenile trout (no common name), 62 mm in total length, also an undescribed species from the Rio Mayo drainage (Arroyo de la Casita), Chihuahua. All of the native Mexican trouts are considered of "special concern" by an international committee of the American Fisheries Society.

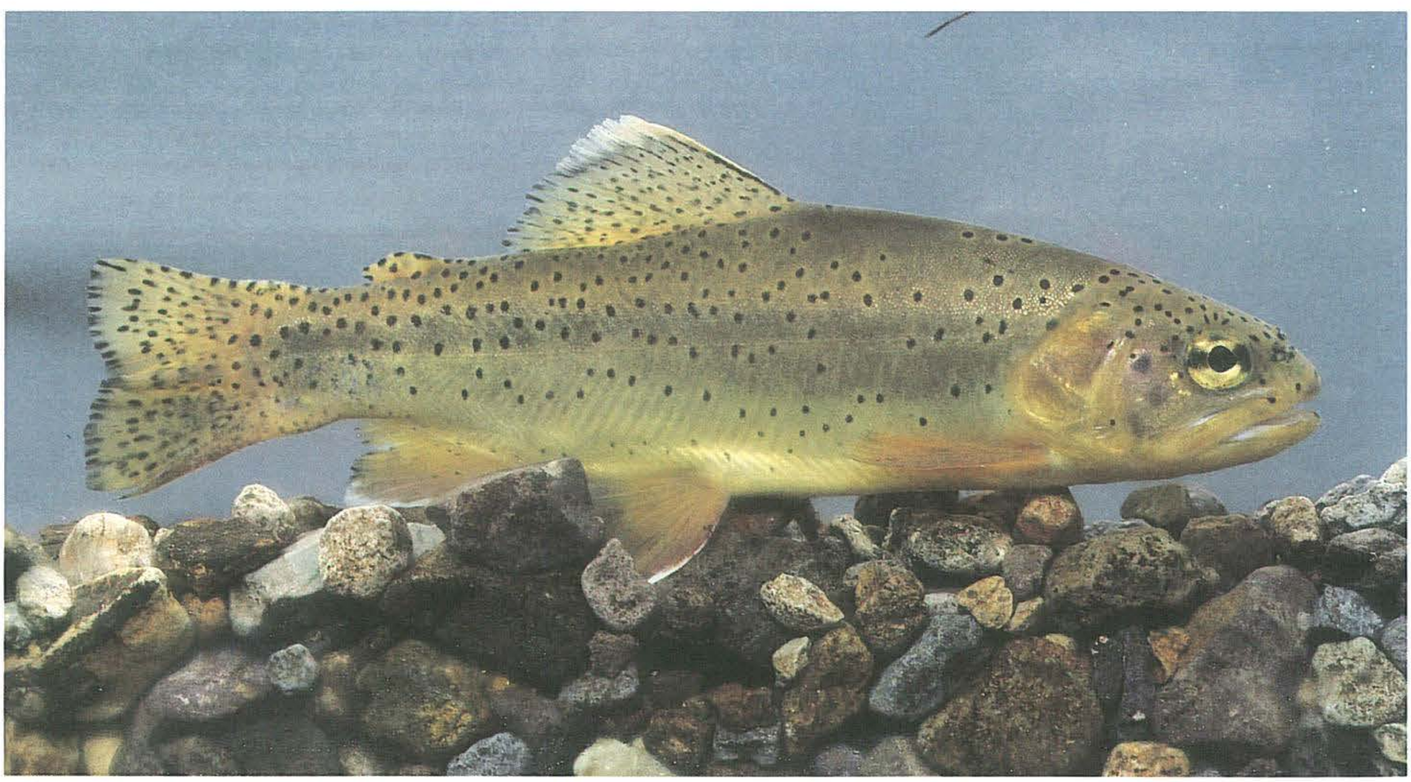
developed large populations that appeared to outnumber and outcompete the indigenous kinds.

Among these problems, hybridization presents the greatest danger to species integrity and survival. By the 1970s, genetic contamination had reduced Apache trout to less than 5.0% of its former range. The Gila trout similarly survives in natural populations in only a few headwater streams. Only inaccessibility to stocking and natural barriers to subsequent upstream movement stopped invasions of non-native trouts and prevented complete loss of these two special natives. Both are federally listed, as threatened and endangered, respectively.

All these trouts have similar ecologies. Large individuals live in pools, while smaller ones remain near obstructions or other cover such as overhanging trees or brush in runs and riffles. All spawn shortly after snowmelt, and young hatch and grow rapidly in the warming waters of early summer. Variations in color patterns are pronounced, even within single populations, some of which may reflect hybridization with rainbow and cutthroat trouts in both the Colorado and Yaqui systems.

In addition to the dangers of introduced relatives that hybridize with them, and the invasions (or stocking) of predatory and competitive species,

Figure 12. Apache trout, 21.0 cm in total length, East Fork of the White River, Arizona. This threatened species generally remains small (less than 20 cm) in smaller streams, but attains 45 cm in artificial lakes.



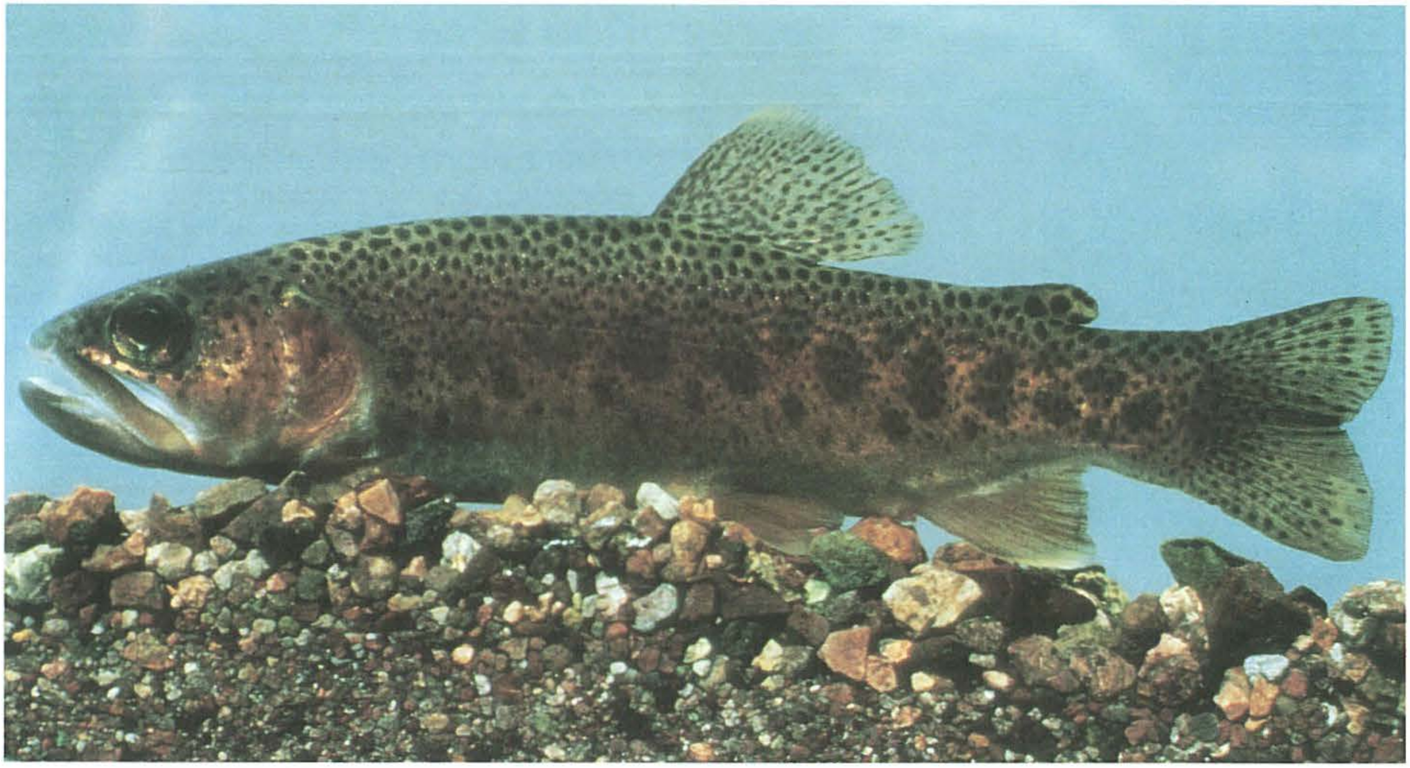


Figure 13. Gila trout, 18.7 cm in total length, Main Diamond Creek, New Mexico. This endangered species persists naturally in only five streams. Similar to Apache trout, the species generally remains small in size in the tiny headwater habitats where it persists.

habitat degradation is an ever present threat to endemic trout populations. Extensive montane logging (Fig. 14), both in the United States and Mexico, has opened stream channels to direct sunlight, altered patterns of organic input, and increased erosion and sedimentation. Sawmill wastes have been a major source of organic pollution in Mexico. Livestock (Fig. 15) compact and denude marshes and meadows, trample stream banks, and remove riparian vegetation.

Figure 14. Clear-cutting can impact headwater streams supporting the threatened Apache trout. Photograph near the crest of Mt. Ord, Fort Apache Indian Reservation, Arizona, 1988.

Figure 15. Domestic livestock seek riparian zones for shade, water, and forage. Their impacts contribute to habitat degradation through vegetation removal, compaction of soils, and decreased bank stability.

Figure 16. Beaver pond on the East Fork of the Little Colorado River, at Phelps Cabin, Arizona. This type of aquatic habitat must have supported large numbers of native trouts in times past.

Disappearance of beaver as a result of overtrapping may also have been a major factor in habitat degradation. Beaver ponds in the White Mountains of Arizona (Fig. 16) now support large numbers of Apache trout. None of these changes has been critically assessed, but higher summer water temperatures, changed nutrient relationships, and increased turbidity and sediment transport may all be predicted; none benefits native trout.

Recovery efforts for native trout in the United States have had public and agency support because of their positive image as game and food fishes, their beauty, and the romanticism with which high mountains and their streams are viewed. The plans are basically to isolate and protect selected populations that represent the phenotypes (and presumably the genotypes) in wilderness or comparable remote areas, and use hatchery strains for restocking other streams within the native ranges. In this way, both species may be managed for their continued survival, as well as for use by man. However, the presence of non-native species will continue to be a problem, which may prove insurmountable. Future management should exclude non-native trouts from the ranges of native species.

To my knowledge, no specific program has yet been developed for native trout conservation in Chihuahua and Sonora, other than (1) inclusion of natural populations in the National Parks at El Salto de Basaseachic, Sonora (Rio Mayo drainage), and San Pedro Martir in Baja California del Norte, and (2) general recognition of the value of the unique Mexican trouts in the Rio Fuerte headwaters to the south, and on Sierra San Pedro Martir.

Other Species

Only a few warmwater fishes ascend high enough to interact on a day-to-day basis with trouts in the United States. The speckled dace/*pecesito moteado* is an exception, since they commonly reproduce up to 2100 m elevation. Spinedaces in the Little Colorado and Virgin rivers also occupy high-elevation habitat along with trouts at the upper limits of their ranges; their ecology is discussed below. Desert mountain-sucker/*matalote del desierto* also go into headwaters, but few are resident there.

In Mexico, Leopold suckers/*matalote del Bavispe* (Fig. 17) seem characteristic of high-elevation trout waters, as is Rio Grande mountain-sucker/*matalote del Rio Bravo* (Fig. 18) in its limited distribution (one stream known) in the Rio Yaqui basin. Five other kinds (see below) reach the upper limit of altitudinal distributions somewhat below the extreme headwaters, but still occur broadly with native trout.

In one example, a trout in the Rio Papigochic sub-basin of the Yaqui basin lives in a stream

Figure 17. The Leopold sucker/*matalote del Bavispe* is listed as a species of special concern. The specimen illustrated is 11.0 cm in total length, from Rio Negro, Chihuahua.

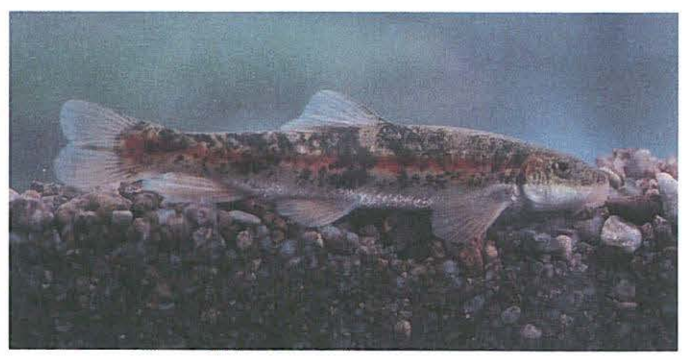


Figure 18. Rio Grande mountain-sucker/*matalote del Rio Bravo*, 13.5 cm in total length, Rio de las Vacas, New Mexico. The red lateral band is characteristic coloration for a fish in breeding condition. This species remains locally common in much of the upper Rio Grande basin in the United States and Mexico, and in a number of independent drainages in the Sierra Madre Occidental of Mexico.

occupied by nine minnows and suckers at the same time and place, all of which are characteristic of "warmwater" habitat. These co-occurrences may be partially explained by a latitudinal effect. High-altitude streams in Mexico are warm enough to support minnows and suckers, but are not (quite) too warm in summer to exclude trout. They also may be an artifact of sampling. Remote streams in Mexico remain inaccessible or unknown to foreign workers unfamiliar with the region, and some of them not yet sampled may be high enough to exclude temperate fishes. It is also notable, however, that non-native trouts have yet to be widely stocked in Mexico, so natives may still occupy natural ranges that include lower-elevation waters. There is good evidence that Apache and Gila trouts descended to lower elevations in the past, where they also encountered "warmwater" species.

Streams at Intermediate Elevations

An Historic Perspective

Creeks and rivers in lower coniferous forests through woodlands and into desert grasslands (from about 1800 to 900 m elevation) support most of the remaining native fish populations in the region. These channels carry surface runoff as well as intercepting groundwaters from the highlands, which enter as springs or seeps along bedrock fracture zones or bedding planes or is lifted from deep alluvial fills when channels cross bedrock dikes (Fig. 19). Many streams are highly erosive in deep, precipitous canyons for parts of their courses (Fig. 20). From an historic perspective, such places have changed little from the way they appeared hundreds of years ago. Other reaches, flowing through broad valleys (Fig. 21), are dramatically different from a century ago due to human activities resulting in changes in the equilibrium of erosion and deposition.

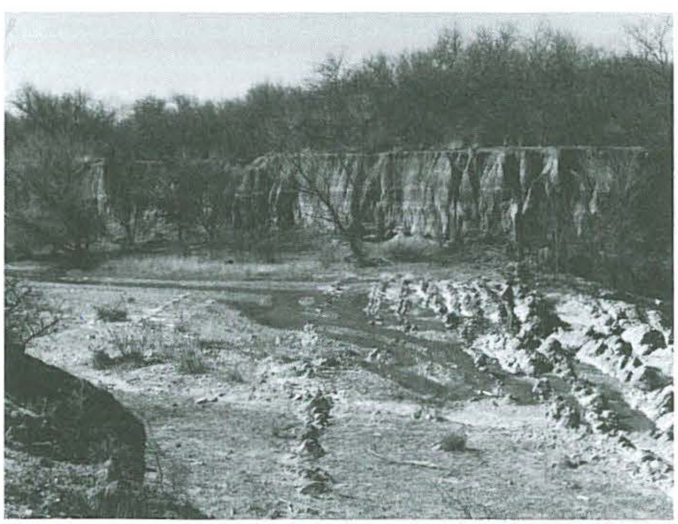


Figure 19. Bedrock dikes exposed by channel incision in Cienega Creek, Arizona, force subterranean flow to the surface, creating refuges for fishes and other aquatic organisms during drought.

Figure 20. Canyons of the Colorado River in northern Arizona were cut in the Colorado Plateau surface through millennia. Forces resulting in these spectacular landforms are now under partial control of mainstream dams. Photograph by D. A. Hendrickson.

A stream at equilibrium transports precisely as much material as produced within its watershed. Thus, as a ton of material weathers and erodes from a headwater mountain, a ton is carried out. In practice, what one sees in a given stream results from the average condition over an undefined period before the observation. In bedrock, canyon-bound segments, transport through the channel may have little to do with how the system appears; apparent equilibrium is dictated by the non-erodibility of bedrock. In alluvial channels on unconsolidated sediments deposited in times past, the stream bed at equilibrium may remain at a constant level, with

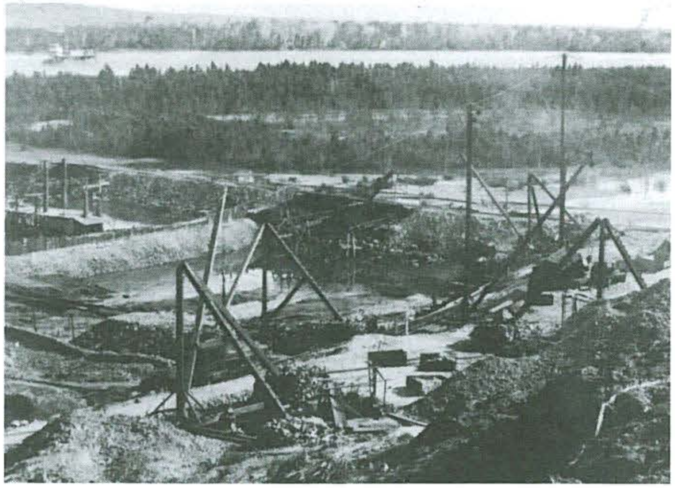


Figure 21. Lower Colorado River, Arizona-California, at Laguna Dam. Upper: Note continuous riparian vegetation and river being navigated by paddlewheeled vessel in 1906. Lower: Riparian vegetation has been replaced in 1975 by agriculture, and the river flows in a constrained, dredged channel. Photographs provided by U.S. Bureau of Reclamation and R. D. Ohmart, respectively.

material forming the bottom at a given place constantly exchanged. If balance shifts to the positive side, the stream channel will build up, or aggrade. A negative shift results in local erosion, or degradation.

In the 1800s, many southwestern streams had aggraded, and flowed near the tops of their banks. Extensive marshes and riparian plant communities slowed water currents, promoting deposition of organic and inorganic materials (Fig. 22). Beaver were common, and their dams contributed to over-all stabilization of the systems. Layers of organic debris interbedded with alluvium and laced together by the trunks and limbs of down trees soaked up flood water, which slowly leaked into the channel during dry times, thereby buffering the impacts of drought.

Figure 22. Marshlands associated with Babocomari Creek, upper San Pedro River basin, Arizona, 1968. This is one of the few, relatively undisturbed cienega habitats remaining in the American Southwest.

A major catastrophe occurred in the 1870s. Livestock, introduced to the region by ranchers, had become abundant. As the uplands desiccated, cattle concentrated near streams and rivers. But even that tactic soon failed, and 75% of all livestock in Arizona are thought to have died of thirst or starvation by 1875. Ranges were severely damaged, so erosion prevailed when a wet cycle began in the 1880s. Deep arroyos were cut from downstream to upstream, incising valley fills so deeply that water tables were drained (Fig. 23; see also Figs. 7, 19).

Figure 23. Cienega Creek, Arizona, 1977: organic deposits (dark bands) formed during periods of marshland development, are interbedded with alluvium deposited from the watershed (light bands) in eroded banks of many incised Southwestern streams.

Marshes and riparian plants were left high and dry, and disappeared. The erosive power was concentrated downward by high channel walls.

Fishes adapted to erosive habitats, those which could live in the hard-rock canyon reaches of streams, were scarcely affected by this change. Flow almost certainly became less reliable as upstream groundwater reservoirs were drained, but the habitat otherwise remained similar to before. On the other hand, fishes depending on constant, cool inflow of groundwater, amelioration of floods, or the presence of quiet habitats along meandering channels, were suddenly and severely impacted.

Ecology of Present Systems

Physical conditions in intermediate-elevation streams are highly variable. Summer water temperatures approach 30° C in afternoon (Fig. 24), and drop to 21.1° C or lower at daybreak. Relatively cool water, despite air temperatures of 43.3° C or more, is due to the high evaporation rates in dry desert air. Only on rare sunny days with high humidity do stream temperatures rise above 32.2° C; thermal death of fishes has been recorded under such conditions. Shading has a profound effect, and a creek with alternating flow through wide, unshaded channels then narrow, dark canyons, may vary along its course at the same time of day. In winter, stream margins often rise to 25° C on sunny days. Channel temperatures rise to 12.1° C, or perhaps more, and rarely drop to less than 5° C at night. Ice nonetheless forms on isolated backwaters on especially cold nights.

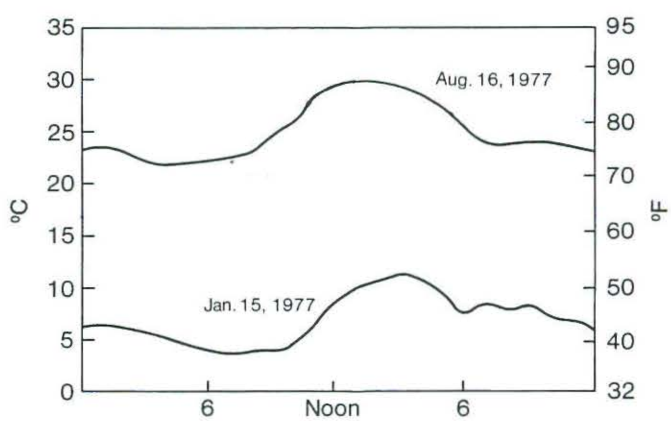
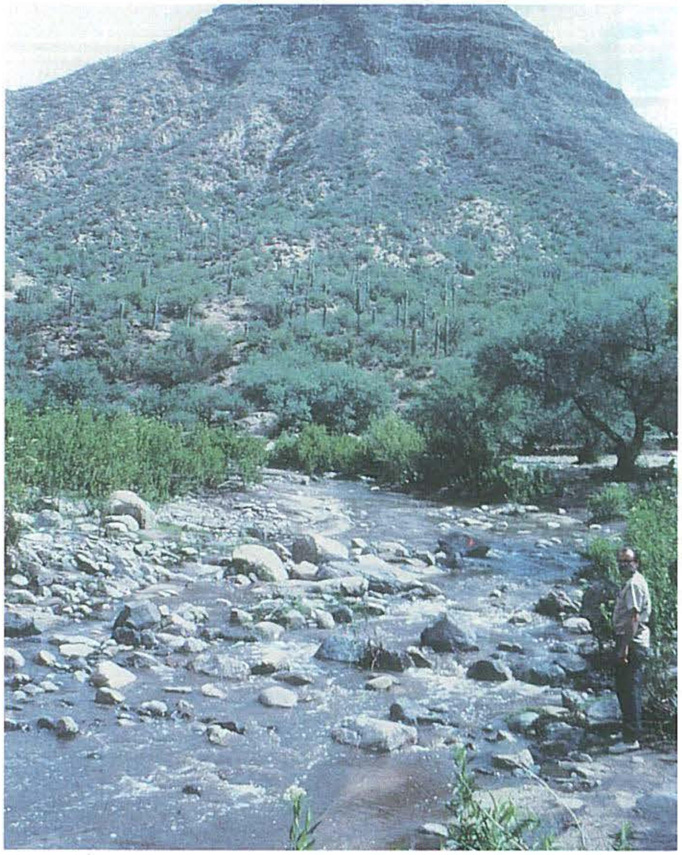


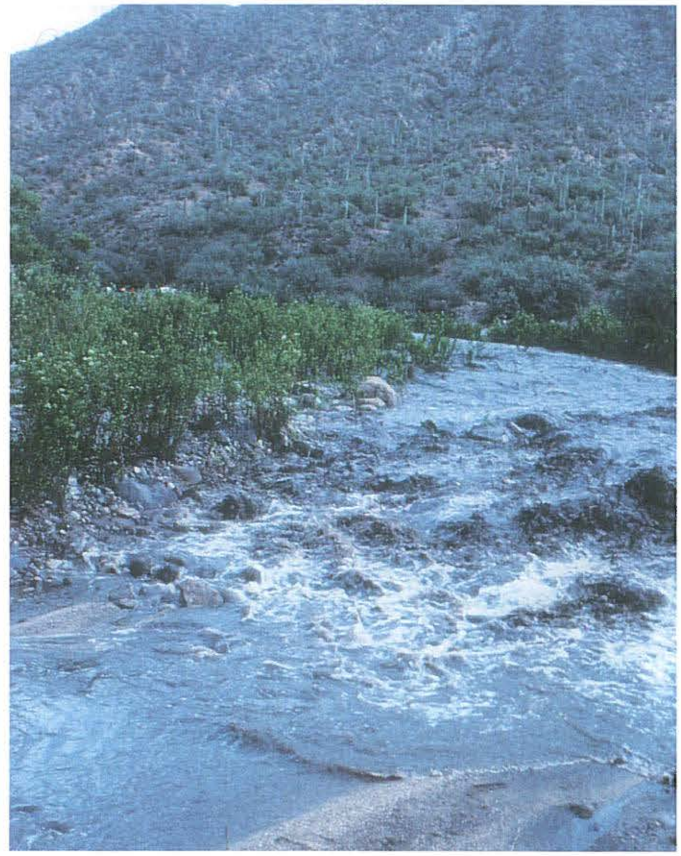
Figure 24. Summer and winter water temperatures over 24-hour periods in Bonita Creek, Arizona.

Figure 25. Above: Boulder substrate in a high-gradient tributary to the Rio de Bavispe, Sonora. Photograph by D. A. Hendrickson. Below: Sand/gravel substrates in a wide segment of Aravaipa Creek, Arizona.

These streams carry remarkable loads of material eroded from the mountains through which they pass. Substrates are typically of boulder and cobble at higher elevations, grading to gravels and sand lower down (Fig. 25). Turbidities are high during floods, but particles tend to be large in size and most streams clear quickly. Because many watersheds are rocky, barren of vegetation, and impervious, sheetflow quickly concentrates into channels to produce abrupt and violent discharges. Unlike streams in more temperate zones, most of the annual water yield of these streams is during flash floods (Fig. 26), rather than as slow, constant discharge throughout the year.

Chemically, most of these streams remain well within the limits for healthy fish populations. They have more total dissolved solids than mountain





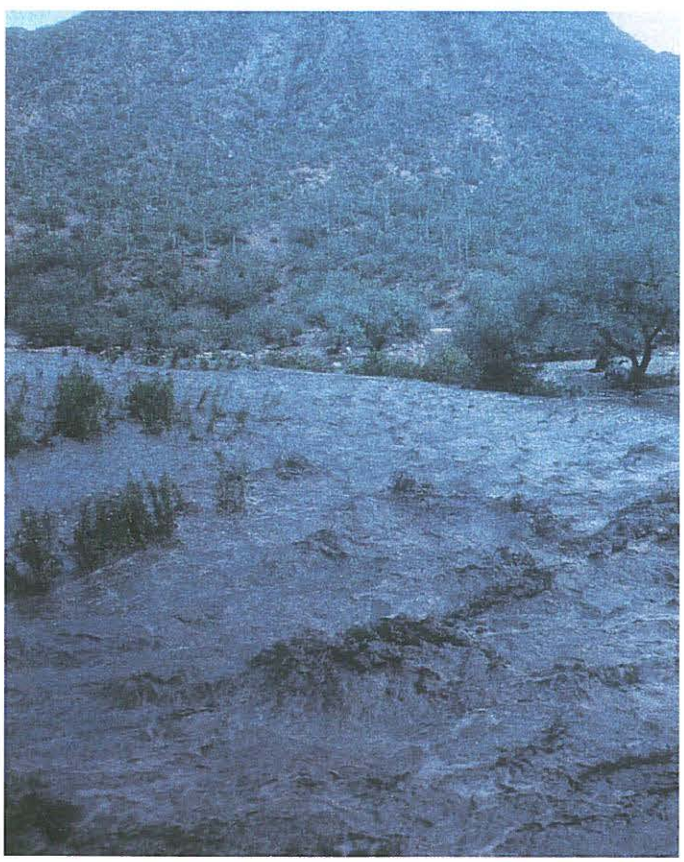


Figure 26. Sequence of flash flooding in Sycamore Creek, Maricopa County, Arizona, 1977. The elapsed time between B and C was that required to advance film between frames. Photographs by S. G. Fisher.

streams, in part because of evaporation and often due to inflow of salty groundwaters. Their chemistry varies with runoff, low in salts at high flow and more concentrated in drought. Other variations, often spectacular, occur with biological activity. All these streams are highly productive. Under intense sunlight, and with clear water at low flow, remarkable changes occur in dissolved gasses and ions associated with algal photosynthesis. Aquatic insects and some other invertebrates with short life histories respond quickly to the rich food source, and secondary productivity is high as well.

Fishes of Intermediate Elevations

Fishes occupying this zone include some species that may have been forced upward with increasing aridity, and another group more closely related to species occupying eastern, more temperate zones. In the natural state, creeks and smaller rivers of the

Figure 27. The spikedace, endemic to the Gila River basin of Arizona and Sonora, is listed as threatened. The specimens illustrated are ca. 70 mm in total length, from the Verde River, Arizona; female above, male below.

lower Colorado basin supported about 18 fish species. Six of these were small, short-lived minnows, and an equal number were larger, longer-lived minnows and suckers. Four even larger and more long-lived minnows and suckers, most common in "big-river" habitats, entered small rivers and may have spawned there, as is discussed later. Last, a pupfish and topminnow in the Gila basin ascended to slightly more than 1500 m elevation. Here, and at lower elevations, they occupied marshes and stream margins, as outlined below along with other low-desert species.

The Rio Yaqui supports 20 species, only three of which are shared with the Colorado. Using the same categories as above, eight were small and short-lived, 12 are larger and longer-lived, but none (perhaps one or two, see later) are clearly "big-river" in ecology. A pupfish lives at higher elevation, and topminnows are represented by a number of species that live from relatively high elevation to the river's mouth.

Short-lived minnows.—Among this group of minnows, spikedace, spinedaces, loach minnow/*charalito ardornado*, and speckled dace are in the Colorado system. All are related to other species of western North America, and all but the last are endemic, commensurate with the long isolation of the Colorado River basin. Longfin dace/*charalito aleta larga*, another species of western relationships, is shared by the Colorado and Yaqui systems. Minnows with eastern relationships—beautiful shiner/*sardinita hermosa*, Mexican stoneroller/*rodapiedras mexicano*, and ornate minnow/*sardinita ornata*—are restricted to the Rio Yaqui and associated basins to the south in Mexico.

The spikedace (Fig. 27) occupies midwater habitats of runs, pools, and swirling eddies, where it feeds on drifting aquatic and terrestrial insects. The species is mottled dorsally, silvery on the sides, and whitened beneath. Males in breeding condition become golden or brassy on their dorsal and lateral surfaces. Spawning is in spring and summer, with younger females spawning once and older females twice each year. Life expectancy is two or three years, and the fish rarely exceeds 75 mm in total length.

Spinedaces (Fig. 28) occur in the Little Colorado and Virgin rivers, and in isolated springs of the

Figure 28. Above: Little Colorado spinedace, 80 mm in total length, from the Little Colorado River, Arizona. Below: Virgin spinedace, ca. 90 mm in total length, from Beaver Dam Creek, Arizona. Both species are considered threatened by the American Fisheries Society endangered species committee.

Figure 29. Male (left) and female (right) loach minnow/*charalito adornado*, 62 and 57 mm in total length, respectively, from Aravaipa Creek, Arizona. This unique, bottom-dwelling minnow is listed as threatened.

ancient White River drainage of eastern Nevada (see below). These are relatively large, silvery minnows, commonly ranging to 125 mm long, that are trout-like in behavior and ecology. Both inhabit quiet water of pools and eddies below riffles and runs, eat aquatic insects and other invertebrates, and spawn in spring and summer. Male breeding colors are mostly seen as yellowish or reddish orange pigments at the bases of the paired fins.

The loach minnow (Fig. 29) is the most secretive yet conspicuously colored minnow species in western North America. Males become brightly pigmented in breeding season (March through September), with colors ranging from blood red to brilliant orange on the lips, fins, and bodies. Females remain relatively drab, but develop yellow pigments on the fins and body. Males appear territorial and defend nests beneath stones on riffles. The species is small, with a large male rarely exceeding 65 mm long. It lives no more than two years, disappearing the third summer after hatching. The habitat is special (Fig. 30), consisting of riffles no more than 15 cm deep over gravel bottoms, and often in association with dense beds of coarse, filamentous algae. Life is spent on the bottom since the air bladder is greatly reduced and their body density is such that midwater swimming is labored and seemingly takes a great amount of energy. This fish feeds almost exclusively on mayfly and blackfly larvae, invertebrate co-inhabitats of its riffle habitat.

Of all native fishes in the Southwest, the speckled dace is the most spectacularly variable in morphology and pigmentation (Fig. 31), as well as in ecology. It remains widespread throughout the Colorado River system, where a special kind adapted for life in canyons of the upper river is duplicated in other erosive habitats such as the Salt River Canyon of east-central Arizona. Even the Paria River, a small tributary entering the Colorado upstream from Marble Canyon, has a special form that is elongated, depigmented, with large fins and reduced, embedded scales (Fig. 31, lower). The Paria River is sand bottomed,

Figure 30. Left: Loach minnow/*charalito adornado* habitat in riffles of Aravaipa Creek, Arizona. Right: Typical positioning response to swift currents over mixed gravel/cobble substrate.

Figure 31. Speckled dace/*pecesito moteado* from three Arizona localities: Upper: Aravaipa Creek, 67 mm in total length; Middle: Beaver Dam Wash (Virgin River drainage), 71 mm; and Lower: Paria River canyon, 70 mm long.

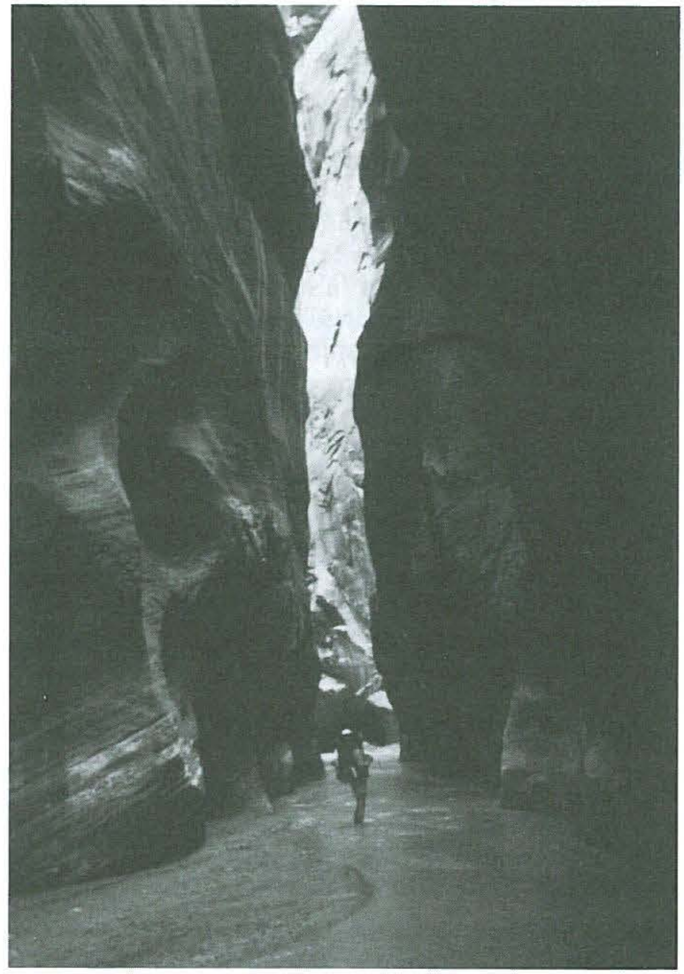


Figure 32. Paria River in Paria Canyon, Arizona. Photograph by G. C. Kobetich.

notoriously turbid, and floods violently through a narrow gorge (Fig. 32); persisting in such a place must require a unique body shape, plus remarkable adaptations at levels other than reflected in morphology.

Speckled dace in some other tributaries, including those lower in the system, are far less spectacular. Many are small and round-bodied, with reduced fins and relatively large, loosely overlapping scales. They live in quiet pools as well as riffles of creeks. Speckled dace are opportunistic carnivores, feeding heavily on aquatic insects and other invertebrates, and only occasionally on plant materials.

The longfin dace (Fig. 33), shared by the Colorado and Rio Yaqui systems, occurs from uplands to

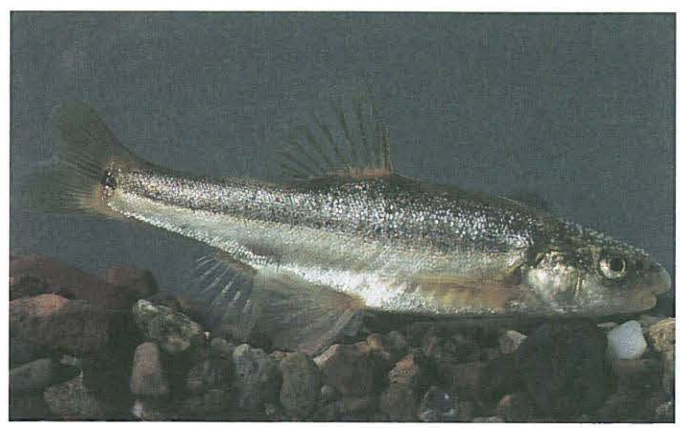


Figure 33. Longfin dace/*charalito aleta larga*, 86 mm in total length, from Aravaipa Creek, Arizona. This minnow, unlike most western fishes, remains relatively abundant through much of its original range. It disperses rapidly from isolated refuges when intermittent desert washes begin to flow after rains, and was thought by early settlers to emerge from the sand.

low-desert streams, enjoying the widest distribution of any species in the region. It has remarkable capability to disperse into new habitats, appearing a few hours or days after flow re-establishes in formerly-dry stream channels. The species is also markedly resistant to drought, persisting in drying pools of the deepest and most permanent parts of a channel (which they find in some unknown manner) even though crowded in habitats that become hot and deoxygenated. Longfin dace once were recorded to survive in tiny volumes of water beneath mats of filamentous algae, then reproduce a few days after when summer rains rejuvenated the stream. They spawn at any time during the year, further enhancing the rapid recolonization of formerly desiccated habitats.

Spawning in Colorado River longfin dace occurs when females come to males over relatively soft, sand bottoms. A swirling spawning act creates depressions, or "nest pits" in the sand (Fig. 34) that are used repeatedly by one or more spawning pairs. Eggs buried in the walls and bottoms of these pits hatch in a few days. Young live at first in the pits, then along stream margins before moving to smooth runs of open sandy areas with the adults. Spawning "pits" and spawning activities have not been observed for the Rio Yaqui form.

Reproductive adults are darkened, and males may develop yellowing of the fin bases and lower head and body. Males have large, strong tubercles—horny projections that develop on the fins, head, and body—which are used to stimulate and hold the female during spawning, and perhaps in combat between males. This species is more omnivorous than most western fishes, feeding opportunistically on algae or invertebrates, when available, and on detritus after floods reduce other food supplies.

Among small minnows in the Rio Yaqui basin, the beautiful shiner is just that (Fig. 35), an attractive member of a widespread group mostly distributed east of the Continental Divide. Males develop intense orange pigments that overlie an almost sky-blue base color on the body. The fins are orange to reddish orange with dark underlying pigments. Males have tubercles of various sizes on the head, paired fins, and caudal peduncle. Females are straw-yellow or bluish. The spawning act has not been recorded, but presumably consists of spreading the eggs over aquatic vegetation, brush, or other cover, or perhaps simply over the bottom. This species is similar in size and ecology to spikedace, living in midwater habitats of pools and runs, along the shorelines in large streams, and tending more to move onto riffles in smaller streams. It also feeds on drifting aquatic and terrestrial invertebrates.

Figure 34. The scattering of light-colored depressions along this sand bar in Kirkland Creek, Arizona, are "nests," formed by whirling movements of longfin dace/*charalito aleta larga* during spawning. Eggs are deposited in the walls and bottoms of the cones. Photograph by W. G. Kepner.

Figure 35. Beautiful shiner/*sardinita hermosa,* male (above) and female (below) (50 and 64 mm in total length, respectively), from the Rio Piedras Verdes, Chihuahua. This species formerly occurred in the Mimbres River, New Mexico, and persisted until the late 1960s in San Bernardino Creek, Arizona. It remains locally abundant in Mexico, but was considered of special concern by the American Fisheries Society.

Figure 36. Mexican stoneroller/*rodapiedras mexicano*, 93 mm in total length, from Rucker Canyon, Arizona. This species is rare in the United States, but remains locally common in Mexico. It is listed as a species of special concern.

Figure 37. Ornate minnow/*sardinita ornata*, male (above) and female (below) (56 and 55 mm in total length, respectively), from Rio Papigochic, Chihuahua. Ornate minnows are widespread in a number of river basins in Mexico, and may represent a complex of species.

Mexican stonerollers (Fig. 36) have cartilaginous sheaths on their jaws for scraping encrusting algae from stones and other solid substrates. Large adults, which may attain lengths of 15 cm or more, live in pools except in breeding season; young frequent riffles and runs. Breeding males not only display bright colors on the body and fins, but also develop an enlarged head and humped back and strong, sharp tubercles on the snout and head. These tubercles are used in combat between males, stimulating and guiding females, and for digging.

The term "stoneroller" comes from the movement of gravel by a male during nest excavation. Stones are pushed about with the head and carried in the mouth, which results in an elongate depression on riffles that is actively defended against other males. Females enter the depression and spawn, then the male protects the eggs until hatching.

Male ornate minnows (Fig. 37) are almost as spectacular as Mexican stonerollers in that their heads become swollen and covered by coarse tubercles. The species is, however, much smaller in size, rarely achieving more than 75 mm long, and develops dark bluish black coloration on the body when in breeding condition. The fins also are darkened, overlying a milky white, opaque pigmentation that lies deep in tissues of the fin membranes. The eggs are deposited on the underside of stones in shallow water and vigorously defended by the male.

Longer lived Suckers and Minnows.—Desert mountain-sucker and Sonoran sucker/*matalote sonorense* (Figs. 38–39) together comprise the most common larger fishes remaining in the lower Colorado basin. Both occupy hard-bottomed habitats from 300 to 2000 m elevation. Adults of both live in pools, with the former commonly moving to swift riffles and runs to feed at night. Young mountain-suckers abundantly inhabit riffles throughout the day, feeding on encrusting algae scraped from stones with well-developed cartilaginous sheaths on the jaws (Fig. 40). Young Sonoran suckers also may be on riffles, but more typically live in runs and quieter eddies. They feed on aquatic insect larvae and other invertebrates, and only rarely on plants. Both species spawn in spring on riffles, where adults congregate in large numbers. Spawning is typically of one larger female and two or more smaller males. A depression in the bottom is formed by lateral movements of the female's body, and adhesive eggs are buried in loose gravels. They develop to hatch in a few days. The Little Colorado sucker (Fig. 41) and tributary populations of bluehead mountain-suckers have similar ecologies in streams of the Little Colorado River basin.

In the Rio Yaqui basin, Yaqui suckers/*matalote Yaqui* (Fig. 42) are widespread from the lowest elevations (on and near the river's delta) to higher than 2000 m in mountain streams. They resemble Sonoran suckers both ecologically and morphologically, and may represent only a subspecies of that Gila River form. Three other species of suckers in the Rio Yaqui basin all tend to be at higher elevation: Leopold sucker and Rio Grande

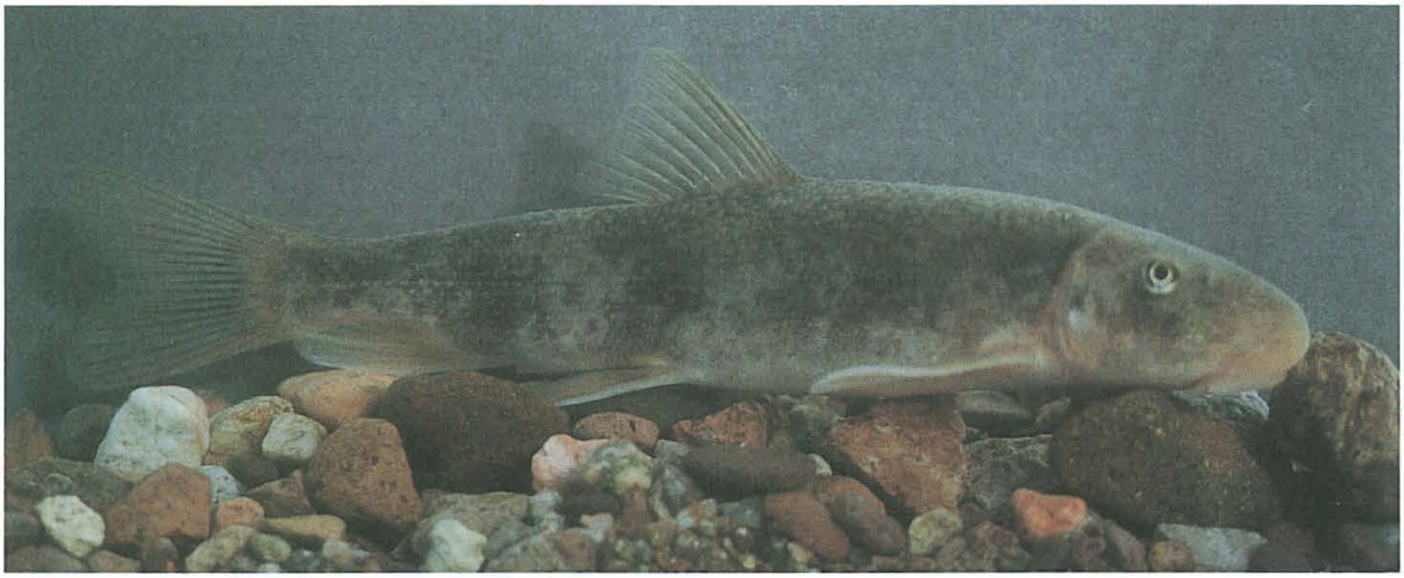


Figure 38. Desert mountain-sucker/*matalote del desierto*, 21.0 cm in total length, from Aravaipa Creek, Arizona. This species remains widespread in intermediate-elevation streams in the Gila, Bill Williams, and Virgin River basins.

Figure 39. Sonoran sucker/*matalote sonorense*, 19.5 cm in total length, from Canelo Cienega, Arizona. Sonoran suckers remain common at intermediate elevations throughout their native range in the Gila and Bill Williams drainages.

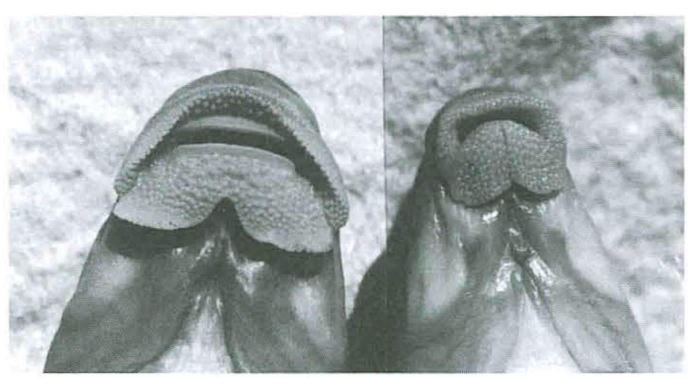


Figure 40. Right: Mouths of desert mountain-sucker/*matalote del desierto*, illustrating the cartilaginous sheaths used to scrape algae and other materials from solid surfaces. Far right: Relatively unmodified jaws of Sonoran sucker/*matalote sonorense*. In both species, the lips are covered by papillae that bear taste buds and other sensory structures to aid in detection of food.

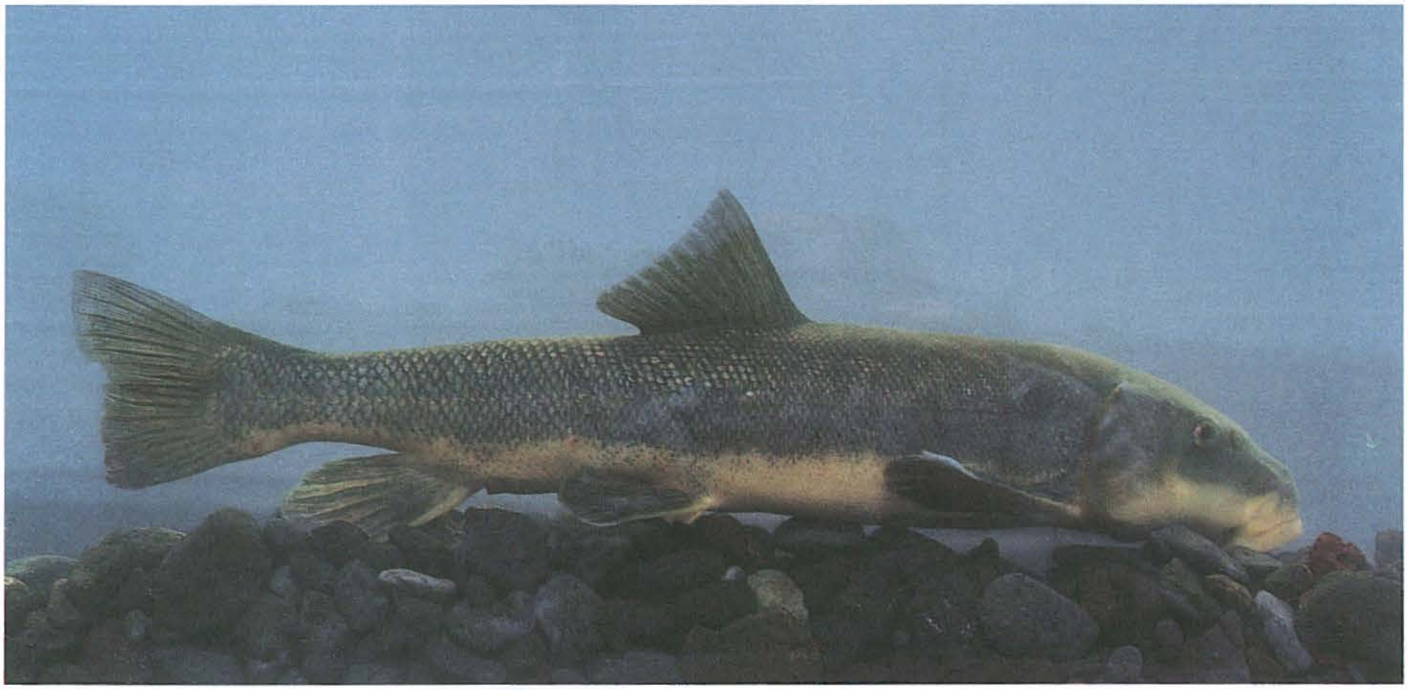


Figure 41. Little Colorado River sucker, 40.5 cm in total length, from Little Colorado River mainstream, Arizona. This distinctive sucker, which seems restricted to the Little Colorado River basin, has not been thoroughly studied and remains unnamed. It is locally common in the upstream parts of its range.

Figure 42. Yaqui sucker/*matalote Yaqui*, 31 cm in total length, from the Rio Sirupa, Chihuahua. This species remains locally abundant in the Rio Yaqui basin in Mexico, but has been extirpated from the United States and is considered of special concern.

Figure 43. Cahita sucker/*matalote cahita*, 16.0 cm in total length, from the Rio Papigochic, Chihuahua. Little is known of this species of stream-dwelling sucker, which was not described until the 1980s. It is considered threatened.

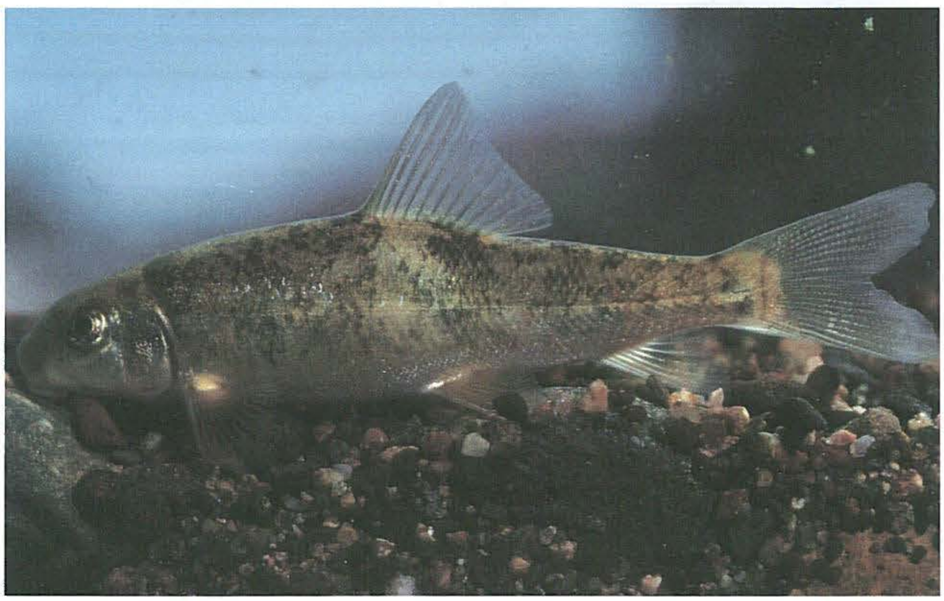


Figure 44. Opata sucker/*matalote Opata*, 15.0 cm in total length, from "Miller's Canyon," headwaters of the Rio Sonora, Sonora. It remains locally common, but the Rio Sonora is rapidly being developed for water supply and the fish is considered of special concern.

mountain-sucker (Figs. 17 and 18) co-occurring with trouts, and Cahita sucker/*matalote cahita* (Fig. 43) rarely taken at elevations lower than 900 m. In contrast, the Opata sucker/*matalote Opata* (Fig. 44) lives generally below 900 m in warm, shallow, sand-bottom desert streams of the Rio Sonora immediately west of the Rio Yaqui basin. Nothing is known of the food or spawning habits of any of the last four species.

As with the suckers, the ecologies of Mexican chubs are remarkably little known despite their widespread distributions and abundance. The Rio Yaqui supports four kinds, roundtail chub/*charalito aleta redonda*, Yaqui chub/*charalito Yaqui*, Desert chub/*charalito del desierto*, and an undescribed species, the first of which is shared with the Colorado system. Gila chub/*charalito del Gila* is found only in the lower Colorado basin, and another species, the Sonoran chub/*charalito sonorense*, is restricted to the small Rio Concepcion basin, a small drainage sandwiched with the Rio Sonora between the Yaqui and Colorado systems.

Roundtail chubs (Fig. 45) are highly variable in size, with some populations achieving only 15 cm as adults and others ranging to almost 65 cm. The species inhabits pools and eddies below riffles, and often occupies quiet waters beneath cut banks or near boulders adjacent to swifter currents. Roundtail are variable in food habits, sometimes feeding on algae and other times becoming piscivorous or even eating terrestrial animals such as lizards that fall into the water. They breed in spring and early summer in

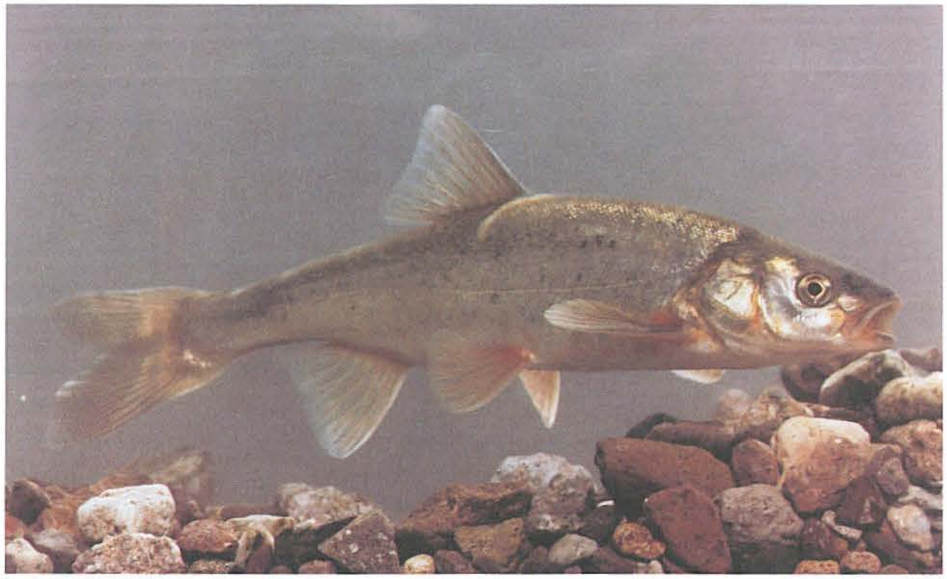


Figure 45. Arizona roundtail chubs/*charalito aleta redonda*, each ca. 17.5 cm in total length: Upper: Aravaipa Creek; and Lower: Virgin River at Littlefield. Roundtail chubs exist as a confusing array of subspecies and local forms. all of which have suffered severe reductions in range. The Virgin chub is listed as endangered.

pool habitats, often in association with beds of submergent vegetation or other kinds of cover such as fallen trees and brush. Males develop sharply bicolored bodies, dark above and whitened below, and have reddening of the bases of the paired fins and often along the lips and on the opercles. Females also may develop darkened bodies and red pigments, although typically not so intense as males. In certain areas, roundtail chubs constitute a significant game fish. Large adults readily take artificial and natural baits, and provide considerable sport on appropriately light fishing tackle.

Yaqui and desert chubs (Figs. 46–47) were only recently separated as distinct species. The former is restricted to the uppermost Rio San Bernardino, mostly in the United States in extreme southeastern

Figure 46. Yaqui chub/*charalito Yaqui,* 55 mm in total length, from Leslie Creek, Arizona. Males of this species become metallic blue-gray in breeding season. Restricted to the drainage of San Bernardino Creek in Arizona and Sonora, it is listed as endangered.

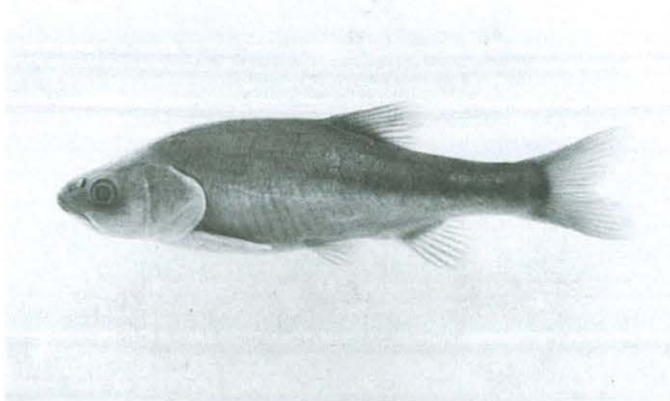


Figure 47. Desert chub/*charalito del desierto,* 150 mm in total length, from Rio Matape. This species was only recently separated and named as distinct from the Yaqui chub. It is widespread in the western Rio Yaqui, Rio Sonora, and Rio Matape, but highly local in occurrence. Photograph by B. D. DeMarais.

Fiqure 48. Undescribed chub/*charalito,* 86 mm in total length, from Rio Papigochic, Chihuahua. In 1978, it was relatively widespread in the Rio Yaqui basin; the American Fisheries Society did not consider it.

Arizona. Desert chub occupies the northwestern Rio Yaqui basin, and the adjacent rios Sonora and Matape. Yaqui chubs are small, usually less than 130 mm total length, and chubby bodied, with small fins and mouths. They occupy pools of creeks, marshes, and other quiet water habitats, often in association with dense aquatic vegetation. Foods consist mostly of small invertebrates, algae, and organic debris. They breed sporadically throughout the summer, with males becoming gray blue when in breeding condition. Desert chubs tend to grow a bit larger, often to more than 15 cm total length. They are similar in ecology, but may more often prefer pools of streams than marshes. Nothing is known of their foods or breeding habits. Even less is known of the undescribed species of chub (Fig. 48) found in the eastern Rio Yaqui basin, other than its general distribution in streams higher than 1400 m.

The Gila chub (Fig. 49) is endemic to the Gila River basin, lower Colorado system, and is also characteristic of pools in small streams, marshes, and other quiet places. Females achieve lengths of 25 cm total length; males rarely grow longer than 15 cm. Foods include both large and small invertebrates, small fishes, algae, and organic debris. As with Yaqui chub, breeding seems to be sporadic throughout the spring and summer. This fish was widely distributed in isolated habitats, occurring in

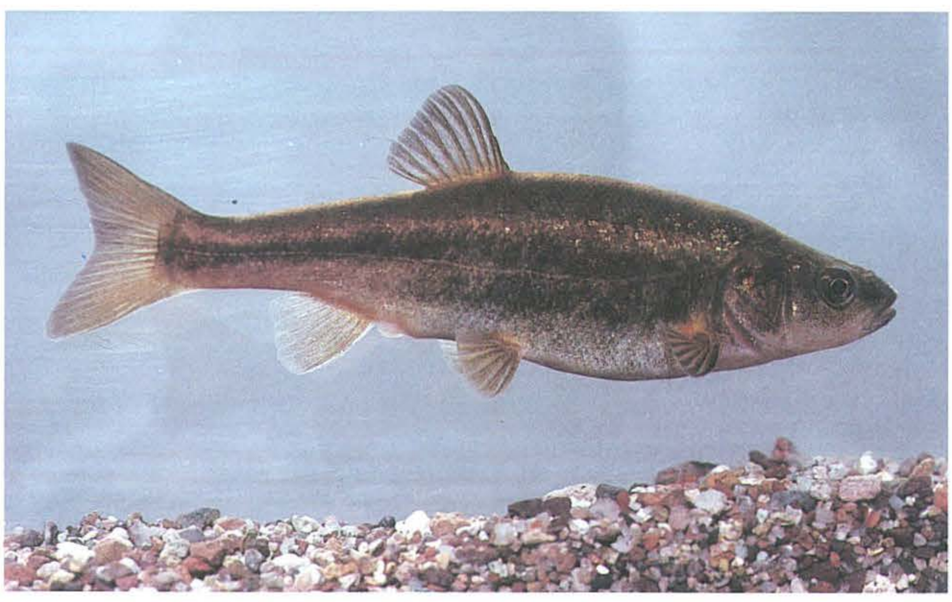


Figure 49. Gila chub/*charalito del Gila*, 14.2 cm in total length, from Canelo Cienega, Arizona. This species is endemic to the Gila River basin, and is considered of special concern. It may be extirpated in Mexico, but still occurs in scattered localities in the United States.

Figure 50. Sonoran chub/*charalito sonorense*, 12.7 cm in total length, from its only locality of occurrence in the United States in Sycamore (or Bear) Canyon, Arizona; it is listed as threatened.

headwaters of essentially all the major tributaries to the Gila River. It is becoming rare, especially where land use practices such as overgrazing lead to incision of floodplains and lowering of water tables, which, in turn, drain marshlands and other stream-associated habitats.

Sonoran chub (Fig. 50) scarcely enters the United States in a single stream that drains southward across the international boundary. It is widespread in the small Rio Concepcion basin in Mexico. When in breeding condition, it is one of the most brightly colored species of chubs, with intense red on the lips, opercles, fin bases, and belly. It occupies erosive creeks, sometimes living under severe intermittent conditions in remnant pools under cliffs. It seems more omnivorous than other chubs, feeding extensively on algae as well as invertebrates. This apparent opportunism may relate more to the severe habitat than to any basic preference—anything tends to be eaten when provisions are scarce.

Other, Special Fishes.—Two special groups of fishes, pupfishes and topminnows, are distributed in part in streams of intermediate elevation in the Colorado and Yaqui systems. Although both these groups are often thought of as "desert fishes" inhabiting isolated springs, neither is exclusively so. Pupfishes are especially misrepresented in this regard. In fact, both groups are quite commonly represented along margins of small to large streams in habitats well above the desert floor. The original elevational range of desert pupfish/*cachorrito del desierto* (Fig. 51) in the Colorado basin was from well below sea level in the Salton Sea area to at least 1500 m elevation in the upper San Pedro River of Sonora. In Mexico, the undescribed, whitefin pupfish/*cachorrito aleta blanco*

Figure 51. Male (above) and female (below) desert pupfish/ *cachorrito del desierto,* 46 and 35 mm in total length, respectively, from Estuario de Santa Clara, Sonora. This endangered species is now restricted to three small, natural localities in the United States, and about the same number of sites on the Colorado River delta in Mexico.

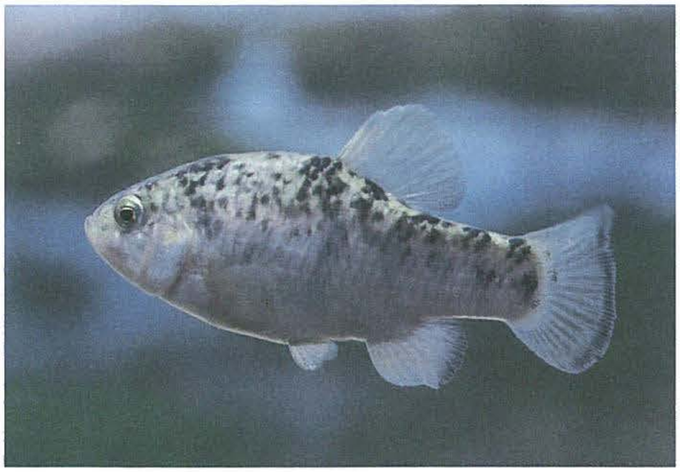


Figure 52. Male (left) and female (right) whitefin pupfish/ *cachorrito aleta blanco*, 47 and 39 mm in total length, respectively, from Ojo de Galeana (Ojo de Arrey), Chihuahua. Pupfish of this general morphology are also widely distributed in the upper Rio Yaqui basin; the form was not considered by the American Fisheries Society.

Figure 53. Female (left) and male (right) of the endangered Gila topminnow/*charalito*, 45 and 30 mm in total length, respectively, from Monkey Spring, Arizona.

depicted in Figure 52 is widespread in streams, springs, and marshes located in grass and woodlands of the northern Mexican Plateau east of the Sierra Madre Occidental. All known occurrences for the species are at elevations higher than about 1400 m.

Topminnows in both the Colorado and Yaqui basins are found from near 1500 m to sea level, although high-altitude occurrences are most commonly associated with outflows of springs. In the Colorado basin, the Gila topminnow/*charalito* (Fig. 53) formerly occurred from Frisco Hot Spring, New Mexico, to near the mouth of the Gila River; it was perhaps most widespread in spring-fed creeks and marshes of southern Arizona between 900 and 1500 m above mean sea level. In the Rio Yaqui basin, the Yaqui topminnow/*charalito* similarly lives in upper parts of the system, to be replaced by two other species near the river's mouth.

As might be anticipated from the common name, topminnows live near the surface in shallow water, and are often associated with aquatic vegetation or other cover. They feed on small invertebrates such as mosquito larvae, microscopic plants, and sometimes detrital materials.

Both pupfish and topminnows reproduce year around in the constant temperatures of springs, but have strong spring-summer reproductive cycles in habitats with seasonally variable temperatures. Pupfish are highly territorial, with males defending small, circular patches of substrate against all other males, and against other species as well. Females remain aloof from males, living and feeding in deeper parts of the habitat. When ready, a female enters the territory of a male to spawn on the substrate. The males inadvertently, although effectively, protect the eggs with their aggressive territorial behavior. Young are generally ignored, so they move and feed throughout the male's territory with impunity. Growth is rapid, and young hatched in early spring can mature and reproduce in mid-summer.

Most fishes deposit their eggs outside the female's body. Topminnows, however, practice internal fertilization and development of young. Sperm packets (spermatophores) are delivered to the female's genital opening by use of a highly modified anal fin of the male. A female can store sperm, so a single sex act can serve to fertilize eggs throughout her life.

Topminnows in the lowermost Rio Yaqui include one kind that differs even more markedly from most other fishes in its mode of reproduction. Most topminnows are bisexual: males and females breed normally. Some, however, have developed systems where males do not exist. Females breed with another kind of topminnow male, producing all female offspring of hybrid origin. The way this system operates remains poorly understood. In any case, young develop within the female's ovaries (Fig. 54) to a large size (up to 10 mm total length), and can swim, feed, and avoid predators a few seconds after birth. As with pupfish, sexual maturation is rapid, sometimes less than six weeks after birth in warm water in summer.

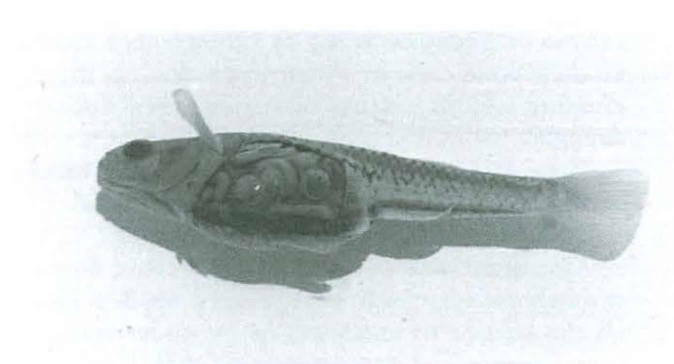


Figure 54. Near-term embryos in a female Gila topminnow/*charalito de Gila* (40 mm in total length) from Monkey Spring, Arizona.

Low Desert Streams

Most low desert streams are now diverted by dams in their headwaters, or have their subterranean supplies interdicted by well fields that pump them dry. Pumpage for irrigation and other uses has lowered water tables more than 50 m in most valleys and more than 200 m in some, and beheading of streams by impoundment in montane parts of the watersheds prevents aquifer recharge. Only streams with reliable spring inflows remain below 600 m, and many of these no longer flow except through manmade delivery channels. Where they do, such as in and below the Grand Canyon, humans are simply using the natural channels for water deliveries from upstream reservoirs. The present section is therefore largely a description of the past, a reconstruction of an original state that may never be re-created. Some native fishes persist in the mainstreams, but only in special places.

All large rivers of the region are (or historically were) characterized by high runoff from spring and early summer snowmelt in distant mountains, and a second period of lesser flooding during summer rains. Prior to man's modifications, the Colorado River near Yuma fluctuated in volume from less than 0.35 to more than 7000 cubic meters per second.

All these streams flow across geologic structure, at least in part, and thus alternately pass through broad alluviated valleys and narrow gorges (Fig. 4). Valleys represent downthrow blocks, and canyons are cut through uplifted blocks that comprise the northeast-southwest-oriented mountain ranges of the region. Water tables in valleys, even in the hottest parts of the Sonoran Desert, were within a few feet of the surface prior to human alteration. Oxbow lakes, marshes behind natural levees (Fig. 55), and underflow that maintained permanent pools during drought were fed by these water tables. Perhaps more importantly, bedrock causing formation of

Figure 55. Topock Marsh along the lower Colorado River, Arizona, is artifically maintained, but must resemble conditions that existed in oxbow lakes, marshes behind natural levees, and backwaters prior to human modifications of the system. Photograph provided by the U.S. Bureau of Reclamation.

canyon reaches also acted as subterranean dams. Underground flow of water was forced to the surface creating reliable reaches of stream, even during drought.

These large desert rivers aggraded their valleys except in time of channel-straightening flood. Substrates of sand and fine gravel shifted continuously with the current. In reaches flowing through valleys, pools were formed by degradation on the outside of meanders or by undercutting of riparian trees, or were associated with large logs or other debris in the channels. Permanent features such as boulders or irregularities in stony walls of canyons caused scour, and deep places persisted despite continuous bedload transport.

Water quality varied radically. Snowmelt produced water low in total dissolved solids, while evapotranspiration in summer and inflows of mineralized springs promoted high salinities. As an example of the last, residents near Yuma reportedly impounded a low flow of the Gila River near the turn of the century to prevent contamination of downstream irrigation supplies by "alkali water". A small flood in the Gila breached the dike, and toxic water flowed into the Colorado River mainstream, supposedly killing fishes for a distance of more than 160 km, all the way from Yuma to the Gulf of California.

Temperatures also must have fluctuated radically, yet extremely high water temperatures likely did not occur because of evaporation into the dry desert air. Dangerously high water temperatures can develop, however, when dark substrates back radiate heat into clear, overlying water, or, as noted before, when unusually high humidities suppress evaporation from water surfaces. Canyon segments remained cooler since stony walls shaded the stream and evaporation resulted in even more rapid cooling when direct sunlight was excluded.

The lowermost portions of regional rivers originally consisted of large, sand-bottomed channels meandering over broad deltas (Fig. 56). Water on undisturbed deltas must have been seasonally warm, silt laden, and rich in organic debris transported from their vast watersheds. Some were lined by dense riparian woodlands (Fig. 57), forests of cottonwoods and willows and understories of arrowweed, seepwillow, and other woody plants. Deltaic channels were so broad, however, that only a small percentage could have been shaded from intense summer sunlight. Rocks and boulders of headwaters had long before been ground to finer particles, and aggradation of silt and sand was the rule except at the highest flow. Organic materials arriving on deltas also had been pulverized; even

Figure 56. View of the Colorado River Delta southward from near the International Boundary in 1975. This vast and complex region has now been largely desiccated as a result of water diversions and depletions upstream. Photograph provided by the U.S. Bureau of Reclamation.

logs washing from mountain forests were mostly reduced to microscopic particles or actually dissolved before nearing the sea. Dissolved and particulate organic material provided fertilizing nutrients not only for deltaic communities, but also for the Gulf of California. Impacts of entrapment of these nutrients by upstream reservoirs on the ecology of the gulf has never been assessed.

Remarkable variation in discharge was the rule. Water spread widely over the broad, nearly level floodplain, and each flood resulted in channel changes. Oxbow lakes and sloughs were formed, only to be filled with organic and inorganic debris during periods of low discharge, then cut again by later flooding events. This was especially true where soft deltaic sediments were marked by complex series of spreading channels or distributaries (Fig. 56). Channels were created and disappeared in days or hours. Aggradation formed natural levees and lakes,

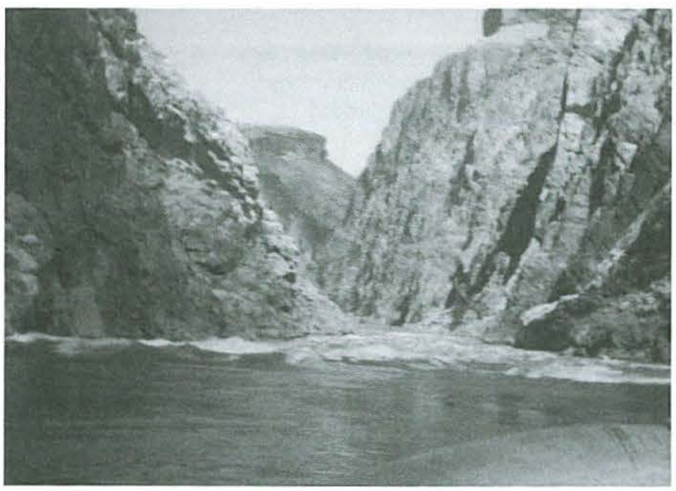
Figure 57. Riparian woodland on the Colorado River Delta, ca. 1890. Photograph provided by R. D. Ohmart.

occasionally even diverting flow into inland basins such as the Salton Sea. The Colorado River Delta was further influenced by a remarkable tidal bore. Tides in the Sea of Cortez exceed 9.0 m at the river's mouth, among the highest in the world. Swift, destructive tidal currents moved with remarkable speed for more than 100 km upstream.

Low Desert, Riverine Fish Communities

Canyons of large desert rivers present two basic types of habitat. Most impressive are the reaches that are termed whitewater in the jargon of river runners, where bottom irregularities cause waves, whirlpools, and other turbulence. The second type is called flatwater, where deep, strong, unobstructed flow occurs, but with little surface roughness (Fig. 58).

Figure 58. Looking downstream from a flatwater reach to a major rapid on the Colorado River in Grand Canyon, Arizona, 1970.



The Colorado River is notorious for whitewater, especially in the Grand Canyon, and the Rio Yaqui flows through similarly constrained reaches through parts of its course. Wider places separating canyons tend to have different faunal compositions, covered below.

Canyons of the Colorado River support a special fish community consisting mostly of humpback chub, speckled dace, bluehead mountain-sucker, and flannelmouth sucker. Of these, only the humpback chub (Fig. 59) is found in whitewater, where it lives in deep eddies associated with large boulders, indentations in canyon walls, or other protecting obstructions. This is one of the most bizarre minnow species in the world, with large, strong fins, leathery skin with deeply embedded scales, and a remarkable hump between the head and dorsal fin. The last reflects a powerful and compact musculature required for movement within its habitat and through rapids separating one eddying habitat from another. Despite years of study, little is actually known of the humpback chub's feeding and reproduction. We know that it lives a relatively long time, perhaps more than 30 years, and that it reproduces in spring/early summer. The fish is rare, and classed as endangered, so few have been sacrificed for biological examination.

Speckled dace (Fig. 31) live along sand and gravel bars of flatwater reaches of the Colorado River. Flannelmouth suckers (Fig. 60) remain in deeper water except when feeding, when they move onto

Figure 59. The largest known population of endangered humpback chub lives in the lowermost Little Colorado River, Arizona. This adult, 36.0 cm in total length, was photographed at Willow Beach National Fish Hatchery.

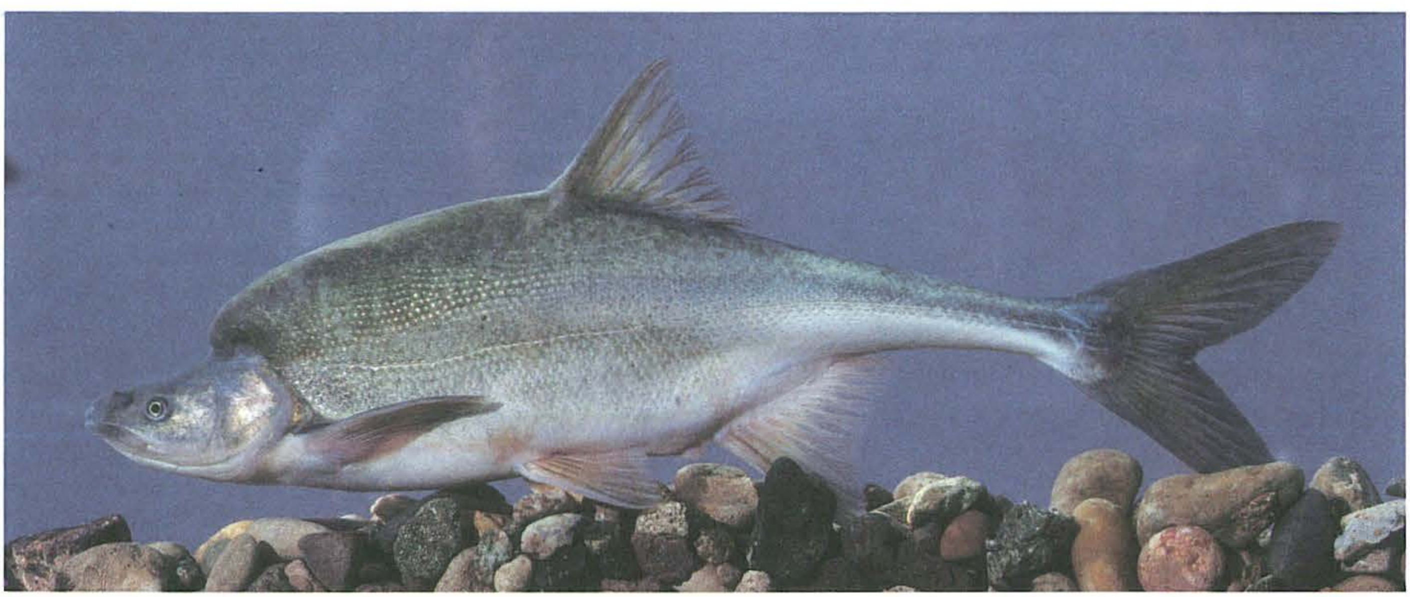


Figure 60. Flannelmouth sucker, 28.5 cm in total length, from the Virgin River, Arizona. This species remains common in the upper Colorado River basin, but has disappeared entirely from the lower basin (including the Gila River drainage) downstream from Lake Mead.

moderate rapids and riffles in pursuit of bottom-dwelling invertebrates, algae, and organic debris. Bluehead mountain-suckers (Fig. 61) tend to feed on harder bottoms, scraping algal films and other organic materials (including clinging invertebrates) from rocks with their modified, cartilaginous jaws. All three of the last species breed in spring on riffles.

Figure 61. Breeding adults of bluehead mountain-sucker, ca. 45.0 and 35.0 cm in total length, from the mouth of the Paria River, Arizona. This species remains abundant within its native range in the upper Colorado River basin. Photograph by W. G. Kepner.

Canyon-bound reaches of the Rio Yaqui are occupied by roundtail chubs, Yaqui suckers, and Yaqui catfish/*bagre del Yaqui* (Fig. 62). Beautiful shiners and Mexican stonerollers live along the banks and in quieter places. It is notable here that little sampling has been done in these reaches, which are mostly isolated and accessible only by river. It will not be surprising if future collectors in the Rio Yaqui and its major tributaries discover new species of swift-water fishes.

The fish community of wider, less dramatic lower parts of the Colorado River, most of which is now dry or otherwise highly modified, consisted of a small number of special kinds, plus in its lowermost reaches a few marine species that entered from the Gulf of California. Freshwater fishes of the lowermost reach included Colorado squawfish/*charalote*, bonytail/*charalito eleganti*, and razorback sucker/*matalote jorobado*, all of which passed readily through canyon reaches, but rarely lived there. All available evidence indicates that squawfish and razorback were abundant and that bonytail was common as well. Flannelmouth sucker, woundfin, and roundtail chub also were present, but are represented by only a few specimens in early collections and must have been relatively rare. Shallow sloughs and backwaters supported desert pupfish. Roundtail chub, Yaqui

Figure 62. Yaqui catfish/*bagre del Yaqui*, ca. 35 cm in total length, from the Rio Sirupa (Rio Aros) mainstream, Chihuahua. This species, considered of special concern, almost certainly lived in the past in San Bernardino Creek, Arizona. It remains relatively common in the Rio Yaqui system.

sucker, and Yaqui catfish are joined by Pacific shad/*sardinita del Pacifico* and Sinaloan cichlid/*mojarra sinaloense* in the lowermost Rio Yaqui. No studies have appeared on the ecology of any of these five species in Mexican waters, but as already covered, the roundtail, sucker, and catfish have conspecific or close relatives in streams of the United States, where some data are available.

Habitats of Colorado squawfish (Figs. 63–64) include deeper pools, eddies, riffles, sloughs, quiet backwaters, creek mouths, swift runs, and shallows along shore. This is the largest North American minnow, achieving lengths of almost 1.8 m and perhaps 45 kg in weight. Young move into embayments and backwaters along the channel, and feed mostly on crustaceans and insects, shifting to

Figure 63. Colorado squawfish/*charalote* caught near the mouth of Cherry Creek, Arizona, near the turn of the century. This endangered species is now extirpated from the lower Colorado River basin. Photograph provided by W. L. Minckley.

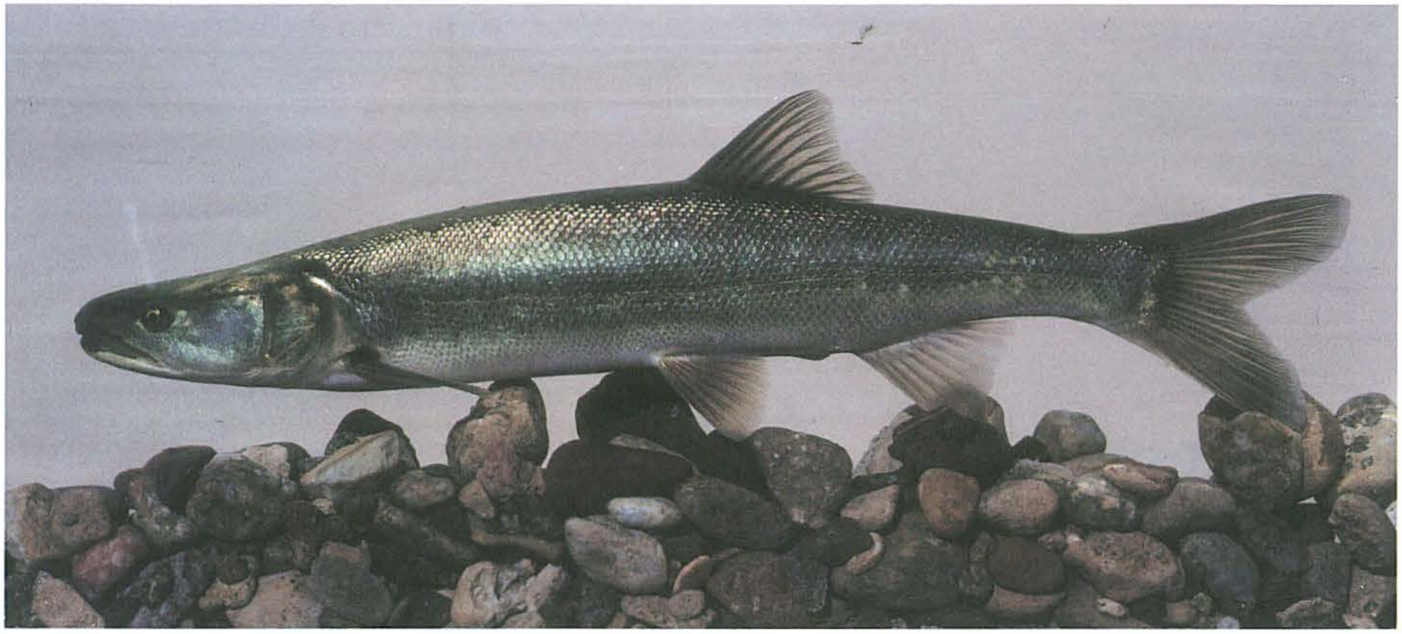


Figure 64. Colorado squawfish/*charalote,* 36.0 cm in total length. The specimen is a hatchery-reared offspring (1974 year-class) of broodfish captured in the Green River basin of Utah.

fishes after becoming longer than 75 to 100 mm. Adults eat other fishes and thus probe and wander extensively in search of food. A squawfish of 90 cm long or more must have devoured almost any other fish in the river.

Squawfish spawn over gravel bars in channels of rivers in spring or summer, after water temperatures exceed 20° to 21° C. They often move long distances to reproduce, and return year after year to the same or a similar spawning area. Major runs in spring into the Gila River, well documented in old newspaper accounts, must have been related to spawning. Breeding squawfish become silvery above and creamy yellow on the belly with an intense array of bright golden flecks on the upper sides.

Razorback suckers (Fig. 65) tended to occupy strong, uniform currents over sandy bottoms. They also lived in eddies and backwaters lateral to the river channels, sometimes concentrating in deep places near cut banks or fallen trees. Large adults approached or exceeded 75 cm in length and more than 5.0 kg in weight. A remnant population of large adults in Lake Mohave, Arizona-Nevada, spawns from late January through April over gravelly bottoms in relatively shallow water (Fig. 66). Males become dark brown to black on the back and develop a russet- to orange-colored lateral band and yellow belly. Coarse, sharp tubercles, which are horn-like outgrowths of skin, are developed on the anal, caudal, and pelvic fins, and on the caudal peduncle. These function to hold the female during the spawning act. Females that have spawned repeatedly may be scarred and abraded from contacts with males and with rocky bottoms. The eggs are adhesive and are deposited in spaces between gravels. They hatch in a few days and young move to the shoreline for a time.

Despite successful reproduction, there is no evidence for successful recruitment of young fish into the Lake Mohave population for more than two decades. Larvae mysteriously disappear before achieving 15 mm total length. The same situation appears to exist in other, riverine parts of the Colorado River basin, and the species is proposed for listing as endangered. Under natural conditions in streams, young fish must have occupied shorelines, then moved with growth into habitats similar to those just described for young squawfish. Razorbacks feed mostly from the bottom, but have elongated, "fuzzy" gillrakers and a subterminal mouth both characteristic of planktonic or detrital feeding habits.

Remarkably little is known of the ecology of bonytail (Fig. 67), and they are almost gone in nature. A small population persists in Lake Mohave, but only a few have been recorded from the upper Colorado River in recent years. As with razorbacks, there are no records of successful recruitment of this species for many decades; specimens caught in nature all appear to be old (35–40 yr) adults. Bonytail are large, streamlined fishes that have long

Figure 65. Male razorback sucker/*matalote jorobado*, 57.5 cm in total length, from Lake Mohave, Arizona-Nevada. This formerly widespread, mainstream species of the Colorado River basin is now reduced to three local populations and scattered individuals. There are no records documented by specimens from Mexico since near the turn of the century. It has been proposed for listing as endangered throughout its range.

Figure 66. Three male razorback suckers/*matalote jorobado* approaching a female in a spawning aggregation in Lake Mohave, Arizona-Nevada. Photograph by Gordon Mueller

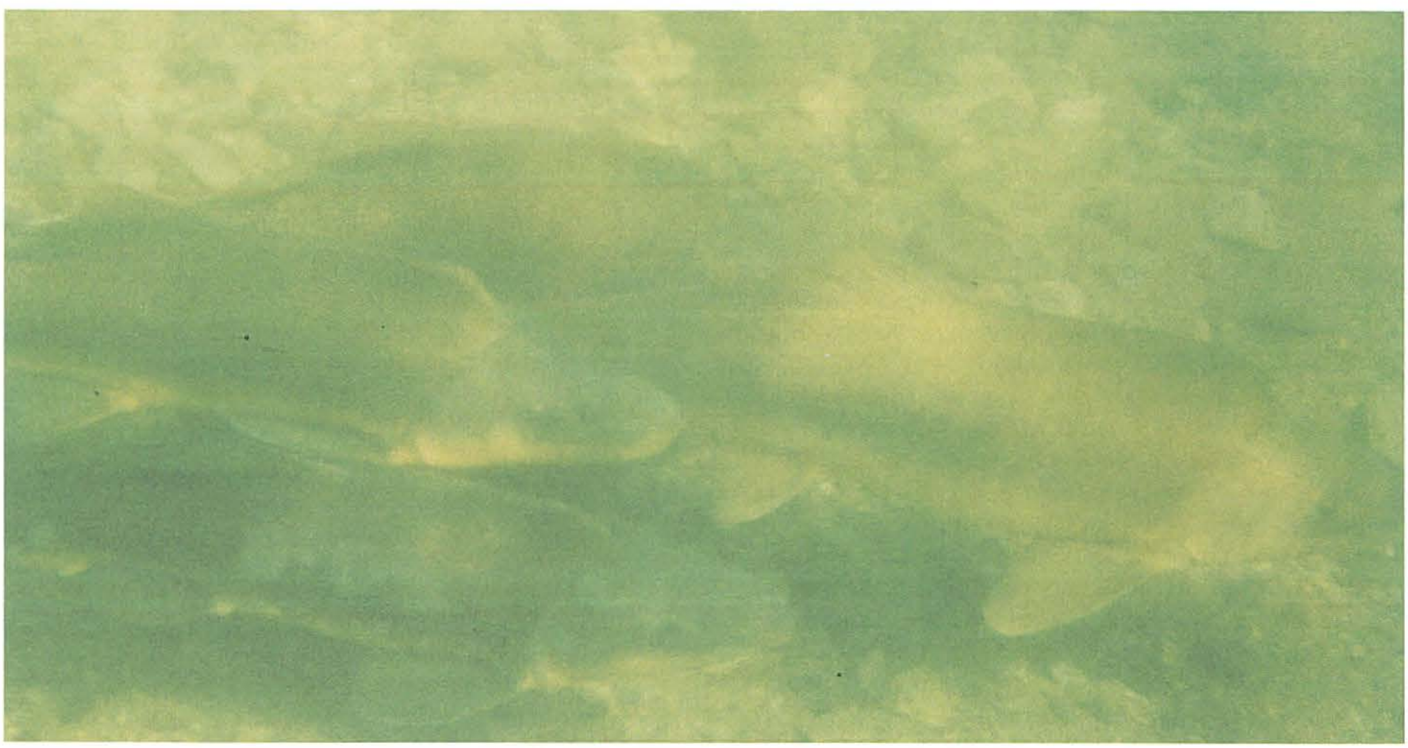


Figure 67. Bonytail/*charalito eleganti*, 52 cm in total length, from Lake Mohave, Arizona-Nevada. This is considered by many workers to be the most endangered freshwater fish in western North America. An attempt is underway to move all individuals encountered in nature into captivity to serve as a broodstock for future reintroductions.

been thought to be adapted to turbulent habitats, similar to those inhabited by humpback chubs. It seems more likely, however, that their body shape makes them most at home in relatively swift but laminar flow, as is still found over smooth sand bottoms in the Colorado River channel. A few adults examined for food habits had eaten a high percentage of terrestrial invertebrates, drifting insects that had been blown by wind or otherwise fallen into the river. Occurrence of adult aquatic insects in stomachs also implies feeding at or near the water surface. The only reproductive activities recorded for bonytail are of aggregations of adults over gravelly "reefs" in artificial impoundments; habitats and activities of young are unknown in nature. The largest recorded bonytail was about 65 cm in length.

Two other species of the mainstream Colorado River attain relatively large sizes. Flannelmouth suckers can grow to nearly a meter in length and roundtail chub to more than 40 cm; both are discussed elsewhere. The next two species are relatively small. Woundfin (Fig. 68) rarely exceed 10 cm long, and desert pupfish rarely exceed 40 mm, even as an extremely large adult. The first three of these were rare in early collections from the lower Colorado River basin, and the last was almost certainly common in more ephemeral habitat too severe for other species, such as on the delta itself. Desert pupfish persist on the delta at present, typically in highly saline pools associated with inflowing springs and seeps.

The woundfin was the only small, short-lived species known from the channel of the lower Colorado River. This species is one of a unique group of North American minnows in having the leading rays of its dorsal fin modified into a stout spine. Other members of this minnow group also have such rays, but not so spectacularly developed. The species is adapted for life in highly turbid water over shifting sand bottoms. Its fins are large and sickle-shaped, and dorsal streamlining is extreme while the lower body is flattened to fit closely to the

Figure 68. Woundfin, ca. 90 mm in total length, from the Virgin River, Arizona. This endangered species, once known from both the lower Colorado and Gila rivers, is now completely restricted to the Virgin River mainstream. Nevada-Arizona-Utah.

bottom. The scales are reduced to bony platelets, some of which form longitudinally arranged ridges that may function to direct water over the body surface and assist in maintenance of position in swift runs. Woundfin select areas with rocky substrate in current for spawning, at a temperature of about 25 ° C. Young grow rapidly, achieving lengths of 20 to 40 mm a month or two after hatching. The species was known from the Gila and lowermost Colorado rivers in the late 1800s but since then has been found only in the Virgin River mainstream.

In the Rio Yaqui, the Pacific shad/*sardinita del Pacifico* (Fig. 69) is a midwater inhabitant of lakes or open parts of rivers. They feed on finely divided detrital material from the bottom or on plankton in the water column, and in doing so act as an avenue for these foodstuffs through the food chain to larger fishes. Shad in freshwaters provide a food base for predatory fishes just as anchovies provide food for larger fishes in the sea. With construction and filling of reservoirs in the Rio Yaqui system, Pacific shad appeared far inland, thus acting as forage for larger fishes in those newly created habitats. The threadfin shad, a similar species from eastern drainages of the United States and Mexico, has recently been introduced into the Rio Yaqui basin, the results of which are not predictable.

The Yaqui catfish (Fig. 62) resembles the common channel catfish of eastern North America. They commonly achieve more than 40 cm in length and a kilogram in weight, and live in relatively deep water during the day, only to move onto riffles and runs at night to feed. The few stomachs that have been examined contained aquatic invertebrates, other fishes, and organic debris. Spawning is apparently similar to channel catfish, with the male defending eggs in a depression or hole in the bank and protecting his newly hatched young for a time. Young live in shallower water than adults, often on riffles among cobble and boulders. Channel, blue, and flathead catfishes from eastern North America have now been introduced into the Rio Yaqui system, and there is already evidence of hybridization between the first and the Yaqui catfish.

Figure 69. Pacific shad/*sardinita del Pacifico*, 17.8 cm in total length, from Marina del Rey, Presa Alvaro Obregon, Sonora. Status of this midwater, possibly estuarine species is speculative. It is known from scattered localities near the sea in western Sonora.

Last among the freshwater fishes characterizing the lowermost Rio Yaqui basin is the colorful Sinaloan cichlid (Fig. 70), which lives in quiet waters of the mainstream, creek mouths, and sloughs and

Figure 70. Sinaloan cichlid/*mojarra sinaloense*, 12.5 cm in total length, from Rio Chico, Sonora. Status of this species is unknown.

backwaters. Cichlids are tropical in distribution, and the lower Rio Yaqui is the northernmost limit of natural occurrence of this group on the west coast of Mexico. Sinaloan cichlids attain lengths of at least 25 cm and weights of 0.3 kg. Nothing is known of its breeding habits, but most species of this group spawn in spring and summer. Young are aggressively guarded by a parent until large enough to fend for themselves. They then move to quiet vegetated areas to feed and grow. Cichlid species sometimes have highly specialized food habits, but Sinaloan cichlids appear to be generalists, feeding on detrital materials, invertebrates, and aquatic vegetation.

Marine Species

It would be remiss not to include a few marine components of the fish faunas of these two river basins, especially since aquatic communities of the deltas received essentially no study before they were highly modified or essentially destroyed by upstream developments. Most fish species from the Gulf of California scarcely penetrated the Colorado River upstream past the zone of tidal influence. Only striped mullet/*lisa* and Pacific tenpounder/*machete* moved far inland. The giant totoaba/*totoaba* (Fig. 71), endemic to the upper Gulf of California, spawns in the Colorado River estuary, and was an important commercial fish in the past. It has almost disappeared due to overfishing and likely as a result of changes following construction of mainstream dams in the United States.

A substantially larger marine fauna existed on the Rio Yaqui delta. Striped mullet (Fig. 72) are common, and comprise a major resource for Mexican fishermen. Other kinds of mullets are present, reflecting the tropical influences in this more southern fauna. Sea trouts are present, and snooks come into distributaries and move as far upstream as the dam at Presa Alvaro Obregon, more than 100 km from the sea. Machete also is present, as are two marine catfishes.

The most upstream record for striped mullet in the Colorado River is near Blythe, California, about 300 km from the sea. Pacific tenpounder (Fig. 73) moved about half that distance, to near Yuma, Arizona. Both occupied the Salton Sea after it filled in 1905–07, but disappeared after a few years, presumably due to lack of reproductive success. Both species now move upstream in the Rio Yaqui to the insurmountable dam forming Presa Alvaro Obregon. There is no information on their distributions prior to construction of that dam. Machete rarely exceed 36 cm long in the lower Colorado River, but they achieve 91 cm or more in length in the sea. Its major prey are small plankton-feeding fishes such as anchovies that school in rich estuarine areas.

Striped mullet form a substantial part of the fish fauna in mouths of major tropical and subtropical rivers worldwide. They remain an important component of the deltaic fish community of the lower Colorado River, feeding mostly on detritus, finely divided organic materials that accumulate in quiet places. Mullet typically spawn in the sea, and

Figure 71. This photograph of a totoaba/*totoaba* being handled on a research vessel provides a perspective of the size of this giant endemic of the Gulf of California. Photograph provided by J. R. Hendrickson.

Figure 72. Striped mullet/*lisa*, 38 cm in total length, from Estuario de Santa Clara, Sonora. This predominately marine species enters the lower parts of major rivers throughout most of the tropics worldwide; it was not considered by the American Fisheries Society.

their young move into estuaries to feed and grow. Young individuals (to 15 cm total length) swarm in the Colorado River estuary; larger (presumably older) fish tend to move farther upstream when water is available. When adult (longer than 35 cm) they disappear from freshwater, moving back to the sea to reproduce.

Fishes of Desert Oases

Springs rising from subsurface sources sometimes form special aquatic habitats in deserts, which may be inhabited by equally special fishes. Springs occur where fractures in the earth allow deep waters to rise to the surface, or as points where water accumulating at higher altitude and percolating through porous strata emerges. Water from deep sources often is hot and charged with gasses and salts otherwise uncommon in a region. Others represent a simple intersection of a local water table with the land surface. Spring water is typically clear and constant in volume. Fishes living in such places have few environmental cues other than daylength—there are no spring floods or summer droughts, seasonal temperature changes, or changes in substrate or turbidity with which to deal. They may thus reproduce throughout the year and grow at a constant rate dependent on population size rather than physical factors.

Figure 73. Pacific tenpounder/*machete*, 15.0 cm in total length, from Estuario de Santa Clara, Sonora. This relative of the tarpon was not considered by the American Fisheries Society.

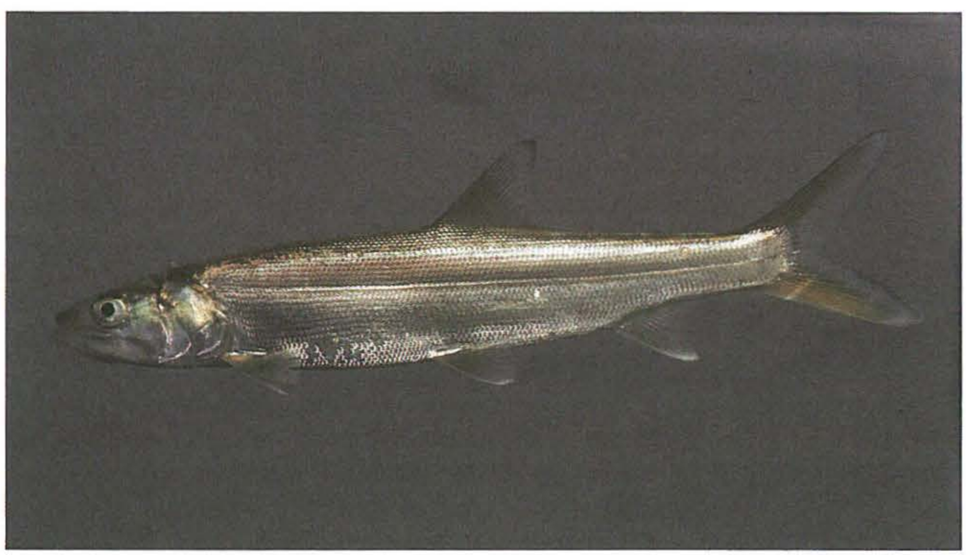


Figure 74. Source pool of Mormon Spring, Nevada, 1981, a major habitat of White River springfish. The spring outflow leads to an extensive bulrush marshland.

Figure 75. Endangered Moapa dace, 55 mm in total length, from the upper Moapa River, Nevada.

Figure 76. White River springfish, 35 mm in total length, from Mormon Spring, Nevada. Various subspecies of this colorful species, most of which are considered threatened or endangered, are distributed in springs of the pluvial White River Valley, Nevada.

Desert springs are often difficult to see until one is immediately upon them. Soils surrounding them are typically too waterlogged or saline to support large, woody vegetation (Fig. 74), and highly tolerant sedges, grasses, and other hydrophytes (or halophytes) may have low growth-forms like that of surrounding desert vegetation. Little erosion occurs, and outflows commonly meander through undercut, sedge-choked solution channels. Bottoms are made up of organic materials and flocculent sediments formed through chemical action.

A series of basins in eastern Nevada now holds a number of disjunct spring systems that once fed the pluvial White River (Fig. 1). This stream, which flowed south to enter the Colorado River, still supports a substantial fish fauna including chubs, speckled dace, spinedaces (one extinct), and a mountain-sucker clearly allied to species and populations of the lower Colorado River, along with a number of other kinds of more obscure relationships. One example of the last is the Moapa dace (Fig. 75), a small minnow restricted to thermal pools and their outflows of the upper Moapa River. This species is rarely found in water cooler than 30° C, and apparently prefers a temperature range of 31° to 34° C. It is classed as endangered because of its extremely limited distribution.

The White River springfish (Fig. 76) also lives in thermal springs and outflows of this same system, and is equally as unique as the Moapa dace. This species is a near relative, or member, of a central Mexican family of livebearing fishes. It differs from Mexican species in retaining the primitive, egg-laying habit. Some springfishes in the White River live at temperatures exceeding 36.7 ° C. and at extremely low oxygen concentrations. Most populations are threatened by introduced fishes, but those living in hot, low-oxygen water have less of a problem since the exotic species cannot invade their special habitat. The Monkey Spring pupfish (Fig. 77) of southern Arizona was not so lucky. Largemouth bass were introduced into their habitat, and within a few months, the native species was gone.

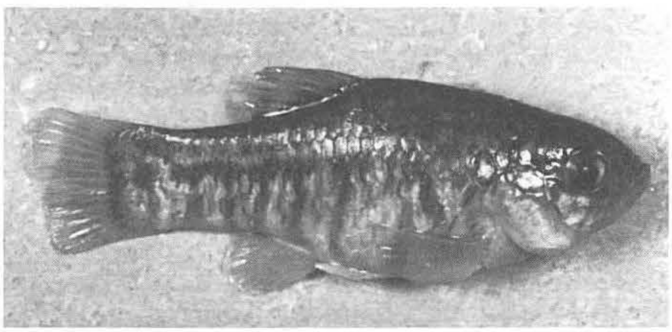
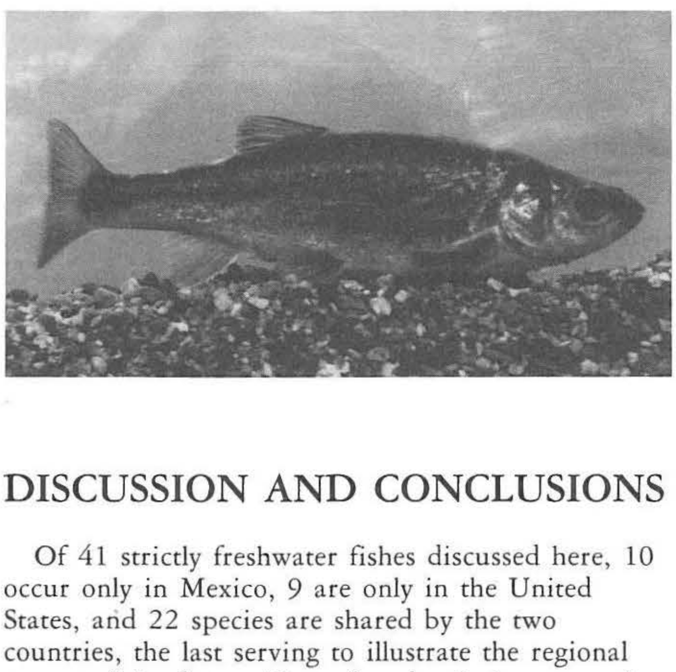


Figure 77. Extinct fishes from the Monkey Spring system, Arizona. Above: Monkey Spring pupfish, 55 mm; Below: Gila chub, 15 cm.



DISCUSSION AND CONCLUSIONS

Of 41 strictly freshwater fishes discussed here, 10 occur only in Mexico, 9 are only in the United States, and 22 species are shared by the two countries, the last serving to illustrate the regional nature of the fauna. Those found only in one or the other country represent in large part local endemics, which demonstrate in their isolation some of the uniqueness of fishes in arid lands. In 1989, 28 (68%) of the 41 taxa were officially recognized (hereafter listed) as threatened, endangered, or of special concern by the American Fisheries Society. Three species from the region (Las Vegas speckled dace, Pahranagat spinedace, and Monkey Spring pupfish, not included in the above compilation) were reported to have suffered extinction.

Definition of just how much trouble these fishes are actually encountering is a major problem. Fishes are difficult to assess from the standpoint of population status. In fact, they are even often difficult to discuss since they live in water, a medium inconvenient for humans to enter. Fishes are furthermore difficult to observe or capture, and even to identify after they are in hand. Lastly, for some reason they are often considered "second-class citizens" when compared with four-legged, furry or feathered beasts; humans identify more with warm-blooded animals that resemble themselves.

Despite this, if one determines that a fish exists only as a hundred or so individuals in a single tiny spring, it can readily be defined as endangered since a single event could destroy it. Widespread species are another matter, and most fishes in this region were, in fact, relatively wide ranging. A fish may become greatly reduced in range, such as the Sonoran topminnow that lived from western New Mexico to the Colorado River then south through Arizona and Sonora. It now occupies fewer than 10 natural localities in the United States. One might also believe this sufficient to define endangerment. However, each existing population consists of hundreds or thousands of individuals, and overall population size may actually number in the millions. This is a substantial number when compared with some endangered terrestrial species such as California Condor or Mexican Wolf, which are reduced to only a few individuals. However, a short-lived species such as topminnow may disappear in a year or less when subjected to an efficient predator such as the introduced mosquitofish, so size of local populations may have little to do with its actual status.

Others, such as bonytail of the Colorado River mainstream, may be equally as rare as California Condor. Fewer than 50 individuals have been caught despite intensive efforts since 1975. This fish is so rare that it cannot be studied in nature. Further, it appears to be hybridizing with other chubs because the few remaining wild individuals cannot find suitable mates. Biologists have no firm ideas why this species has disappeared. As with both the condor and wolf, artificial propagation has been initiated to perpetuate the bonytail, although it has been difficult to capture enough individuals to establish a viable broodstock.

An intermediate state between the topminnow example and that of bonytail involves the razorback sucker, which enjoys one population that exceeds 50,000 individuals in Lake Mohave, Arizona-Nevada, yet is almost gone from the remainder of its formerly extensive range (that included much of the Colorado River system). Larvae are produced by the thousands in Lake Mohave, but disappear before even attaining the juvenile stage. There is no evidence for recruitment of young fish into the adult population for at least 30 years, and researchers have concluded that they are eaten by introduced predators. Wild-caught and hatchery-produced fish are fertile, however, and the species readily responded to artificial propagation.

In the United States, it is obvious that modifications of rivers, drying of reaches below dams, channelization, and diversion of large volumes of water from place to place, destroy habitat and eliminate the fauna. Stabilization of rivers is similarly disruptive to natural communities, and changed temperatures and flow regimes below dams exclude native fishes. Major impacts have further been associated with use and misuse of watersheds. Overgrazing, logging, and other practices have promoted increased erosion and sediment transport. Chemical modifications include changes in nutrient relations due to damming and watershed uses, and dumping of injurious substances by industrial and domestic activities.

Modifications in Mexican river systems are not yet so extensive, but are of the same kinds and magnitudes. For example, the Rio Yaqui system is not yet as completely dammed and diverted as the Colorado. Some changes in Mexico are, however, equally as severe as any in the United States. Heavily logged watersheds promoted widespread erosion and pollution reported by Aldo Leopold and others in the 1930s, and the pressure of grazing and other destructive land-use has long been evident. As in the United States, diversion dams desiccate long reaches of channel, effluents from mines and smelters influence tributaries and mainstream alike, and domestic sewage pollutes many streams below towns and cities.

Native fishes tend to remain in places where physical and chemical modifications are minimal or non-existent, and natural stream conditions and native fishes still go hand and hand in Mexico. However, in the United States, a substantial number of native species are disappearing from rivers and creeks that appear in a natural state, which seems inconsistent. What differences exist in conditions in the two countries that cause different biological results? The introduction and establishment of non-native fishes, which replace natives through competition for food, space, or other resource, or simply devour them, seems the most logical answer.

Historic evidence points toward a development of a depauperate fish fauna in harsh riverine environments of the American Southwest over the past 5 to 10 million years, and maybe longer. Evolution selected for ecological generalists—specialization through attainment of generalized traits—with parallel development of highly attuned interactive capabilities among a few species. Non-native fishes had to carve out new niches in their new world, and in the process replaced the natives. Perhaps as importantly, native fishes had co-evolved in communities that lacked carnivores other than those developed from among their own ranks (i.e., the Colorado squawfish). Predatory fishes common to other parts of North America did not occur—gars, bowfins, pikes, most catfishes, sunfishes, and basses disappeared early in the geologic history of this region, or were never present. The native fauna had never before experienced pressures from piscine predators.

Since essentially all the introduced fishes were characteristic of quiet water, preadapted for life in artificial impoundments, human stabilization of rivers and construction of reservoirs in western United States prepared the region for establishment of an exotic fauna. Construction of impoundments was accompanied by stocking of non-native fishes from eastern North America and elsewhere. Most game fishes are predators—northern pike, larger catfishes, largemouth, smallmouth, striped, white, and yellow basses, crappies, and walleye. Mosquitofish, introduced for control of pestiferous insects, is a notorious predator on small fishes as well. Forage fishes stocked to feed the introduced predators—threadfin shad, a whole series of minnows called shiners (red, redside, golden shiners), fathead minnows, smaller sunfishes (bluegill, green, redear), etc.—are potential predators as well as probable competitors. The impacts of omnivorous fishes like common and grass carps, African cichlids (tilapias), and bullhead catfishes are relatively unknown.

A tremendous loading of aquatic habitats occurred and continues, so that the original fish fauna of the Colorado River has been increased from a total of 32 species to more than 80. Furthermore, fishes that were introduced were generally transported from zones of faunal saturation, places such as the Mississippi River valley, Atlantic coastal drainages, and tropical Mexico and Africa, where hundreds rather than tens of species were naturally present. It is logical that fishes which developed and existed in association with large faunas should be more capable of dealing with biological adversity than one that had not before seen another species of its own genus. The native fish fauna, lacking experience with alien species, was disadvantaged, especially when non-native fishes became abundant.

Relative inaccessibility and a time lag in construction of reservoirs in Mexico has isolated that region from introduced fishes. Populations of non-native fishes are only now becoming available to invade and populate Mexican watersheds, and interactions among introduced and native species in that country are only beginning. The bottom line is, when non-native fishes become dominant, native fishes disappear. This pattern has been repeated with minor exceptions throughout western United States, and may be predicted with confidence in Mexico.

This ends the presentation, with the hypothesis that biological interactions are the ultimate factor causing disappearance of native fishes in the United States, even where physical and chemical conditions resemble the natural state. The "how" of species replacement has been avoided, other than by pronouncement and inference, and is left to future research. Unique possibilities exist to test these ideas through experimentation under field conditions, and to apply the findings to perpetuation of native fishes and natural aquatic systems, if humans chose to do so.

APPENDIX I. SELECTED REFERENCES ON AQUATIC HABITATS AND FISHES OF THE AMERICAN SOUTHWEST

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APPENDIX II. LIST OF COMMON AND SCIENTIFIC NAMES

NATIVE SPECIES

Tarpons and tenpounders, Family ELOPIDAE

Pacific tenpounder/*machete*	*Elops affinis*

Anchovies, Family ENGRAULIDAE

Shads, Family CLUPEIDAE

Pacific shad/*sardinita del Pacifico*	*Dorosoma smithi*

Salmons and trouts, Family SALMONIDAE

Apache trout	*Oncorhynchus apache*
Mexican golden trout/*trucha dorada mexicana*	*Oncorhynchus chrysogaster*
Gila trout	*Oncorhynchus gilae*
San Pedro Martir trout/*trucha de San Pedro Martir*	*Oncorhynchus mykiss nelsoni*
Yaqui trout/*trucha de Yaqui*	*Oncorhynchus* sp.[1]

Minnows, Family CYPRINIDAE

Longfin dace/*charalito aleta larga*	*Agosia chrysogaster*
Mexican stoneroller/*rodapiedras mexicano*	*Campostoma ornatum*
Ornate minnow/*sardinita ornata*	*Codoma ornata*
Beautiful shiner/*sardinita hermosa*	*Cyprinella formosa*
Humpback chub	*Gila cypha*
Sonoran chub/*charalito sonorense*	*Gila ditaenia*
Bonytail/*charalito eleganti*	*Gila elegans*
Desert chub/*charalito del desierto*	*Gila eremica*
Gila chub/*charalito del Gila*	*Gila intermedia*
Yaqui chub/*charalito Yaqui*	*Gila purpurea*
Roundtail chub/*charalito aleta redonda*	*Gila robusta*
Undescribed chub (Rio Yaqui)	*Gila* sp.
Pahranagat spinedace	*Lepidomeda altivelis*
White River spinedace	*Lepidomeda albivallis*
Virgin spinedace	*Lepidomeda mollispinis*
Little Colorado spinedace	*Lepidomeda vittata*
Spikedace	*Meda fulgida*
Moapa dace	*Moapa coriacea*
Woundfin/*charalito*	*Plagopterus argentissimus*
Colorado squawfish/*charalote*	*Ptychocheilus lucius*
Las Vegas speckled dace	*Rhinichthys deaconi*
Speckled dace/*pesecito moteado*	*Rhinichthys osculus* subspp.[2]
Loach minnow/*charalito adornado*	*Tiaroga cobitis*

Suckers, Family CATOSTOMIDAE

Yaqui sucker/*matalote Yaqui*	*Catostomus bernardini*
Cahita sucker/*matalote cahita*	*Catostomus cahita*
Sonoran sucker/*matalote sonorense*	*Catostomus insignis*
Flannelmouth sucker/*matalote*	*Catostomus latipinnis*

NATIVE SPECIES (Continued)

Leopold sucker/*matalote del Bavispe*	*Catostomus leopoldi*
Opata sucker/*matalote Opata*	*Catostomus wigginsi*
Little Colorado sucker	*Catostomus* sp.
Desert mountain-sucker/*matalote del desierto*	*Pantosteus clarki*
Bluehead mountain-sucker	*Pantosteus discobolus*
Rio Grande mountain-sucker/*matalote del Rio Bravo*	*Pantosteus plebeius*
Razorback sucker/*matalote jorobado*	*Xyrauchen texanus*

Ariid catfishes, Family ARIIDAE

Bullhead catfishes, Family ICTALURIDAE

Yaqui catfish/*bagre del Yaqui*	*Ictalurus pricei*

Livebearers, Family POECILIIDAE

Gila topminnow/*charalito*	*Poeciliopsis o. occidentalis*
Yaqui topminnow/*charalito*	*Poeciliopsis o. sonoriensis*
Common name unknown	*Poeciliopsis monacha*
All-female topminnow	*Poeciliopsis monacha-occidentalis*
Common name unknown	*Poeciliopsis prolifica*

Killifishes, Family CYPRINODONTIDAE

Desert pupfish/*cachorrito del desierto*	*Cyprinodon macularius*
Whitefin pupfish/*cachorrito aleta blanco*	*Cyprinodon* sp.
Monkey Spring pupfish	*Cyprinodon* sp.

Mexican livebearers, Family GOODEIDAE

White River springfish	*Crenichthys baileyi*

Mullets, Family MUGILIDAE

Striped mullet/*lisa*	*Mugil cephalus*

Cichlids or Mojarras, Family CICHLIDAE

Sinaloan cichlid/*mojarra sinaloense*	*Cichlasoma beani*

Drums and sea trouts, Family SCIAENIDAE

Totoaba/*totoaba*	*Cynoscion macdonaldi*

Snooks, Family CENTROPOMIDAE

NON-NATIVE SPECIES

Gars, Family LEPISOSTEIDAE

Bowfins, Family AMIIDAE

Pikes, Family ESOCIDAE

Northern pike	*Esox lucius*

NON-NATIVE SPECIES (Continued)

Shads, Family CLUPEIDAE	
Threadfin shad	*Dorosoma petenense*
Salmons and trouts, Family SALMONIDAE	
Rainbow trout	*Oncorhynchus mykiss*
Cutthroat trout	*Oncorhynchus clarki*
Brown trout	*Salmo trutta*
Brook trout	*Salvelinus fontinalis*
Minnows, Family CYPRINIDAE	
Common carp	*Cyprinus carpio*
Grass carp	*Ctenopharyngodon idellus*
Red shiner	*Cyprinella lutrensis*
Golden shiner	*Notemigonus crysoleucus*
Fathead minnow	*Pimephales promelas*
Redside shiner	*Richardsonius balteatus*
Freshwater catfishes, Family ICTALURIDAE	
Black bullhead	*Ameiurus melas*
Yellow bullhead	*Ameiurus natalis*
Channel catfish	*Ictalurus punctatus*
Blue catfish	*Ictalurus furcatus*
Flathead catfish	*Pylodictis olivaris*
Sunfishes, Family CENTRARCHIDAE	
Green sunfish	*Lepomis cyanellus*
Bluegill	*Lepomis macrochirus*
Redear sunfish	*Lepomis microlophus*
Smallmouth bass	*Micropterus dolomieui*
Largemouth bass	*Micropterus salmoides*
White crappie	*Pomoxis annularis*
Black crappie	*Pomoxis nigromaculatus*
Temperate basses, Family PERCICHTHYIDAE	
White bass	*Morone chrysops*
Yellow bass	*Morone mississippiensis*
Striped bass	*Morone saxatilis*
Perches and darters, Family PERCIDAE	
Walleye	*Stizostedion vitreum*
Cichlids (tilapias), Family CICHLIDAE	
Blue tilapia	*Oreochromis aurea*
Mossambique mouthbrooder	*Oreochromis mossambica*
Zill's tilapia	*Tilapia zilli*

[1]This common name is applied, collectively, to trouts of Sonora and Chihuahua (rios Yaqui, Mayo, and Casas Grandes basins).

[2]Systematics of the speckled dace complex has defied interpretation for years. A number of subspecies are described, some of which are listed as imperiled, and others remain widespread and relatively abundant.