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Southwestern Fishes and the Enigma of "Endangered Species"

Man's invasion of deserts creates problems for native animals, especially for freshwater fishes.

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Increasing public interest in man's pressure on the world's biota is evident from the number of agencies now actively involved in attempts to conserve what remains. These range from small, private conservation clubs to large established groups such as The Nature Conservancy and the International Union for the Conservation of Nature and Natural Resources. Activities of some organizations have been complemented by action on the part of some state and federal departments. For example, in January 1967 the Nevada Game and Fish Commission accepted responsibility for preserving the unique, endemic fishes of that state, and acted to protect habitats of a number of forms, and in December 1967 California initiated similar action (*1*). The U.S. Bureau of Sport Fisheries and Wildlife has defined rare and endangered species, and has begun to catalog them (*2*). A laboratory for studying and preserving such organisms is established at the Bureau's Patuxent Wildlife Center in Maryland.

Concern for natural environments has therefore spread from individuals through state, local, and federal governments, to become international in scope; with such a diversity of interest, it is not surprising that there are some problems. Emotion and lack of understanding often obscure the picture, and these factors, coupled with gross lack of basic biological information on many species, promote confusion and conflict. In this article we outline some of our ideas on the problem of "endangered species," discussing certain freshwater fishes of the Southwest as examples. We do not aspire to solve problems or smooth conflicts—perhaps we shall confuse the issues for some. If so, we hope the confusion leads to constructive inquiry.

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Kinds of Species

In considering "endangered species" one is immediately confronted with a need to understand, and to be able to explain, diverse abundances and degrees of dispersion. Except for domesticated animals, not considered here, the only objective definition of "endangered" must be one given in terms of an organism's ability to maintain its populations in nature. If the organism is to accomplish this, suitable habitat must be continuously available.

Recognizing some subjectivity and overlap, we divide organisms into four broad categories with respect to habitat needs:

1) Species having habitats produced by or changed by man, which have responded to man's influence by extending their range and abundance.

2) Organisms which have not responded to man's influence and which inhabit large geographic areas and are at present common.

3) Animals which require large, special habitats.

4) Species living in small, unique habitats as relicts or isolated endemics.

Category 1 is irrelevent to our discussion, except where introduced or invading forms are detrimental to indigenous species.

Category 2 likewise needs little discussion. This category includes animals, tolerant of environmental extremes, which occupy broad spectra of available habitats in their native ranges. Influences of man on animals of category 2 are fairly direct, and decreases in gross abundance (as opposed to decreases in number per unit area of suitable habitat) must already have occurred in most species. However, because of the wide ecological tolerances of these species, modifications of habitat must be extensive to extirpate them. Even if local decimation occurs, their broad, general distributions insure against extinction. There may in the future be cause for concern for animals of this category, but at present those of other categories bear far greater pressure.

Animals of category 3 are intimately dependent on some major feature or features of their environment. This dependence automatically places them in an untenable position if the feature they need is also needed by, or modified by, man. A familiar example is the American bison, which man actively eliminated in the natural state, converting its grasslands for agriculture and for grazing herds of domestic meat-producing animals. Bison now are essentially domesticated and are common, but for a few years they were certainly endangered. A number of other spectacular species are known, even by laymen, to be endangered. Large amounts of money and hundreds of hours of time are spent in perpetuating these forms, especially if they are of commercial, sporting, or esthetic importance.

Many fishes are included in category 3. In fresh waters, those kinds that depend on, or move through, large, strongly flowing rivers are especially noteworthy. No species of Pacific salmon (genus *Oncorhynchus*) is immediately endangered, yet certain runs of these fishes have declined or disappeared because of man-made obstruction of rivers or modifications of spawning grounds; such phenomena are well documented. Similar effects are known, but less well substantiated, in a number of "big-river" fishes of North America. More subtle, but perhaps even more important, are changes in the quality of water, induced by impoundment. Siltation behind dams, concomitant reductions in silt loads of rivers, increased penetration of light, changes in temperature relations—all contribute to form a new habitat, which elicits faunal change. The channelization of rivers often has opposite effects and modifies riparian habitats drastically (*3*). In the American Southwest, complete drying of streams or of riparian habitats may destroy whole faunas (*4*). In all instances, faunal shifts that occur must, by definition, involve relative changes in abundance. Some species may be eliminated, others may be reduced in numbers, and some may be benefited.

Animals in category 4 are the easiest to define, simply because of the generally small, unique habitats in which they live. Such habitats often lack biological diversity. Minor changes may therefore effect major fluctuations in species abundance. Because of its isolation, an island is an especially likely site for such a catastrophe; indigenous organisms are few, and the system is ecologically unsaturated. Aggressive exotic species that travel with man have, when successfully established, a profound and usually detrimental influence. This was exemplified by the rapid destruction of a major part of the isolated avifauna on the Hawaiian Archipelago in the late 1800's and early 1900's (*5*). In most respects, desert springs are similarly isolated, insofar as many aquatic animals are concerned—often even more so than oceanic islands (*6*). Series of springs in desert regions form aquatic archipelagos that differ from their oceanic analogs in that they often contain organisms that are relicts of past ages, rather than organisms resulting from chance invasion and subsequent differentiation. The restricted and ecologically simplified nature of these habitats leaves them especially susceptible to faunal destruction, especially when the springs are located in areas of rapid population growth, where the demand for water exceeds the supply.

Status of Selected Fishes

Faunal depletion in aquatic habitats of the American Southwest is the simple rule. Much surface water is directly removed for use by man. Most of the remaining natural waters are highly modified, physicochemically or biologically. Because of these factors, big-river fishes (category 3) present a special, pressing problem in the region. Table 1 illustrates the gross changes that have occurred in the fish fauna of a major stream in Arizona, the Salt River, near its downstream end at Tempe (Fig. 1). Extirpation of a major part of the fauna between 1890 and 1926 is evident, corresponding to early modifications of the stream by Caucasian man and impoundment of Roosevelt Lake on the river in 1910. A chain of impoundments was then progressively created on the Salt River between Tempe and Roosevelt. The Verde River, a major confluent of the Salt, maintained some water in the channel at Tempe for a while. Bartlett Reservoir on the Verde was closed in 1939, however, and this, in combination with construction of another dam, resulted in almost total desiccation of the channel of the Salt River by the late 1950's (*7*). Only subsurface percolation of water, mostly from underflow of municipal waste waters, maintained isolated fish habitats along the nearly dry stream. Such habitats persist today. Introduced fishes became increasingly established after 1926, and extirpation of additional native fishes quickly followed.

All the species that occupied the Salt River at Tempe in 1890 exist today somewhere in the Colorado River basin. The variation in their success in maintaining populations is, however, great; some species remain abundant, others are reduced in number, and a few are on the verge of extinction. This variation illustrates some of the problems involved in the study and definition of "endangered species."

Two large species especially relevant

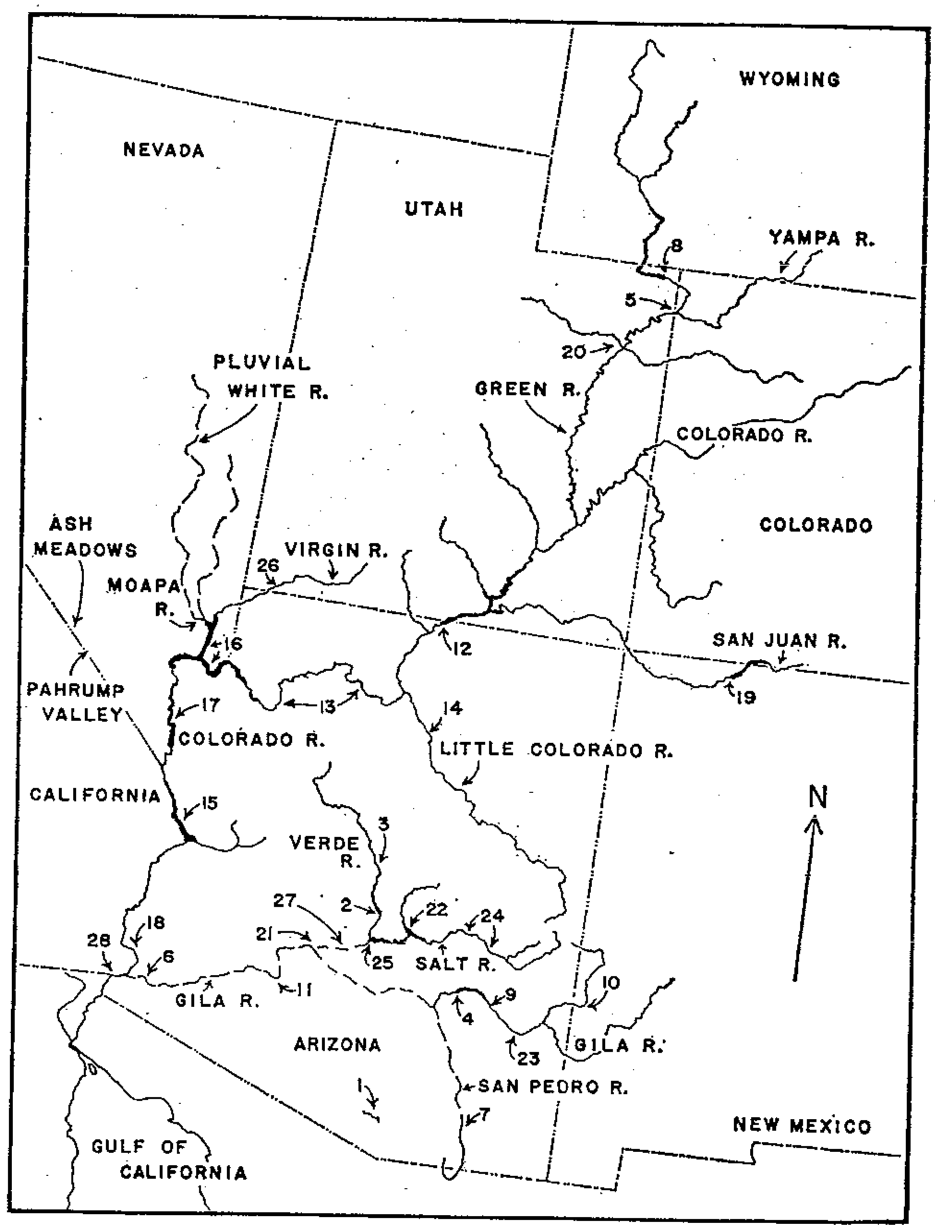

Fig. 1. Sketch map of the Colorado River basin, southwestern United States, showing rivers and localities mentioned in the text. (1) Arivaca Creek; (2) Bartlett Dam; (3) Camp Verde, Arizona; (4) Coolidge Dam; (5) Dinosaur National Monument; (6) Dome, Arizona; (7) Fairbank and Tombstone, Arizona; (8) Flaming Gorge Dam; (9) Ft. Thomas, Arizona; (10) Frisco Hot Spring; (11) Gila City (= Gila Bend), Arizona; (12) Glen Canyon Dam and Lee's Ferry, Arizona; (13) Grand Canyon; (14) Grand Falls; (15) Lake Havasu; (16) Lake Mead; (17) Lake Mojave; (18) Martinez Lake; (19) Navajo Dam; (20) Ouray, Utah; (21) Phoenix, Arizona; (22) Roosevelt Lake and Roosevelt, Arizona; (23) Safford, Arizona; (24) Salt River Canyon; (25) Saguaro Lake; (26) St. George, Utah; (27) Tempe, Arizona; (28) Yuma, Arizona.

to this discussion are the Colorado River squawfish, *Ptychocheilus lucius*, and the humpback sucker, *Xyrauchen texanus*. The status of these fishes above Grand Canyon, particularly in the Green River, has been outlined by Vanicek (*8*). Both species were effectively eliminated from about 250 miles (400 kilometers) of the mainstream and 250 miles of tributaries of the Green River above the Flaming Gorge Dam site by fish-control operations in 1962, some kill being observed downstream as far as Dinosaur National Monument (*9*). Neither species is now found above the dam, or in the 65-mile stretch of cold tail-waters between Flaming Gorge Dam and the mouth of the Yampa River in Dinosaur National Monument. Both squawfish and humpback sucker, however, are common in the Green River between Echo Park (Yampa River) and Ouray, Utah. Koster (*10*) reported adult squawfish (and possibly humpback suckers) from the San Juan River, in New Mexico, in 1959. He pointed out, however, that the segment of river from which the fish were obtained was soon to be flooded by the construction of Navajo Dam. Squawfish ran to the base of Grand Falls on the Little Colorado River in years past (*11*), but that area is now essentially dry. We have seen, or heard of, two adult or subadult squawfish taken from the Colorado River between Glen Canyon Dam and Lee's Ferry in the period 1962–66. No humpback suckers have been seen in that segment of the river, but one hybrid, *Xyrauchen texanus* × *Catostomus latipinnis*, was taken below Glen Canyon in 1966 [such hybrids have previously been reported by Hubbs and Miller (*12*)]. On the basis of these data and of a general account by Sigler and Miller (*13*), it appears that both squawfish and humpback suckers are persisting above, and in, Grand Canyon. We leave further documentation of their status in that area to others.

For the region below Grand Canyon our data are specific. Colorado River squawfish were abundant at Yuma in the early 1900's, and in the lower Gila River near Dome in 1920 (*4*). They persisted in the lower Colorado mainstream until the 1940's (*14*), but since 1950 they have become increasingly uncommon. We have heard of only two specimens from the lower Colorado in the period 1962–67.

In historic times, squawfish lived in the Gila River mainstream as far east as Ft. Thomas, in the San Pedro River at least to Fairbank (*15*), and in the Verde River to Camp Verde (*16*), and presumably they were present throughout the Salt River Canyon and above it (*4, 17*). We have collected intensively in the Gila River basin since 1963 and can attest to the virtual, and perhaps actual, extinction of both squawfish and humpback sucker there. The headwaters of the Gila River were blocked by Coolidge Dam in 1929 (*7*); the river is now a dry wash throughout most of its lower course. The formerly large San Pedro River rarely flows in its lower part, and is a small creek near its headwaters. The Verde and Salt rivers are effectively impounded, and the upper Verde has diminished flow and is entrenched in its floodplain (*16*). Only the Salt River, in its central canyon, seems a suitable habitat for either squawfish or humpback sucker. No adult squawfish has been taken from the Roosevelt area on the Salt River since 1937 (*4*). Dammann (see *17*) saw two adults taken in the Salt River Canyon in 1948, however, and Miller (*4*) caught two young squawfish near the same locality in 1950. Branson *et al.* (*18*) reported seven juvenile specimens seined in the canyon in 1959. We and other workers known to us have failed to obtain any squawfish or humpback suckers since 1963, during intensive studies of that area, and John K. Andersen (*19*) of the U.S. Bureau of Sport Fisheries and Wildlife, who has worked in the canyon for the past few years, has not taken either of these fishes in his sampling program, or seen either in fishermen's creels.

The habitats of humpback suckers and squawfish are similar, though the suckers are more likely to frequent marshes, lakes, and quieter parts of rivers. Humpback suckers have been less commonly reported than squawfish, perhaps because humpback are less easily taken by conventional fishing methods. The recent status of the species in part of the upper Colorado is given by Vanicek (*8*). Below Grand Canyon it appears to be maintaining a fairly constant abundance. Norman Wood (*20*) of the Nevada Game and Fish Commission has found no changes in the numbers of humpback observed in lakes Mead and Mojave over the last 15 years. However, his conclusion is based on casual observations made during fish-population census, and no actual data are available. Spawning aggregations of this species were observed several times in the lakes (*21*), most recently in March 1967 in a shallow cove of Lake Mojave (*20*). The sucker also persists farther downstream, in Lake Havasu and below, perhaps as far as Martinez Lake (where, according to local testimony, one was seen in 1966), but it is becoming increasingly rare.

The upstream limit of range of humpback suckers in the Gila River basin was probably similar to that of squawfish. The suckers were abundant enough to be marketed in Tombstone, as "buffalo fish," prior to the 1880's (*4, 15*); presumably these specimens were caught in the adjacent San Pedro River. We know of no records of humpback suckers from the Gila River mainstream above Phoenix, or from the Verde River, but large populations formerly were present in the Salt River. According to Hubbs and Miller (*12*), the fish was common near Roosevelt, Arizona, prior to the closure of Roosevelt Dam. In 1926, many suckers were seined in Roosevelt Lake and in Tonto Creek upstream from the lake, but none is now found in either area (*22*). The large populations persisted until the 1950's in lakes downstream from Roosevelt; commercial fishermen took 6 tons of humpback from Saguaro Lake in 1949, but none was found when the lake was drained in 1966 (*22*).

We point out again that both these fishes appear to be maintaining populations in some areas of the Colorado River basin, yet the relatively well-documented decline of both in the Gila River basin is instructive, and may foreshadow their extinction elsewhere. Large fishes like squawfish and humpback sucker have long life expectancies, and the presence of large adults may not indicate a "healthy" population. The large average size of humpback suckers in the Salt River impoundments in 1949 [some weighed more than 14 pounds (6 kilograms) and were more than 30 inches (75 centimeters) long (*12*)] may have foreshadowed their imminent decline through lack of reproductive success. Despite observations of the spawning of humpback in the lower Colorado River lakes, no specimen shorter than about 15 inches has been caught in recent years (*20–22*).

One can hardly say that such fishes are "maintaining their populations," and only long-range trends are available as a basis for estimating their status. There are few basic data available on the physiological, ecological, or behavioral requirements for their continued reproductive success. It is easy to say that such big-river fishes disappear as a result of impoundment, the implication being that the presence of a dam is directly responsible. Yet these fishes are becoming extirpated in areas, like the Salt River Canyon, where such modifications are yet to be made. Our lack of information on species requirements for reproductive success and on such matters as the effects of introduced fishes on native species is discouraging.

Another kind of big-river fish—the small, streamlined woundfin, *Plagopterus argentissimus*, adapted to life in sandy, swift, turbid, downstream parts of the lower Colorado basin—occurred in the Salt River at Tempe (Table 1) and in the Gila River at Yuma, Dome, and Gila City, in the period 1890–95 (*4*, *23*). Elsewhere in the system this species was not recorded by early (or later) collectors. The last reproducing population of the monotypic genus *Plagopterus* now lives in the lower Virgin River of southwest Utah, northwest Arizona, and southeast Nevada. A few stragglers have been caught in the lower Moapa River (Nevada) in recent years (*24*).

Plans by the U.S. Bureau of Reclamation to construct a dam on the lower Virgin River 8 miles above St. George, Utah, would affect about 80 of the approximately 90 miles of river habitat suitable for this species. Planning calls for flow in the Virgin River downstream to be maintained only by return irrigation flow and springs in and below "the narrows," about 12 miles below St. George (*25*). The Bureau estimates that, downstream from the proposed dam, turbidity will decrease, salinity will increase, and flow in the river will be equalized. Equalization of flow means that, on the average, flow will be decreased in every month, but the decrease will be less in the summer than in the winter. Assuming that the Virgin River Dam is funded and constructed and that predictions of the downstream effects are borne out, we are still unable to confidently predict what will happen to *Plagopterus*. We do know, however, that *Plagopterus* disappeared from the Gila River early in this century, presumably because of the first man-induced changes; that despite its ability to invade the somewhat smaller Moapa River it has not become established there; and that it is fulfilling its life cycle only in the lower Virgin River. These facts suggest that any change in river condition is likely to be detrimental. Such change should be avoided until some attempt has been made to define habitat requirements for the species.

The Gila spinedace, *Meda fulgida*, is endemic in the Gila River basin, requires another kind of habitat, and demonstrates yet another type of sensitivity to man's activities. The spinedace frequents moderately swift currents flowing over gravel bottoms at or near the lower ends of riffles, and is midwater in habit (*23*, *26*). In this respect it resembles any number of small cyprinids of more eastern drainages. At one time it occurred throughout the upper Gila River basin (Fig. 2B). Many streams in which it formerly lived still flow strongly, and the habitats seem totally suitable for its continued life, yet in recent years it has not been taken anywhere in the Verde River drainage, where it was abundant in the past. The aggressive, introduced red shiner,

Table 1. Fishes recorded from the Salt River, Maricopa County, Arizona, in the city of Tempe, in the period 1890–1967. Dashed lines span the period during which a species probably inhabited this segment of the stream; (O) occurrences documented by specimens in museums or recorded in the literature; (X) probable occurrence of a species at a given time, on the basis of collections made before that time or in other parts of the drainage, both upstream and downstream from Tempe.

Species	Year of collection or probable occurrence					
		1900	1920	1940	1960	
Native species						
Gila elegans	O					
Meda fulgida	O					
Plagopterus argentissimus	O					
Ptychocheilus lucius	X					
Rhinichthys osculus	O					
Catostomus latipinnis	O					
Xyrauchen texanus	O					
Agosia chrysogaster	X	---	O			
Gila intermedia	X	---	O			
Gila robusta	X	---	O			
Poeciliopsis occidentalis	O	---	O			
Cyprinodon macularius	O	---	O	X	O	
Catostomus insignis	O	---	X	X	O	O
Pantosteus clarki	O	---	X	X	O	O
Introduced species						
Gambusia affinis			O	O	O	O
Lepomis cyanellus			O	X	O	O
Cyprinus carpio				O	X	O
Ictalurus melas				O	O	O
Lepomis macrochirus				O	X	O
Pomoxis nigromaculatus				O	X	X
Poecilia latipinna					O	O
Micropterus salmoides					O	O
Dorosoma petenensis						O
Carassius auratus						O
Notemigonus crysoleucus *						O
Notropis lutrensis						O
Pimephales promelas *						O
Ictalurus natalis						O
Ictalurus punctatus						O
Lebistes reticulatus *						O
Poecilia mexicana *						O
Xiphophorus variatus *						O
Lepomis microlophus						O
Tilapia mossambica *						O

* These species were taken prior to severe flooding in the Salt River channel at Tempe in the winter of 1965–66, but not subsequently.

Notropis lutrensis, has seemingly replaced it throughout that system (Fig. 2A). The red shiner spreads rapidly, naturally and from fishermen's bait buckets. In view of this, and of proposals to build the Charleston Dam on the upper San Pedro River and the Hooker Dam on the Gila River in New Mexico, the outlook for *Meda* appears bleak.

The Gila topminnow, *Poeciliopsis occidentalis*, provides another example of the influence of an exotic fish on a native species. The Gila topminnow also was at Tempe in 1890, where it undoubtedly lived in marshes along the stream rather than in the channel itself. Records show that this fish ranged from a high-elevation habitat adjacent to Frisco Hot Spring in western New Mexico (*27*) to an area near Dome, Arizona (*28*). These, plus records from most of the central and southern parts of the Gila basin (Fig. 3), leave no doubt that the topminnow once lived throughout the Gila drainage, and perhaps in suitable habitats along the lower Colorado as well. Its decline was rapid. Gila topminnows were considered by Hubbs and Miller (*28*) to be "one of the commonest fishes in the southern part of the Colorado River drainage." Today the fish persists only in one spring area in Santa Cruz County, Arizona.

The diminution in the range of this fish is attributable in part to desiccation of habitat, especially in places like the lower Gila River. Arroyo cutting in the 1880's (*4, 29*), must have destroyed much of its preferred quiet-water habitat even before man began to use the water. The introduction and spread of the mosquito fish, *Gambusia affinis*, throughout most of the basin over the last 40 years appears to have been the most important factor, however, in the overall decline of the native fish. The aggressive *Gambusia* has played a part in the decline of a number of fishes in the West and in the destruction of populations of fishes in other areas (*30*). In the best-documented examples of replacement of *Poeciliopsis* by *Gambusia*, the sequence is rapid. In the formerly fishless Arivaca Creek, in Arizona, topminnows were introduced in 1936. In 1957 they were extremely common, but, in 1959, mosquito fish of unknown origin had totally replaced them (*4*). The sequence was similar in an artesian-spring area near Safford, Arizona. Gila topminnows abounded in canals and ponds of that area in 1962. In 1963, specimens of *Gambusia* were taken in the area, and in the same pond as *Poeciliopsis*. In our intensive survey, only the introduced mosquito fish was found in 1966. Restriction to a single, isolated drainage seems a precarious position for the Gila topminnow; this formerly abundant, endemic species now qualifies for category 4, even though it was originally a category-3 species.

In discussing fishes in category 4, we use as examples species naturally isolated in aquatic systems of closed basins, or isolated, by habitat preference or physiological attributes, or both, to springs or springlike environments. Alterations induced by man, a major cause of declining populations in categories 2 through 4, are particularly important to fishes in category 4. Minor changes in a small spring, for example, may influence the entire population of a species. The acute susceptibility of such forms to catastrophe is evident in the recent compilations of extinct fishes of the United States (*2, 4*); three of the six fishes listed were in restricted waters in Nevada, and a fourth, *Cyprinodon bovinus*, was in an isolated spring in Texas.

Empetrichthys merriami, the Ash Meadows killifish, one of the two known species of the cyprinodont genus

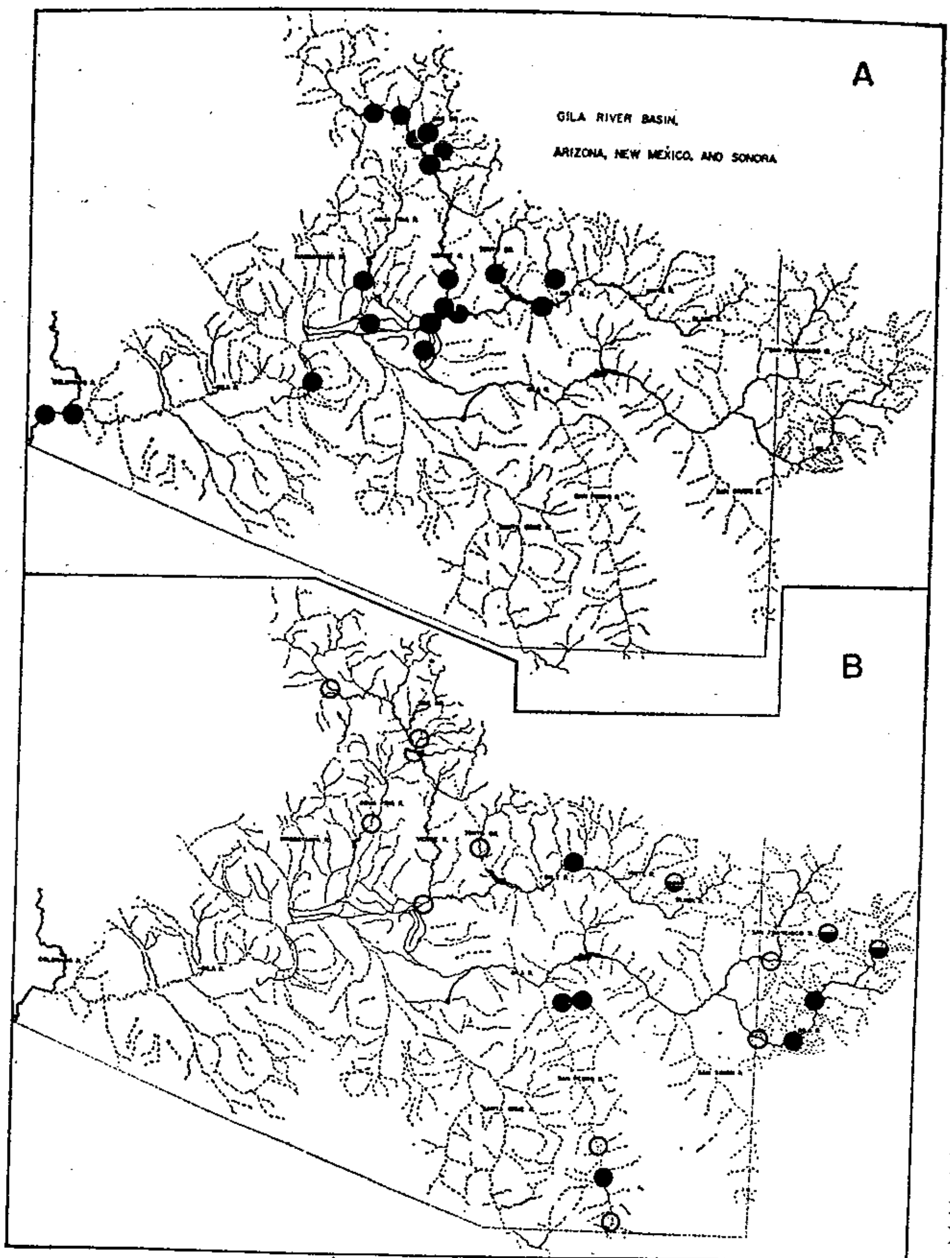

Fig. 2. (A) Present distribution of the introduced red shiner in the Gila River basin. (B) Present and past distribution of the native Gila spinedace in the Gila River basin. Open circles are localities of former occurrence where the present absence of the fish has been confirmed; half-solid circles are localities that we have not reexamined; solid circles are localities where the spinedace persists.

Empetrichthys, is extinct. Three distinct subspecies of the other known species of the genus, *E. latos,* the Pahrump killifish, have been described from the three isolated springs of Pahrump Valley, Nevada. One of the springs (Pahrump Spring) failed in 1958, presumably because of lowering of the water table by pumping for irrigation. A second spring (Raycraft Spring) was filled by a rancher in an attempt at mosquito control. This spring would probably have gone dry from the same cause as Pahrump Spring had it not been filled. The third spring, Manse Spring, which supports the typical subspecies *E. latos latos,* remains, but goldfish (*Carassius auratus*) were recently introduced (*31*). Thus, two of the original three known stocks of *E. latos* are extinct, and the third is subjected to competition from an exotic species. The species is maintaining itself at present. In July 1967 an attempt was made to remove the fish from the spring and count the entire population; population size was estimated to be about 1300. Most of the goldfish were removed at this time.

This species appears capable of maintaining its population in the face of some competition, but obviously cannot withstand the virtually total destruction of its habitat. Table 2 gives data that in part explain the destruction of habitat and the extinction of the two subspecies of *Empetrichthys latos.* There is clearly a relationship between increased cultivation, number of wells, volume of water used for irrigation, and lowering of the water table. The first wells were drilled in 1910; by 1916, flow at Manse Spring was reduced to about half its original volume. Water use nearly doubled during the period 1946–59, and increased by a factor of 7 to 8 between the periods 1937–40 and 1940–46. Such large increases in pumpage inevitably result in failure of surface waters. The estimated annual recharge in Pahrump Valley is 22,100 acre-feet (27 million cubic meters) (*32*). Withdrawal of nearly 41,000 acre-feet annually virtually guarantees continued decline of the water table, eventual failure of Manse Spring, and extinction of the last population of the genus *Empetrichthys.* If the spring flow continues to decline at its present rate (since 1959 the mean annual rate of flow has shown a decline of 0.14 cubic foot per second), Manse Spring should fail in 10 to 11 years. The trend of increased pumpage in Pahrump Valley suggests that the rate of decline of spring flow will accelerate and that elimination of the fauna may be expected in less than 10 years.

The status of the Moapa dace, *Moapa coriacea,* is less readily defined than that of *Empetrichthys.* The minnow was abundant in the headwaters of the Moapa River, Nevada, when the first collections were made in 1933 (*33*). Its abundance was apparently maintained at least until the early 1950's (*34*). In our studies, which began in 1964 (see *24, 35*), the species was found to be rare. The low population density of *Moapa* closely followed the introduction and establishment of the shortfin molly, *Poecilia mexicana,* in the river. After 2 years the population of *Moapa* suddenly became more dense. In this case there was no physical deterioration of the habitat, thus changes in habitat were obviously not a factor in either the decline or the recovery of this species. The maximum and minimum annual mean discharge over the past 25 years, measured at the approximate lower extent of the habitat suitable for *Moapa,* fall within 3.3 cubic feet (0.1 cubic meter) per second of the 25-year mean discharge (*36*). The stream flow is, therefore, remarkably stable. The major problem is alteration of the biotic habitat by the introduction

Table 2. Water discharge and utilization in Pahrump Valley, Nye and Clark counties, Nevada, in the period 1875–1967. Data for 1875 are from Malmberg (*32*); for 1916, from Waring (*41*); for the years 1917–46, from Maxey and Robinson (*42*); and for the years 1951–67, from the Nevada State Engineer (*43*).

Year or period	Manse Spring (ft^3/sec, av.)	Pahrump Spring (ft^3/sec, av.)	Raycraft Spring (ft^3/sec, av.)	Thousands of acres irrigated	Pumpage (in thousands of acre-feet)	Number of wells operating	Depth of water table (ft)
1875	6.0	7.9					
1916	3.2	4.7	0.002	0.5	4.3	15	
1917–37					3.3–4.6		
1937–40	3.1				2.2–3.5		
1940–46	3.1	5.5			2.2–16.3		
1951	2.6				16.1	39	37
1952						39	30–60
1959	2.5	0.0	0.0	5.8	25.6	45	
1960	2.4			6.2	27.4	39	
1961	2.0			6.5	30.1	55	
1962	1.9			6.5	29.2	54	
1963	1.8			7.8	31.9	59	
1964	1.9			7.7	37.5	62	
1965	1.2			8.2	36.5	64	
1966	1.5			7.6	37.9	71	70–85
1967							75–84

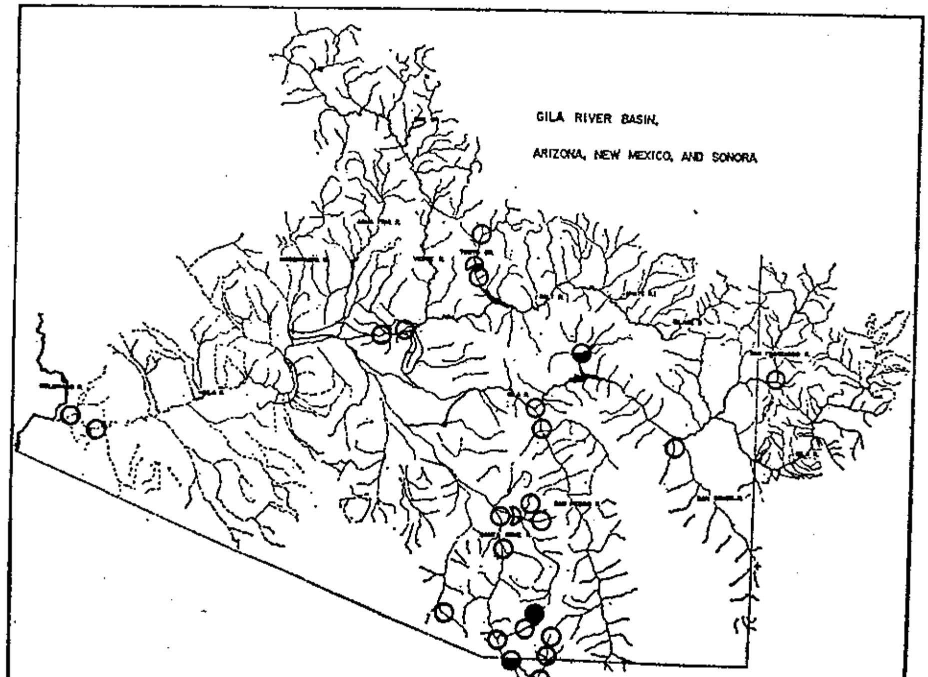

Fig. 3. Present and past distribution of the Gila topminnow in the Gila River basin; the symbols are the same as in Fig. 2.

of exotic species. The introduction of *P. mexicana* resulted in a decrease in the population density of *Moapa*, apparently through an increase in parasitism (*35*) and possibly through direct competitive interaction. A primary danger to *Moapa* is the possibility that additional introductions will cause another population decline from which it might not recover; such circumstances are not predictable.

The White River springfish, *Crenichthys baileyi*, presents still a different problem. This species occurs as a number of disjunct populations along the course of the Pluvial White River, in Nevada. No careful taxonomic evaluation of all populations of the species has been made, yet marked physiological differences are known, and morphological differentiation is apparent. Some populations exhibit the highest tolerance to high temperatures and to low concentrations of dissolved oxygen known in fishes (*37*). Some stocks of *C. baileyi*, like stocks of *Moapa*, have become depleted following the introduction of aquarium fishes. In this case, too, a major factor in the decline seems to be the original species' greater susceptibility to existing parasites in the presence of competition from exotic species, or the introduction of new parasites along with the introduced fish (*35*). Populations have been severely reduced—and in one instance the population became extinct—following the introduction of largemouth bass, *Micropterus salmoides*, and mollies, *Poecilia mexicana*. During the past 3 years, three springs in Nevada have been selected for comparative ecological research as "controls" because they were uncontaminated by exotic fishes. In each instance, after no more than 2 months of work, exotic species suddenly appeared. This further illustrates the magnitude of the problem.

It is difficult to decide which populations of a fish like *Crenichthys baileyi* are to be preserved. In many respects this fish is intermediate between categories 3 and 4. Yet, known physiological and morphological differences indicate that several populations provide an exceptionally high amount of information and that each may be scientifically important.

Numerous other examples of fishes in category 4 could be cited. The precarious status of *Gambusia gagei*, which was almost destroyed by the introduction of *G. affinis* into its warm-spring habitat in Big Bend National Park, was documented by Hubbs and Broderick (*38*). *Cyprinodon diabolis*, a unique species represented by no more than 700 individuals in Devil's Hole, Nevada, now is protected in Death Valley National Monument. This species has been affected, but scarcely disturbed, by man.

Some changes effected by man are not automatically detrimental to native fishes. Placement of the desert dace, *Eremichthys acros*, on the list of endangered species (*2*) resulted from a premature judgment concerning the impact of irrigation development (*39*) rather than from an objective evaluation. Subsequent work in Soldier Meadows, Nevada, indicates expansion of populations of *E. acros* into the recently constructed irrigation ditches. This species belongs to category 4, but is not endangered, both because it successfully extends its populations into habitats built by man and because several populations exist. On the other side of the slate, a reminder that a number of fishes have become extinct in recent years seems appropriate. Some are *Empetrichthys merriami*, *Lepidomeda altivelis*, *Lepidomeda mollispinis pratensis*, the Crystal Spring population of *Cyprinodon nevadensis mionectes*, the Hiko Spring population of *Crenichthys baileyi*, the Pahranagat Valley population of *Pantosteus intermedius*, *Empetrichthys latos pahrump*, and *E. l. concavus*. Exotic fishes obviously contributed to the extinction of the first six, whereas habitat destruction is clearly responsible for the extinction of the two last-named species.

Conclusions

Declines in the populations of native fishes in the American Southwest are largely due to habitat changes associated with man's modification of various aquatic environments. Early decimation of the fauna was mainly a result of large-scale physical change, such as the diversion and impoundment of rivers and downcutting of streams in their formerly stable floodplains [that is, arroyo cutting, a possible result of a combination of man's actions and climatic phenomena (*4*, *29*)]. More subtle physical or chemical changes, the lowering of water tables through the use of subsurface water for irrigation, eutrophication and other pollutional effects, and biological phenomena associated with the ever-increasing introduction of exotic species—all are accelerating the extirpation of remnant populations.

Present populations of most native fishes are locally dense, especially in isolated habitats occupied by fish of category 4. Given a reasonable degree of environmental stability, these fish certainly are capable of maintaining themselves. However, some species belonging to category 3 present a different problem. They have at present retreated to the most inaccessible parts of their ranges, where simple surveillance of their status is a major operation. Some of these fishes can spread rapidly when water conditions improve. Their populations may be greatly depleted in one year, or perhaps they withdraw from a major part of their possible range over a longer period, but after a few years of high precipitation and stabilized stream flow they may spread and repopulate almost all available habitats. Such a population resurgence was recently documented by Minckley and Carufel (*40*) for the formerly depleted Little Colorado spinedace, *Lepidomeda vittata*, in the period 1963–66, and is known for other forms.

It seems to us that many people and agencies currently involved in the study and promotion of "endangered" species are only partially realistic. This is evidenced, for example, by their concern for "peripheral" species, those represented in a given state or country by an isolated or remnant population peripheral to the main body of the gene pool. In fishes, the inclusion of the Mexican stoneroller (*Campostoma ornatum*), the Atlantic salmon (*Salmo salar*), and a number of other forms in the U.S. list of endangered species (*2*), even as "peripheral" species, seems unwarranted. One invariably meets opposition on suggesting that each population of a desert fish such as *Crenichthys baileyi* should be preserved. But if each isolated spring population of *C. baileyi* is not "worth saving," why then be concerned with the different river populations of *S. salar*? The distinction is apparent: *Salmo* is well known to many people and is of importance to sportsmen; *Crenichthys* is neither. We are simply dealing with an interaction of supply (meaning maintenance in nature, in this context) and demand (meaning the interest of the people concerned).

The validity of a decision as to whether or not a species is "endangered" depends on many factors. For example, working style, prior information, thoroughness, and time available may differ greatly from collector to collector. It may be nearly impossible to seine fishes that are readily taken by means of electrofishing methods or gill nets. Data obtained in winter, when a given species retires to deep pools, may "document" its extinction, but in June the fish may swarm in shallow, more accessible places. We know three students who worked more than half a mile of stream in southern Arizona with electrofishing equipment in an attempt to catch the Yaqui chub, *Gila ditaenia;* they failed. The area they sampled was less than a fourth of a mile upstream from the canyon in which the species was abundant, and in which it remains abundant today; the stream was flowing in the area of sampling only as a result of persistent rainfall. Such errors are to be expected in any field operation, especially if specific data are not generally available.

A program of study on the more obscure "endangered" species is hampered (i) by a lack of information (information concerning the species in question and information disseminated to the public); (ii) by misinformation (or unavailability of unpublished data) largely resulting from a lack of time on the part of people in the field; and (iii) by apathy on the part of the public and of professional workers. Lack of communication, even among active scientists, may result in grievous errors. Making a collection of fishes from a desert spring may not seem a serious matter; however, if another worker is systematically sampling the already small population for a life-history study, activities of a collector unaware of this sampling could produce results that are spurious, to say the least. Errors in judgment may also cause problems. For example, an ichthyologist who may wish to eradicate exotic fishes from a spring so that the native form may be reestablished had best consider the effects of his efforts on other organisms; in preserving a fish species, a genus or higher taxon of invertebrate animal might be destroyed. Such a happening is not consistent with a successful, progressive program. Persons studying fishes are perhaps delinquent in not reviewing the endemicity and distributions of other animal groups. However, scientists working on other groups appear, with some notable exceptions, relatively unaware of changes taking place in many habitats, and have yet to become active in documenting depleted populations.

What are needed are broad, comprehensive studies geared toward realization of three major objectives. (i) thorough documentation of the past and present population status of native animals, with publication of data and wide dissemination of topical reports; (ii) accumulation of basic information on ecologic requirements of depleted animal species and, if possible, preparation of descriptive life histories for such animals; and (iii) possible laboratory study and maintenance of populations of depleted species in seminatural conditions, in case nothing can be done to maintain their habitats in nature. This laboratory maintenance is simple in some instances, especially in most fishes of our category 4, but is exceedingly complex and time-consuming in the case of larger species of category 3. After the objective of documentation is realized we will have information on depleted species that will speak for itself. We will then be in a position to project trends and consider probabilities on the basis of facts rather than observational interpretations. This documentation will lay the groundwork for study to satisfy the second objective. Populations large enough to sustain themselves under pressures of research collecting may be found, and detailed, meaningful information may be compiled. Laboratory study and maintenance (the third objective) may or may not be necessary, but the development of facilities and techniques for maintaining certain animals will insure their availability for future study and will provide substantial information in itself. A number of fishes are currently being studied under such a program, but much additional effort is needed, on fishes and on other groups as well.

The problems we have discussed are not unique to fishes, or to the American Southwest. However, they are acute in the Southwest because of the increasing population pressure on the limited aquatic environment. Most water laws, for instance, permit "beneficial" use of water without regard to the needs of wildlife. Habitat destruction is generally regarded as the vested right of the landowner, and, if immediate economic gain can be realized, as the duty of governmental agencies. The problem of endangered species therefore is only one result of attitudes and measures which at present permit, or even demand, exploitation of resources that the environment has not the capacity to restore. Pumpage of water in Pahrump Valley in excess of the annual recharge does not differ, in kind, from farming practices that result in the washing away of topsoil; from the use of prime farming land for building cities; from lumbering that destroys forests; and from a hundred other catastrophic practices. These practices attempt to "answer a demand," instead of recognizing the more fundamental problem—that of meeting the long-term need of a population that will ultimately be forced to restrict its use of resources so as not to exceed the carrying capacity of the environment. Possibly the most compelling reason for preserving species is the value such a program has in demonstrating the importance of restraint. An "endangered species" program is imperative, not only for the sake of the species studied but also because of what it can teach us about the possibilities for continued survival of other species, including man.

In the narrower sense, in the program discussed here we are dealing directly with the western aquatic fauna, poorly known and viewed by many people as unimportant. These animals are difficult to observe and to exhibit, and are generally considered less worthy of preservation than organisms of value to sportsmen or to industry. Native aquatic animals of the American Southwest are unique and endemic—part of an ancient, relict fauna that provides important scientific information. Changes that have occurred and are occurring are amplified and accelerated by the scarcity of water. A great natural experiment of evolution, also amplified and perhaps accelerated by isolation in desert aquatic habitats, appears about to become an exercise in extinction, if man will have it so.

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Population Regulation and Genetic Feedback

Evolution provides foundation for control of herbivore, parasite, and predator numbers in nature.

David Pimentel

Although within a relatively short period man has learned how to put himself into space, he still is not certain how the numbers of a single plant or animal population are naturally controlled. Aspects of this problem have been investigated since Aristotle's time, they were given important consideration in Darwin's *Origin of Species*, and yet the unknowns far outweigh the discoveries. If we knew more about natural regulation of population, we would be in a better position to devise more effective and safer means of control for important populations of plant and animal pests. We might also be better able to limit the growth of human populations, although that problem is exceedingly complex because of the social activities and nature of man.

Population Characteristics

Before considering how populations in nature are regulated, we should review various characteristics of animals and plants—as individuals and as populations. Do populations of animals in nature fluctuate severely or are they relatively constant? Stability and constancy have been proposed as characteristics of natural populations. Speaking about birds, Lack (*1*) says, "of the species which are familiar to us in England today, most were familiar to our Victorian great-grandparents and many to our medieval ancestors; and the known changes in numbers are largely attributable to man." He continues, "All the available censuses confirm the view that, where conditions are not disturbed, birds fluctuate in numbers between very restricted limits. Thus, among the populations considered above, the highest total recorded was usually between two and six times, rarely as much as ten times, the lowest. This is a negligible range compared with what a geometric rate of increase would allow." Discussing the stability in animal populations in general, MacFadyen (*2*) writes: "it is generally agreed that the same species are usually found in the same habitats at the same seasons for many years in succession, and that they occur in numbers which are of the same order of magnitude."

Further evidence for the thesis that species populations are relatively constant is found in a study of the changes in the fauna of Ontario, Canada (*3*). When Snyder (*4*) evaluated the bird fauna, he found that, over a period of about 70 years, two species became extinct, 23 species increased in number, and six species decreased in number. This represents a total change of only 9 percent of 351 bird species found in Ontario (*5*) and agrees favorably with an 11-percent change (*6*) for 149 species of birds over a 50-year period in Finland. These data suggest that there is relative constancy in the abundance of species populations. The word "relative" must be emphasized because changes in numbers must be related to a species' real potential for fluctuations; to para-

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