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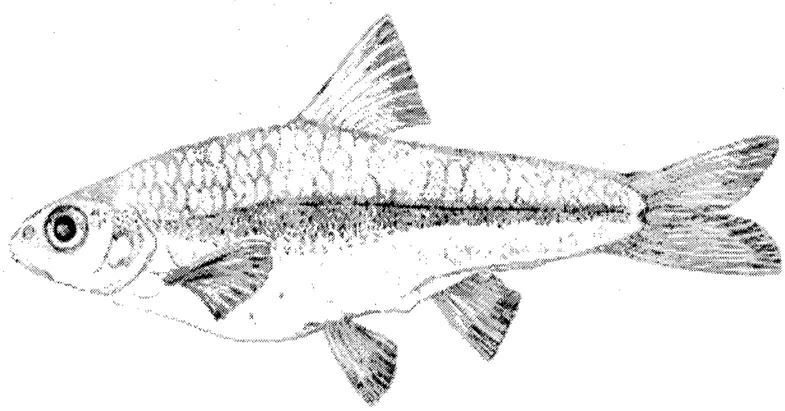

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Pupfishes of the Northern Chihuahuan Desert: Status and Conservation

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Abstract

Twelve species of pupfish (Genus *Cyprinodon*) generally are recognized in the northern Chihuahuan Desert. Eight of these are restricted to relatively small spring systems, whereas the remaining four occur in springs and riverine situations. The present abundance and distribution of pupfishes in the region is only a remnant of what must have been present prior to anthropogenic watershed deterioration and depletion of groundwater. Today, most spring-dwelling pupfishes are succumbing to losses of springflows, primarily as a result of pumping of groundwater, and the riverine species are adversely affected by a diversity of anthropogenic factors. The diversity of both groups has declined as a result of introgressive hybridization with a non-native pupfish, the wide ranging coastal species *C. variegatus*. The rapidity with which native stocks can be lost as a result of such hybridization is dramatically illustrated by events following the introduction of *C. variegatus* into the Pecos River Basin in the 1960s. A similar threat is posed by transport of any non-native pupfish into waters occupied by an endemic pupfish.

Introduction

In this paper, we review the history, current status, and conservation efforts for the 12 species of pupfish (Cyprinodontidae: *Cyprinodon*) generally recognized in the northern Chihuahuan Desert. The genus ranges west to east from the Death Valley System to the West Indies and north to south in coastal waters from Cape Cod, Massachusetts to Venezuela. In the past century, seven of the 25 species of *Cyprinodon* in the arid southwest have been driven to extinction in the wild. The first of these events occurred sometime between 1903 and 1953 when *C. latifasciatus* of the Parras Basin in Coahuila disappeared as a result of a variety of anthropogenic factors, including destruction of springs (Miller, 1964). Most recent extinctions occurred in the 1980s and early 1990s with the loss of five *Cyprinodon* species in the Sandia and Potosí basins of southern Nuevo Leon, all as a result of groundwater pumping and resultant loss of springs (Contreras-B and Lozano-V, 1996), including a complex of small to large springs that was unknown to ichthyologists until 1983 (Lozano-V and Contreras-B, 1993). The seventh known species of *Cyprinodon* to go extinct in historic times is the Monkey Springs pupfish, which was extirpated as a result of groundwater pumping and other human activities (Minckley, 1973; Minckley et al., 2002). Although extinct in the wild, three of the seven species are being maintained in various aquarium facilities (Lozano-V and Contreras-B, 1993).

In the following accounts, we present a basin-by-basin account of the pupfishes in the northern Chihuahuan Desert, eight of which are restricted to single springs or spring systems, whereas the other four occur in riverine situations and associated springfed waters. Regardless of extent of range, however, the pupfishes of the northern Chihuahuan Desert are declining. This reflects a variety of anthropogenic factors, but loss of springs, apparently as a result of groundwater pumping, and genetic introgression by non-native pupfish are the most immediate causes of concern.

PECOS RIVER BASIN

Cyprinodon bovinus (Leon Springs pupfish).—The waters supporting *C. bovinus* occur in Diamond Y Draw (= Leon Creek in some publications), a "flood" tributary of the Pecos River that has rarely, if ever, reached the river in historic times. Until 1965, the species was unknown to science except for the original collection, in 1851, of 16 specimens from Leon Springs near the present Fort Stockton, Pecos County, Texas. In 1965, W. L. Minckley found it approximately 15 km downstream of Leon Springs. In the intervening time, an area immediately downstream of, and fed by, Leon Springs had been dammed (about 1910) and the resulting "Lake Leon" was stocked with carp and game fish. In 1938, Carl Hubbs failed to collect the species in the Leon Springs area. By 1958, Leon Springs had gone dry because of over-pumping of the aquifer (Brune, 1975). The species was declared extinct by the late 1950s (Hubbs, 1957; Miller, 1961). Its rediscovery was verified in a re-description of the species (Echelle and Miller, 1974), and it was listed as a federally endangered species in 1980, with most of the occupied areas designated as critical habitat (Federal Register, 45:54678). Since 1990, most of the area occupied by *C. bovinus* has received protection as a preserve of 607 hectares (Diamond Y Spring Preserve) managed by The Nature Conservancy of Texas.

Since its re-discovery, *C. bovinus* has occupied two separate systems of surface water separated by 1-2 km of dry land: an "upstream watercourse" receiving flow from Diamond Y Spring and several smaller springs and seeps, and a "downstream watercourse" receiving flow from Euphrasia Spring, several small seepage springs, and groundwater seepage. Both of the two watercourses are 2-4 km long, with length of watercourse varying considerably over the years.

The primary threats to *C. bovinus* include pollution, loss of habitat, and introgressive hybridization with an introduced congener. Both watercourses supporting *C. bovinus* occur in the Fort Stockton Oil and Gas Field, an area of intense petrochemical extraction activity for about 50 years. Thus, there is a continuing threat of pollution (Kennedy, 1977; Gehlbach, 1981). In 1974, the Soil Conservation Service (Natural Resources Conservation Service) constructed an earthen berm that protects the headpool of Diamond Y Spring from surface spills (Hubbs 1980). In 1992, a ruptured pipeline released crude oil in a nearby area, creating sufficient concern that the oil company dug a trench downslope of the spill to help slow contamination of the watercourse.

In recent years, both watercourses supporting *C. bovinus* have been 1-2 km shorter than they were in the 1970s (Hubbs et al., 1978; Echelle and Echelle, 1980). This may be the combined result of the drought conditions in the region during the past five years and continued over-pumping of groundwater in the basin. In addition to the reduced size of the watercourses, densities of pupfish now seem lower than they were in the past. In the 1970s, the pupfish was abundant in a diversity of open-water situations in Diamond Y Draw (Kennedy, 1977; Hubbs et al., 1978; Echelle and Echelle, 1980). Reduced densities seem to reflect a loss of open-water habitat as a result of encroachment by bulrush because of reduced water flow.

The problems posed by introductions of non-native pupfish emerged as the most important immediate threat to *C. bovinus* shortly after R. D. Suttkus collected *C. variegatus* from the lower watercourse in 1974. By January 1976, hybrid morphotypes occurred throughout the lower watercourse. This led to an intensive effort to eliminate hybrids, with some attention to protecting the invertebrate community (Hubbs et al., 1978). The effort included treatment of the lower watercourse with rotenone, re-introducing *C. bovinus* from the upper watercourse, and subsequent seining and selective removal of suspected hybrids (Hubbs, 1980). The absence of morphological traits indicating hybrids (Hubbs, 1980) and the absence of alleles of *C. variegatus* in a genetic survey of the population (Echelle et al., 1987) indicated that the renovation was successful in restoring *C. bovinus* to the lower watercourse (for a more detailed review see Minckley et al., 1991). In retrospect, it was extremely fortunate that, during the 1976 renovation, *C. bovinus* from the upper watercourse was used to establish a captive stock at Dexter National Fish Hatchery and Technology Center in New Mexico (DNFH).

A second introduction of *C. variegatus* into Diamond Y Draw in the late 1980s or early 1990s led to contamination of both the upper and the lower watercourse of Diamond Y Draw (Echelle and Echelle, 1997). In response, the U.S. Fish and Wildlife Service (FWS) approved and, with help from various agencies and the Rio Grande Fishes Recovery Team, implemented a plan to restore the native pupfish genome. The renovation occurred in two phases that differed in approach. Antimycin A was used to eliminate all fish (including two non-natives, *Gambusia geiseri* and *C. carpio*) from the Diamond Y Spring outflow in August 1998. Prior to the renovation, large samples of the native fishes *G. nobilis* and *L. parva* were removed and transported alive to DNFH; after dissipation of the toxin, they were released back into the watercourse. Similar precautions were taken to protect known invertebrate species of concern. To provide additional protection for the remainder of the fauna, two small areas supporting pupfish were left untreated; one of these was contaminated by *C. variegatus*, but the population seemed sufficiently small that it was decided to try diluting the introgressed genome by releases of pure *C. bovinus* from DNFH. Renovation of the downstream watercourse was initiated in March 2000 and involved removal of all pupfish captured by intensive seining, dipnetting, and trapping. Both watercourses received large numbers of pupfish from the captive DNFH stock of *C. bovinus* immediately after renovation and in the following year.

Subsequent genetic surveys indicated that the renovation efforts were largely successful in both watercourses (AAE and AFE, unpublished data). There was no evidence of introgression in the upper watercourse except for the small population not treated with ichthyotoxins. Levels of introgression in the lower watercourse were reduced to possibly acceptable levels. Further releases of *C. bovinus* from the DNFH stock are planned for the future, with emphasis on the known areas of persistent contamination.

Since establishing the Diamond Y Preserve, The Texas Nature Conservancy (TNC) has attempted to restore the watershed to more natural conditions. Their activity includes renovation of old oil/gas pads, management of livestock to reduce their impact on the aquatic system, and using tractor equipment in 2000 to uproot all salt cedars (*Tamarix* sp.) in the lower watercourse. TNC is searching for appropriate ways to improve conditions for the pupfish without compromising the habitat for other rare, native species.

Cyprinodon pecosensis (Pecos pupfish).—The geographic range of *C. pecosensis* once included saline floodplains and springs, lakes, gypsum sinkholes, and other waters associated with the Pecos River from Bitter Lake National Wildlife Refuge and Bottomless Lakes State Park near Roswell, New Mexico, downstream for about 650 river-km to the mouth of Independence Creek in Texas (Echelle and Echelle, 1978). The present distribution represents less than 20% of the historic range. The only known natural population remaining in Texas (but see below) is in a portion of Salt Creek, a saline tributary of the Pecos River just south of the New Mexico border. In New Mexico, the species occurs most abundantly in saline waters of the Pecos River floodplain near Roswell, primarily on the Bitter Lake National Wildlife Refuge and Bottomless Lakes State Park.

There is only sketchy knowledge of the distribution and abundance of Pecos pupfish prior to the extensive habitat alteration that had occurred by 1950, but anthropogenic factors have undoubtedly caused a considerable loss of habitat for the species. The factors contributing to such losses were reviewed by Hoagstrom and Brooks (1999). Native Americans used water from the Pecos River for agriculture in the headwaters of the river prior to 1600, but human-induced alterations of aquatic habitats in the basin probably escalated considerably in the late 1800s. Since that time, a variety of anthropogenic factors drastically reduced the habitat available to pupfish. These include construction of dams on the mainstem of the river and tributary streams, introduction of salt cedar, overpumping of aquifers, over-grazing by domestic animals, erosion, pollution, and draining of wetlands (Hoagstrom, this volume). An apparently indirect effect of human activity are fish kills that have occurred sporadically in the lower Pecos River in Texas since the 1950s, including several kills from 1985 to 1989 that extended over hundreds of river kilometers (Rhodes and Hubbs, 1992; Childs et al., 1996). The latter series of kills apparently resulted from toxins released during blooms of a chrysophyte alga (*Prymnesium parvum*) that probably reflect a response to anthropogenic nutrient enrichment (Rhodes and

Hubbs, 1992). Although not documented in detail, such kills undoubtedly resulted in temporary depletions of the pupfish population.

Until recently, and despite losses of habitat and extensive fish kills, *C. pecosensis* seemed reasonably secure because of its relatively large range and locally high abundances. However, the status of the species changed abruptly with the introduction, sometime between 1980 and 1984 (Echelle and Connor, 1989), of *C. variegatus* into the basin, probably in Red Bluff Reservoir on the New Mexico/Texas boundary (Childs et al., 1996). Collections of pupfish from the Pecos River at four Texas localities in March 1980 showed no morphological evidence of influence by *C. variegatus*. But less than five years later, in August 1984, collections of six specimens each from two sites separated by about 200 river-km comprised *C. pecosensis* x *variegatus* hybrids (Echelle et al., 1987). The genotypes for allozyme loci indicated that samples consisted of individuals that were minimally second-generation hybrids.

A broader geographic survey in 1985 detected locally panmictic hybrid populations throughout approximately 430 river-km of the Pecos River in Texas, where, depending on locality, alleles typical of *C. variegatus* represented 18 to 84 percent of the genome (Echelle and Conner, 1989). Subsequent monitoring revealed that hybrids were ubiquitous in the Pecos River and peripheral waters (reservoirs, irrigation canals, and gravel pits) in an area that extended downstream from near Loving, New Mexico to at least the vicinity of Pandale, Texas, approximately 55 km downstream of the historic range of *C. pecosensis* (Wilde and Echelle, 1992, 1997; Echelle et al., 1997; AAE and AFE, unpubl. data). Childs et al. (1996) suggested that the genetic structure of the hybrid swarm is explained by genetic swamping, possibly mediated by selection for *C. variegatus* or *C. pecosensis x variegatus* hybrids during a period of increasing population size, such as those that would have followed the fish kills mentioned earlier in this account. The role of selection is being confirmed experimentally by J. Rosenfeld (pers. comm.) in A. Kodric-Brown's laboratory at the University of New Mexico.

Until recently, the population in Salt Creek, a tributary of the Pecos River near the New Mexico/Texas boundary, was considered effectively free of contamination except near the mouth of the creek where there were low frequencies of alleles typical of *C. variegatus*. However, in March 2001, morphological and genetic evidence of hybrids extended approximately 19 river-km upstream in Salt Creek (AAE and AFE, unpubl.). Pure populations of Texas stocks of *C. pecosensis* exist only in two artificial ponds supporting stocks transplanted from Salt Creek (Garrett, this volume) and, as of March 2001, in a headwater reach of Salt Creek (AAE and AFE, unpubl. data).

Endangered species status was proposed for *C. pecosensis* in 1998, primarily because of the threat from hybridization (Federal Register, 63:4608). In 2000, the proposal was withdrawn (Federal Register 65:14513) in response to a Conservation Agreement between the states of New Mexico and Texas, the FWS, and the U.S. Bureau of Land Management (Federal Register, 65:71424). In this agreement, "The signatory agencies . . . made commitments to protect known extant populations of pure Pecos pupfish, expand the distribution of the species within its native range by establishing new populations, and to prohibit the use of . . ." *C. variegatus* as baitfish in the Pecos River area. To date, various measures have been taken to protect populations, including, among other proactive measures, constructing fish barriers in two locations, initiating a study of the life history of the pupfish, enacting the necessary baitfish regulations, and establishment of two captive populations of the Texas stock in artificial ponds (Garrett, this volume).

Cyprinodon elegans (Comanche Springs pupfish).—This pupfish is known only from springfed systems in two separate flood tributaries of the Pecos River in Trans-Pecos Texas, Comanche Draw and the Toyah Creek Basin. Unlike the other two pupfishes endemic to the Pecos River drainage, which occur in saline to moderately saline waters, *C. elegans* is known only from relatively fresh waters (about 1-3 ppt total dissolved solids). The species was described from 32 specimens taken in 1851 at Comanche Springs, Fort Stockton, Texas. Because of over-pumping of groundwater, the six large springs of the Comanche Springs complex were dry by 1956 (Brune, 1981; Scudday, this volume) and the morphologically divergent (Echelle, 1975) local population of *C. elegans* was extirpated (Hubbs, 1957; Miller, 1961).

The species still exists about 90 km to the west in the Toyah Creek Basin near Balmorhea and Toyahvale, Reeves and Jeff Davis counties, where there is a system of three large artesian springs (Phantom Lake, San Solomon, and Giffin springs) and smaller springs that feed the irrigation canals for Reeves County Water Improvement District No. 1 (Garrett and Price, 1993; Garrett, this volume). Genetic and morphological studies indicate that the Phantom Lake Spring population is divergent from the populations in waters fed by Giffin and San Solomon Springs (Echelle, 1975; Echelle et al., 1987).

The species occurs in a small segment (< 1 km) of Toyah Creek, a large, swimming pool fed by San Solomon Spring at Balmorhea State Park, and two semi-natural refugia at the park. The remainder of the species is almost entirely confined to a system of earthen and concrete irrigation canals that is fed primarily by the artesian springs and serves approximately 2428 ha of agricultural land (LaFave and Sharp, 1987). During cooler months of the year, much of the flow is diverted into Lake Balmorhea, an artificial reservoir. The canal system supporting *C. elegans* extends through an area about 3 to 4 km wide and 15 km long, but the species is primarily restricted to areas of more permanent water in the main canals, in sections where the current is slower and the substrate more heterogenous.

The springs now supporting *C. elegans* originally would have fed large, marshy habitats (ciénegas) that drained into Toyah Creek. However, such ciénegas would have been eliminated by the development of the system of irrigation canals for agriculture (Garrett, this volume). Traces of canals built by Native Americans occur in the vicinity of San Solomon Springs (Brune, 1975, 1981), but large-scale diversion of springflows probably started in the 1870s when the area was developed for agriculture to supply the military at Fort Davis (Young et al., 1993). Such activity culminated with the amalgamation, in 1914, of local canal companies into the Reeves County Water Improvement District No.1 and reconstruction of the canal system by the U.S. Bureau of Reclamation in 1946 (Young et al., 1993). A variety of other fishes are known from the area, including at least eight introduced species, most of which are restricted primarily to Lake Balmorhea where they were released either to support the sport fishery or as accidents associated with release of gamefishes. Since the 1960s, Lake Balmorhea has supported a dense, non-native population of *Cyprinodon variegatus*, probably as a result of accidental transport (Stevenson and Buchanan, 1973).

The presence of an introduced population of *C. variegatus* in Lake Balmorhea threatens existing populations of *C. elegans* with both hybridization and competition for resources. A hybrid zone between the two occurs in an earthen canal where Lake Balmorhea receives flow from the irrigation system (Stevenson and Buchanan, 1973; A. F. Echelle and Echelle, 1994). Upstream migration of *C. variegatus* from the reservoir into most of the spring system is precluded by physical barriers. However, in the summer of 1988, *C. variegatus* had moved by way of a recently dug canal from the vicinity of the lake into East Sandia Spring, a small spring near the periphery of the spring-system in the region. A large sample of the introduced species was taken from the headpool of that spring in July 1988 (A. F. Echelle and Echelle, 1994), but sometime after that, and for unknown reasons, *C. variegatus* disappeared from the spring. To our knowledge there is no historical record of *C. elegans* from the headpool of East Sandia Spring, but on 20 March 2001 two specimens were found just downstream of a small culvert in the outflow. There is some indication of male sterility among hybrids in Lake Balmorhea, but the presence of backcross progeny demonstrates that genetic introgression by *C. variegatus* is a serious concern should *C. variegatus* gain access to areas outside of the lake (A.F. Echelle and Echelle, 1994). In 1998, Texas Parks and Wildlife Department expended considerable effort to eliminate *C. variegatus* from the lake; although more than 5 million *C. variegatus* were initially eliminated, the fish quickly reestablished in the lake (Garrett, this volume).

The ultimate threat to *C. elegans* is habitat loss due to declining springflows. Periodic losses of pupfish due to management of the irrigation canals supporting the species (Davis, 1979) is a relatively trivial matter. Some springs in the Balmorhea-Toyahvale area have gone dry and flows from all springs in the area have declined since the early 1900s (Brune, 1981; A. F. Echelle et al., 1989). The two largest of the existing springs, Phantom Lake and San Solomon springs, showed a steady decline in recent decades (A. F. Echelle et al., 1989; Schuster, 1997) and surface flow from the former ceased in 2000 (N. Allan, pers. comm.). In

2001, the Bureau of Reclamation and the U.S. Fish and Wildlife Service installed a pump to maintain the small pool at the head of Phantom Lake Spring, but this is a short-term solution that is unlikely to support the fish populations if water levels continue to decline (N. Allan, FWS, pers. comm.).

Cyprinodon elegans has been a federally listed endangered species since 11 March 1967 (Federal Register, 32:4001). Three aquatic refugia have been constructed for *C. elegans* and other endemic forms. Two using flows from San Solomon Spring were constructed at Balmorhea State Park by the Texas Parks and Wildlife Department; one, constructed in 1974, is a meandering, slow-flowing channel about 120 m long (Echelle and Hubbs, 1978) and the other is an artificial, 1-ha ciénega constructed in 1996 (Garrett, this volume). A refugium at Phantom Lake Spring was built in 1993 through the cooperation of several state and federal agencies. For this refugium, some of the water emerging from Phantom Cave, a hillside cavern, is diverted from an irrigation canal into an artificially constructed channel and side-pool habitat that is about 110 m long (Young et al., 1993). In the Phantom Lake Spring refugium, the abundance of the pupfish peaked rapidly in the first year and then declined somewhat with increasing growth of vegetation, possibly as a result of the elimination of open patches of bottom substrate for spawning (Winemiller and Anderson, 1997). This refugium has been ineffective since 1999 as a result of the loss of springflows. However, the two refugia at Balmorhea State Park support large populations of *C. elegans* in semi-natural settings (Garrett, this volume). Captive stocks of the Phantom Lake Spring population have been maintained at the Uvalde National Fish Hatchery in south-central Texas since 1990.

Río Conchos-Middle Rio Grande

Cyprinodon eximius (cachorrito del Conchos, Conchos pupfish).—*Cyprinodon eximius* comprises at least four forms that may deserve taxonomic recognition (Miller, 1976). These include populations in the Río Conchos and Río Saúz (Chihuahua), a form in Devils River (Val Verde County, Texas), and a form in Rio Grande tributaries upstream of Devils River (Presidio and Brewster counties, Texas, and Chihuahua). A protein electrophoretic survey provided genetic support for the distinctiveness of the Devils River population from other populations of the species (the Río Saúz population was not examined). The Devils River population was fixed for unique alleles at three of 30 loci examined; a population from Alamito Creek, a more upstream tributary of the Rio Grande, was allozymically similar to two samples from the Río Conchos (Echelle and Echelle, 1998). An undescribed pupfish in Ojo de Villa López, an isolated spring near the Río Florido (Río Conchos drainage), may deserve species-level recognition (Contreras-B, 1991), but in overall appearance it resembles *C. eximius* and is genetically similar to that species (Echelle and Echelle, 1998).

The various forms of *C. eximius* occupy a variety of habitats ranging from constant temperature springs to eurythermal marshes and riverine situations. The riverine forms can occur in relatively diverse assemblages of native fishes. For example, samples taken in 1901 from the Río Chihuahua at Chihuahua City, and from the Río Conchos at Camargo, Chihuahua, Mexico produced 12 and 16 species, respectively (Contreras-B, 1977), and, in 1994-1995, the species was taken with 8 to 19 species at four sites in the Río Conchos Basin (Edwards et al., 2001; Edwards et al., this volume). Although general collections from a site can produce a diversity of fishes, the pupfish tends to occupy shallow, quiet waters with relatively few species (Davis, 1980; Valdes-Cantu and Winemiller, 1997). Possibly because of differences in fish assemblage complexity, the species is rare in the mainstem of the Rio Grande and more common in tributaries. In a series of 18 collections downstream of the mouth of the Río Conchos, Hubbs et al. (1977) found only a single specimen in the mainstem and this was at a site just downstream of Alamito Creek, where the species is more abundant.

In a 1994-1995 survey of 11 localities in the Río Conchos Basin, Edwards et al. (2001) found *C. eximius* abundant at a site in the Río Chuviscar and present, but less abundant, at one location each in the Río Conchos and two tributaries, Río San Pedro and Río Santa Isabela. The Río Florido was dry at sites visited during that survey, whereas, in 1989, a collection of *C. eximius* was taken from that river near Villa López (Oklahoma State University Collection of Vertebrates, catalog number 18240). Populations associated with tributaries of the Rio Grande between the Río Conchos and Devils River are restricted primarily to the downstream termini of small streams, although specimens are occasionally taken from associated waters in the Rio Grande (Hubbs et al., 1977). The tributary streams are particularly vulnerable to habitat loss from dewatering as a result of upstream impoundments or pumping of groundwater. Construction of Amistad Reservoir in the 1960s inundated most sites of historic occurrence for the population in Devils River, and it was considered extirpated until its rediscovery in an 11-km reach of Devils River at the headwaters of the reservoir (Davis, 1980). In 1979, specimens from this area were transported to Dolan Creek in a successful effort to re-establish the population in Dolan Springs, a small (< 1 km) springfed area of historic occurrence in the Devils River drainage approximately 25 km upstream of the reservoir (Hubbs and Garrett, 1990).

The population of *C. eximius* in the Río Saúz Basin once was considered extinct because of drying of the habitat (Miller, 1961), but it was collected in 1964 from an impounded, possibly springfed, pond 75 km S of El Sueco, Chihuahua (Minckley and Koehn, 1965). In 1968 and 1975 it was collected in Estacíon Saúz and springs near Laguna Encinillas, but, in 1995 the former locality was dry, as was most of the surrounding area (SCB, unpubl.). The present status of this population is unknown.

Cyprinodon macrolepis (cachorrito escamudo, largescale pupfish).—This species is endemic to a rather large springfed pool, Ojo de la Hacienda Dolores, and its outflow, 12.5 km S-SW of Jiménez, Chihuahua, Mexico. Miller (1976) noted that the outflow "no doubt" once connected with the Río Florido, which supports *C. eximius*. Now the outflow has been highly modified into a number of irrigation distributaries and is isolated from the river. There is evidence from protein electrophoresis for past hybridization and genetic interaction between *C. macrolepis* and the population of *C. eximius* in the Río Florido (Echelle and Echelle, 1998), but the two species have maintained marked differences in color pattern and morphology (Miller, 1976).

During our visit in 1989, the species was common in the spring and the outflow immediately downstream of the headpool. The spring headpool is a locally popular recreation area and has been modified for swimming, with the edges shored up by rock walls. We are unaware of any analysis of the trend of the hydrograph for the springs.

Cyprinodon pachycephalus (cachorrito cabezón, bighead pupfish).—Two populations of "big-headed" pupfish occur in separate thermal-spring systems of the Río Conchos Basin (Minckley and Minckley, 1986): one described as *C. pachycephalus* in Baños (= Ojo) de San Diego, a small springfed system tributary to the Río Chuviscar, 57 km E of Ciudad Chihuahua, Chihuahua, Mexico, and an undescribed population in a spring near the Río Conchos at Julimes, 22 km SSE of Baños de San Diego. The taxonomic status of the latter population has not been determined, but they may represent the same species (Minckley and Minckley, 1986).

Baños de San Diego was described by Smith and Chernoff (1981) and Minckley and Minckley (1986). It comprises a small system of thermal springs that emerges on a small hilltop, and, prior to human alterations, must have emptied into the nearby Río Chuviscar (Minckley and Minckley, 1986). The system includes several small, commercially operated swimming pools and baths. Outlets from the springheads coalesce to form a small, partially braided, stream channel about 2 m wide and less than 3 cm deep. The spring run has been widened in places to form bathing pools, and, in 1971, it emptied into an artificial pond adjacent to the Río Chuviscar. However, by 1980 the spring outflow was diverted into a canal for irrigation (Smith and Chernoff, 1981). Water temperature is 43.8°C to 44.0°C in the springheads and cools as it moves downstream. The pupfish occurs throughout the springfed system alongside a possibly undescribed species (Contreras-B, 1991) related to the blotched gambusia (*Gambusia senilis*). Gonadal condition and other observations led Smith and Chernoff (1981) to conclude that *C. pachycephalus* and the local form of *Gambusia* are not stressed by the high temperatures and that the two exhibit "the highest long-term temperature tolerances known for any teleost."

The only other fishes reported from the Baños de San Diego system are the more widespread pupfish *C. eximius*, a few putative *C. eximius* x *C. pachycephalus* hybrids, and longear sunfish *Lepomis megalotis*, all of which were restricted primarily to the tailwater pond in 1971 (Minckley and Minckley, 1981); none of these were reported by Smith and Chernoff (1981) from their visit in 1980. However, collections from the tailwater pond by one of us (SCB) in 1982 and by his student, Héctor Leal Sotelo, in 1984 included 16 species, including two non-natives, *Cyprinus carpio* and *Ameiurus melas*.

The status of this species is precarious because of its restricted habitat and the general trend toward loss of springflows as a result of over-pumping of groundwater in arid regions of the southwest (Contreras-B and Lozano-V, 1994). Human modifications of the habitat did not seem to threaten the species in 1989, when AAE and AFE visited Baños de San Diego. However, the present status of the species and the undescribed Julimes population is not well known.

TULAROSA BASIN

Cyprinodon tularosa (White Sands pupfish).—*Cyprinodon tularosa* is restricted to the Tularosa Basin in New Mexico where it occupies four isolated bodies of water, three on the White Sands Missle Range (Malpais Spring, Mound Spring, and Salt Creek) and one on Holloman Air Force Base near Alamogordo, Otero County. The Mound Spring and Lost River populations both represent translocations by local people in the late 1960s and early 1970s (Pittenger and Springer, 1999). Genetic analyses indicate that Salt Creek was the source for both introductions (Stockwell et al., 1998). Pittenger and Springer (1999) determined from historical records that Malpais Spring and Salt Creek have been modified by human activities, but Springer (FWS, pers. comm.) suggests that this might not have been associated with notable loss of habitat for the pupfish. The present, sharply incised nature of upper Salt Creek apparently occurred as a result of overgrazing and gully erosion sometime after the late 1800s (Pittenger and Springer, 1999; Springer, FWS, pers. comm.).

Habitats of *C. tularosa* show a wide range in salinity (1.5-60 ppt), temperature (3.0°C to 33.4°C) and environmental stability (Stockwell and Mulvey, 1998). Stockwell and Mulvey (1998) demonstrated a correlation between salinity and genotype at an allozyme locus that appears to reflect adaptation to salinity differences among habitats. In addition, parasitic infection in the White Sands pupfish is apparently a function of salinity (Stockwell et al., 1998). *Physa*, the intermediate host of diplostome trematodes, cannot tolerate salinities above 9 ppt. As a result, pupfish in the relatively fresh Malpais Spring were highly infested (up to 100%) with white grub (*Posthodiplostomum minimum*), whereas the pupfish in Salt Creek were free of this parasite.

No other fish species occur in habitats supporting *C. tularosa* (Miller and Echelle, 1975). However, isolated waters in the vicinity of present populations do support introduced species: western mosquitofish (*Gambusia affinis*) at three sites, largemouth bass (*Micropterus salmoides*) at two, and goldfish (*Carrasius auratus*) at one (Pittenger and Springer, 1999).

Cyprinodon tularosa is considered a federal species of concern (Federal Register, 50:64481). Malpais Spring (266-ha wetland), Salt Creek (33-km stream) and Lost River (5-km stream) all support substantial pupfish populations, whereas the population in Mound Spring (two small ponds) is relatively small (Pittenger and Springer, 1999). Threats include introduction of exotic species, dewatering, and pollution, as well as disruption of the habitat by feral horses and off-road vehicle use. A conservation team organized in 1994 recommended establishment of additional populations in the Tularosa Basin. Stockwell et al. (1998) recommended that the Malpais Spring and Salt Creek forms be treated as separate units of conservation because loss of either one would result in a marked decrease in genetic diversity of the species. As previously mentioned, the Salt Creek form is represented in Mound Spring and Lost River. The Malpais Spring population, however, apparently has not been replicated.

LAGUNA DE GUZMÁN BASIN

Cyprinodon fontinalis (cachorrito de Carbonera).—*Cyprinodon fontinalis* is known only from a series of five springs and their outflows near Ejido Rancho Nuevo in the Bolsón de los Muertos of the Guzmán Basin in northwestern Chihuahua. The springs are described in some detail and mapped by Smith and Miller (1980, 1981). They are separated by a maximum distance of only about 5 km. Ojo de Carbonera, the only spring habitat relatively unmodified by humans, includes a complex of spring-heads and flows about 100 m (less than 10 cm deep) before entering irrigation canals. In this system, *C. fontinalis* occurs most abundantly in small solution holes and along undercut banks of the spring outflow. The species also occurs in irrigation ditches and in four impounded springs. The only native fish sympatric with *C. fontinalis* is the largemouth shiner (*Cyprinella bocagrande*), which is known only from Ojo Solo (Chernoff and Miller, 1982), one of the five major springs supporting the pupfish. Black bullhead (*Ameiurus melas*) and western mosquitofish (*Gambusia affinis*) have been introduced into the area (Smith and Miller, 1980).

The species probably declined after human modifications to the habitat, including introductions of mosquitofish (*Gambusia affinis*), black bullhead (*Ameiurus melas*), and largemouth bass (*M. salmoides*), and construction of irrigation ditches and small impoundments of the springs (Smith and Miller, 1981). In the late 1970s, pupfish were more abundant in the relatively undisturbed Ojo de Carbonera than elsewhere in the area (Smith and Miller, 1980). The species was abundant at Ojo de Carbonera when we visited the area in 1989. An important threat is the possibility for increased pumping of groundwater for irrigation, a factor that has contributed to failure of springflows in nearby areas (Smith and Miller, 1981).

Cyprinodon albivelis (cachorrito dorsal blanca, whitefin pupfish).—This species occurs in the western highlands of Chihuahua, primarily in the headwaters of the Río Papigóchic, a tributary of the Río Yaqui on the Pacific versant, and in a small springfed situation, Ojo de Arrey, in the Río Santa María sub-basin of the Laguna de Guzmàn Basin. There is some question regarding whether the latter population is native or a result of a modern introduction from the Río Papigóchic, but Minckley et al. (2002) suggested, on the basis of genetic considerations (Echelle and Dowling, 1992; Echelle and Echelle, 1993a) and gill raker counts, that it probably is a native population.

The species was widespread and abundant in the Río Papigóchic system in 1978 (Hendrickson et al., 1981) and in 1982 and 1986 (SCB and MLLV). In 1989, it was locally abundant at a site in the Río Papigóchic and at two different springs in the Ojo de Arrey system (AAE and AFE), and, according to Minckley et al. (2002), P. J. Unmack found the latter population "intact in 1999." Minckley et al. (2002) noted that ". . . local stocks . . . [probably] have disappeared due to increased human activities, . . . [but they had] no reason to believe the species is as yet in jeopardy."

Cyprinodon pisteri (cachorrito de Guzmán, Guzman pupfish).—This species (= "Palomas pupfish" in some publications; e.g., Echelle and Echelle, 1998) occurs relatively widely in the Guzmán Basin, and apparently introduced populations once occurred just across the U.S./Mexico boundary in New Mexico (Minckley et al., 2002). The Lago de Guzmán complex comprises the ríos Casas Grandes, Santa María, del Carmen (= Río Santa Clara), and the Laguna Bustillos Basin. In March 1990, Propst and Stefferud (1994) surveyed these basins for the occurrence of Chihuahua chub (*Gila nigrescens*), and collected the pupfish at one or more sites in each, except that the species was absent from their nine sample sites in the Río Santa Clara. Minckley et al. (2002) noted that "the species is catholic in habitat, occupying springs, marshes (ciénegas), shorelines and cutoff channels of rivers and creeks, even colonizing ephemeral canals and ditches along roadsides."

Anthropogenic factors such as habitat destruction, degradation and fragmentation, pollution, and nonnative species have adversely affected native aquatic communities over a large portion of the Guzmán Basin (Propst and Stefferud, 1994). Minckley et al. (2002) observed that, although the Guzmán pupfish is relatively widespread, losses have occurred with the drying of a diversity of aquatic habitats at lower elevations in the Guzmán Basin. They cite Brand (1937) as follows: "The increasing use of spring and river water for irrigation in the *haciendas* and *colonias* of the region has contributed markedly to the lessened flow of the rivers in their lower courses. Many of the abundant springs that fed this system ~80 years ago have failed." However, some losses of habitat, including, by about 1975, the type locality, a springfed ciénega near Las Palomas, are attributable to over-pumping of groundwater on both sides of the international boundary (Minckley et al., 2002).

CUATRO CIÉNEGAS

Cyprinodon atrorus (cachorrito del Bolsón, bandfin pupfish).—*Cyprinodon atrorus* occurs primarily in physicochemically variable, often ephemeral habitats in the Bolsón de Cuatro Ciénegas de Carranza (Cuatro Ciénegas Basin), Coahuila, México. However, the species also occurs in stable, springhead environments in the southeastern end of the Cuatro Ciénegas Basin, where the other pupfish of the basin (*C. bifasciatus*) is absent (Arnold, 1972). The two Cuatro Ciénegas pupfishes hybridize in areas where they come into contact either naturally or because of human-constructed irrigation canals (Miller, 1968; Minckley, 1977). However, such hybridization is restricted to local zones of contact and, outside these zones, the two species are maintaining their morphological and genetic distinctiveness (Echelle and Echelle, 1998; E. Carson, pers. comm.).

The species can be locally very abundant, but is considered rare because of its restricted distribution (Williams et al., 1989). The amount of habitat available for pupfish must have been much more extensive at the turn of the century, when Cuatro Ciénegas was a closed basin with no outflow (Rodriguez Gonzáles, 1926, as cited by Calegari, 1997). Now, however, canals transport water outside the valley (Minckley, 1969, 1977). Canalization of springs and their outflows for agriculture and industry, mostly outside the basin (Contreras-B, 1991), undoubtedly has reduced the amount of habitat available to this fish. In November 1994, the federal government designated Cuatro Ciénegas as a National Protected Area, affording some protection for the system. The species remains abundant, despite a long history of human activity in the basin, including agriculture, gypsum mining, tourism, and a recent increase in manufacturing plants (Calegari, 1997). Uncontrolled tourism and continued economic pressures on the human population pose a variety of threats (Contreras-B, 1991; Calegari, 1997), and there is some concern that groundwater pumping is threatening spring flows by causing the water table to fall (Grall, 1995). The ultimate impact of introduced species, including African cichlids (*Oreochromis* sp. and *Hemichromis guttatus*), water hyacinth (*Eichornia crassipes)*, and Asian snail (*Melanoides tuberculata*), remains to be seen.

Cyprinodon bifasciatus (cachorrito de Cuatro Ciénegas, twoline pupfish).—*Cyprinodon bifasciatus* occupies an arc of constantly warm springs and their outlet pools and streams in the valley floor around the northern tip of Sierra de San Marcos, an area of karst topography where there are cenote-like, springfed sinkholes ("pozas") that range up to 200 m in diameter and more than 10 m deep (Miller, 1968; Minckley, 1969, 1977). Ecologically, the species is largely segregated from *C. atrorus*, the other pupfish of the Cuatro Ciénegas Basin, but they meet and hybridize in peripheral areas (see account for *C. atrorus*).

The species is considered vulnerable to extinction because of its restricted distribution and rather specialized habitat requirements (Williams et al., 1989). Some of the pozas have been developed for picnicking and swimming, but these activities do not seem to pose serious threats to the species. See the account for *C. atrorus* for additional comments on introductions of non-native species and other human activities in the basin.

DISCUSSION

None of the 12 pupfishes endemic to the northern Chihuahuan Desert, as defined for purposes of this symposium, has gone extinct. However, two species, *C. bovinus* and *C. elegans* have declined in range by at least 50% and, without intensive management, native stocks of the former would have been lost to introgressive hybridization. The latter factor has eliminated native stocks of *C. pecosensis* over about 80% of its historic range. With one major exception, most of the remaining species have undergone various degrees of range contraction as a result of a variety of anthropogenically induced losses and physical alterations of habitat. The exception is *C. tularosa*, which is confined within a military reservation with highly restricted access. The range of this species has expanded within its general area of endemicity as a result of transplantations by local people (Pittenger and Springer, 1999) into previously unoccupied waters in the Tularosa Basin.

It is well understood that introduced non-native fishes are a major factor in the decline of native fishes in southwestern North America (Moyle et al., 1986; Allendorf and Leary, 1988; Propst et al., 1992) including northern Mexico (Contreras-B et al., 1976; Contreras-B and Escalante, 1994; Contreras-B, 2000). Correspondingly, depletion of pupfish populations via competition and predation by non-natives has been inferred for various situations in southwestern North America (Soltz and Naiman, 1978; Schoenherr, 1981). However, the potential for losses as a result of genetic introgression by non-native pupfish may have been underestimated until recently. The rapidity with which this factor can cause losses of native stocks is dramatically demonstrated by events following the introduction, in the 1960s (Stevenson and Buchanan, 1973), of *C. variegatus* into Lake Balmorhea. Apparently because of physical barriers, the locally endemic pupfish, *C. elegans*, has been little affected, but the presence of a dense, nearby population of the non-native poses a continual threat for this species (A. F. Echelle and Echelle, 1994) and other endemic pupfishes of the region. Genetic markers indicate that the Lake Balmorhea population of *C. variegatus* has been the source for subsequent introductions into both Diamond Y Draw (Echelle and Echelle, 1997) and the Pecos River (Childs et al., 1996) which support, respectively, the endemic species *C. bovinus* and *C. pecosensis*. As described in our accounts for the pupfishes of the Pecos River Basin, the resulting rate and extent of genetic introgression has generated a great deal of concern and costly, sometimes futile, management activity for the endemic pupfish species.

Smith (1981) argued convincingly that pupfishes in desert environments are hardy generalists ultimately derived from estuarine ancestors pre-adapted to survive the Post-Pleistocene desiccation of pluvial Pleistocene waters (Miller, 1981) of southwestern North America. After surviving and thriving during the post-Pleistocene expansion of desert, the pupfishes in the Chihuahuan Desert have been exposed to dramatically rapid anthropogenic reductions in habitable surface waters since the early 1800s. Since those years, arid grasslands were replaced by shrub desert over large portions of the desert southwest, an effect largely attributable to Anglo-American settlement, agriculture, and domesticated livestock (York and Dick-Peddie, 1969; Gehlbach, 1981; Hendrickson and Minckley, 1984). The rate of desertification, with losses of springs and ciénegas and reduced persistence of natural stream habitat, was hastened by the more recent advent of mechanized construction of dams, canals, and water diversions, and groundwater pumping.

Groundwater pumping may be the ultimate threat to most of the spring-dwelling pupfishes of the Chihuahuan Desert. In the past few decades, groundwater pumping has delivered the *coupe de grace* to many springs in the northern Chihuahuan Desert (Scudday 1977, this volume; Brune, 1981; Contreras-B and Lozano-V, 1994), and springs of the region continue to fail (Contreras-B and Lozano-V, 1994; Sharp et al., this volume). In southern Nuevo León, just south of the region treated in our species accounts, five species of *Cyprinodon* and the monotypic genus *Megupsilon*, the closest relative of *Cyprinodon* (Echelle and Echelle, 1993b; Parker and Kornfield, 1995), were driven to extinction in the wild within 15 years of the advent of intensive groundwater pumping (Contreras-B and Lozano-V, 1994, pers. observ.). In the northern Chihuahuan Desert, groundwater pumping seems directly responsible for losses of two of three morphologically divergent populations of *C. elegans* and significant losses of populations of *C. bovinus* and the Guzman pupfish. In addition, there almost certainly have been losses of populations that may have occupied now-dry springs whose original faunas were unknown to science (W. L. Minckley, pers. comm.; SCB and MLLV, unpubl. data).

Persistence of habitats suitable for the great variety of often locally endemic aquatic and semi-aquatic organisms in desert ecosystems (Williams et al., 1985) is especially threatened when drought conditions are superimposed onto a landscape already depleted of water resources by human activities. This probably explains the recent failure of Phantom Lake Spring

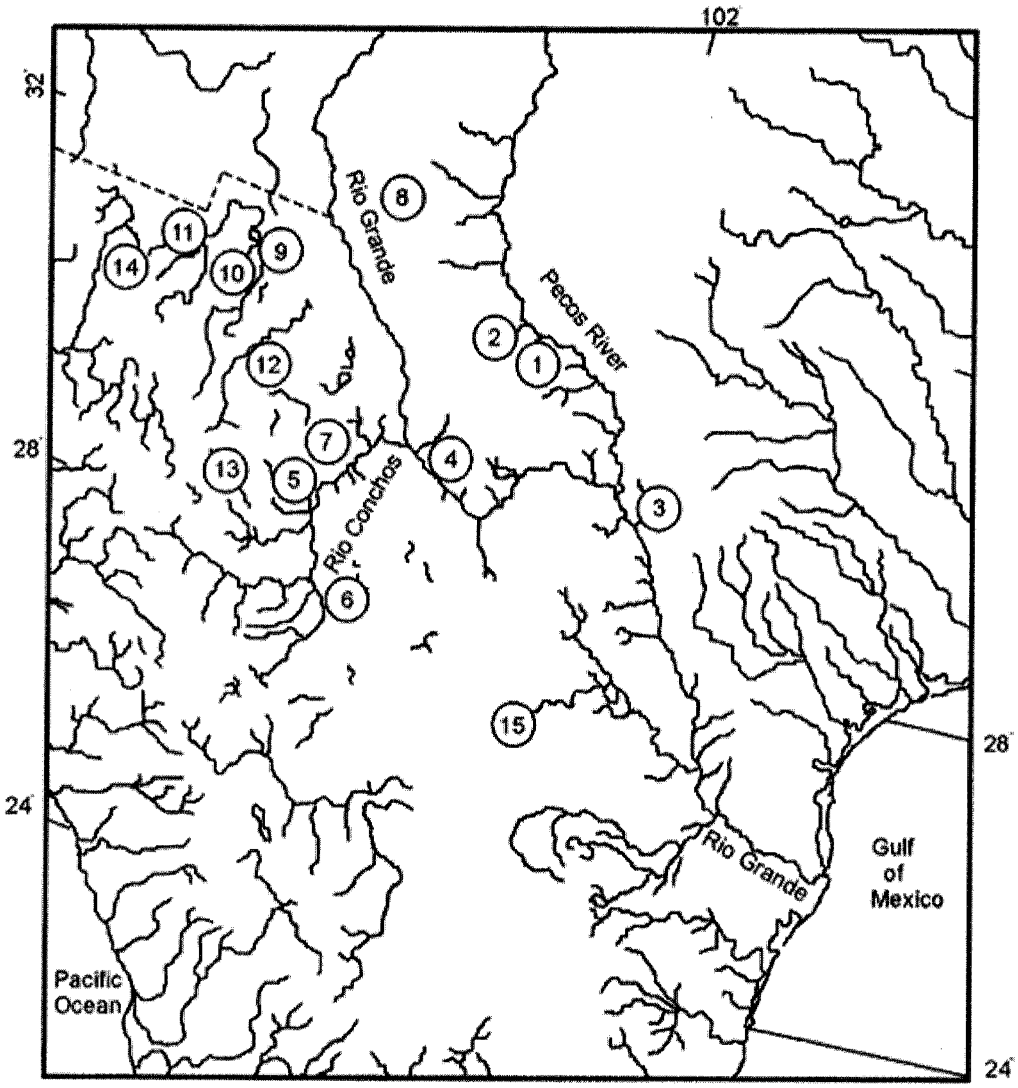

Figure 1. Basins and springs mentioned in the text. 1 = Diamond Y Draw, 2 = Toyah Creek, 3 = Devils River, 4 = Alamito Creek, 5 = Baños de San Diego, 6 = Ojo de la Hacienda Dolores, 7 = Río Saúz, 8 = Tularosa Basin, 9 - 13 = Laguna de Guzmán Basin, 9 = Bolson de los Muertos, 10 = Río Santa Maria, 11 = Río Casas Grandes, 12 = Río del Carmen, 13 = Laguna Bustillos, 14 = Río Papigóchic, 15 = Cuatro Ciénegas.

and the decline in surface waters in Diamond Y Draw, both of which are described earlier in this paper. It remains to be seen whether surface waters in these situations will rebound when the present drought ends. Regardless, with time and continued over-pumping of groundwater, these spring systems and others will fail as part of a trend of such failures in the past few decades (Brune, 1975, 1981; Contreras-B and Lozano-V, 1994; Sharp et al., this volume). This can be avoided only if society decides that these aquatic ecosystems are worth preserving, perhaps for their own sake or for their aesthetic appeal or what they signal about water availability for future human needs.

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