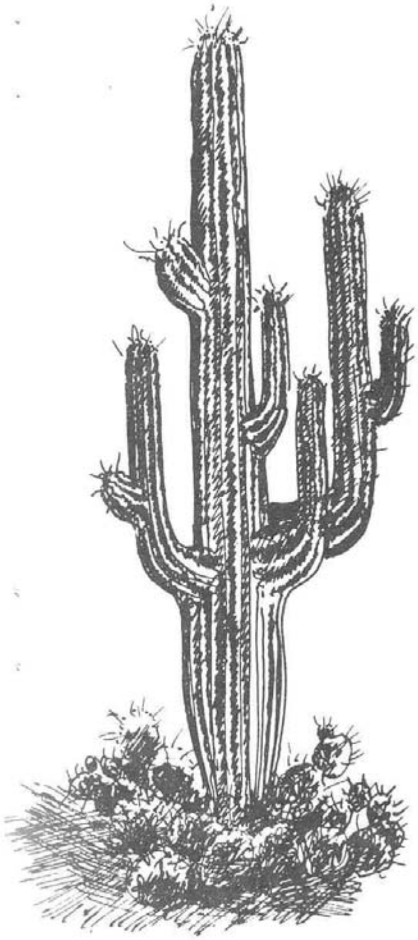

Cooperative National Park Resources Studies Unit

ARIZONA

TECHNICAL REPORT NO. 24

STATUS OF CYPRINODON MACULARIUS EREMUS,
A NEW SUBSPECIES OF PUPFISH FROM
ORGAN PIPE CACTUS NATIONAL MONUMENT, ARIZONA

Robert Rush Miller and Lee A. Fuiman

University of Arizona
Tucson, Arizona 85721

Western Region
National Park Service
Department of the Interior
San Francisco, Ca. 94102

COOPERATIVE NATIONAL PARK RESOURCES STUDIES UNIT
University of Arizona/Tucson - National Park Service

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COOPERATIVE NATIONAL PARK RESOURCES STUDIES UNIT
UNIVERSITY OF ARIZONA
125 Biological Sciences (East) Bldg. 43
Tucson, Arizona 85721

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Robert Rush Miller and Lee A. Fuiman

The University of Michigan
Museum of Zoology and Department of Biology
Ann Arbor, Michigan 48109

And

Dunstaffnage Marine Research Laboratory
P.O. Box 3
Oban Argyll PA34 4AD, Scotland

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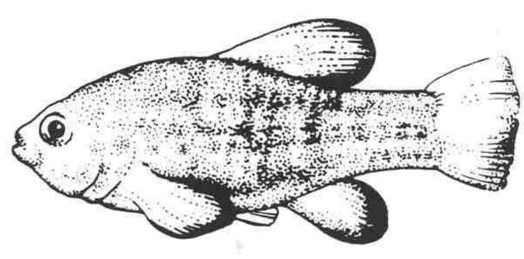

Quitobaquito Science Series #5 - August 1987
Technical Editors: Peter S. Bennett, Research Scientist
and
R. Roy Johnson, Sr. Research Scientist

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ABSTRACT

A new subspecies of pupfish, genus Cyprinodon, is described from Organ Pipe Cactus National Monument, Arizona. It is distinguishable from 10 other populations of the desert pupfish, Cyprinodon macularius, occurring throughout the natural range of that species. Especially interesting is its distinction from pupfish populations inhabiting other parts of the Rio Sonoyta basin that lie mostly in Sonora, Mexico. The new subspecies is diagnosed by males having a longer, wider and deeper head and a broader and deeper body. Females have a deeper head, a slightly deeper body, a longer dorsal-fin base, and a shorter anal fin. None of these differences is affected by allometric growth. Principal components analysis is applied using 26 measurements on 12 populations throughout the range of Cyprinodon macularius, including one undescribed relative.

The Quitobaquito pupfish is illustrated in black and white and in color. Data are given on its past and present habitat, food habits, temperature and low-oxygen tolerance, population size, sex ratio, parasites and reproductive biology. Its origin is attributed to selection for a localized niche after disjunction of a small, initial population.

Remarks on conservation and management are presented both for the new pupfish and for Cyprinodon macularius as a whole. The latter is an endangered species now surviving in Arizona only in Organ Pipe Cactus National Monument and extinct in most of its California range. It still occurs in Rio Sonoyta, Sonora, but its status in many other parts of northwestern Mexico is uncertain. The distribution and depletion of the desert pupfish are discussed and the species range is plotted. Cyprinodon m. californiensis is not accepted as a valid subspecies.

RESUMEN

Se describe una nueva subespecie del pez "perrito" genero Cyprinodon, de Organ Pipe Cactus National Monument, Arizona. Se distingue de las otras 10 poblaciones de perritos de desierto, Cyprinodon macularius, que constituyen la especie en toda su area de distribucion. De particular interes son sus diferencias con poblaciones de perritos que habitan la cuenca del Rio Sonoyta comprendida en su major parte en Sonora, Mexico. La diagnosis de la nueva subespecie es: los machos tienen la cabeza mas alargada, ancha y alta, y el cuerpo mas ancho y alto (que en otras poblaciones). Tambien las hembras presentan una cabeza mas alts y un cuerpo ligeramente mas alto, con la base de la aleta dorsal mas larga y la aleta anal mas corta (que en otras poblaciones) . ninguna de las medidas es afectada par crecimento alomentrico. Se efectuo el analisis de componentes principales usando 26 medida de 12 poblaciones al traves del area de distribucion de Cyprinodon macularius, incluyendo una forma cercana no descrita.

El perrito de Quitobaquito se ilustra aqui en blanco y negro, y a color. Se proporcionan datos de su habitat pasado y presente, habitos alimenticios, temperature, tolerancia a la hipo-oxigenacion, tamano de la poblacion, abundancia relativa de sexos, parasitos y biologia de su reproduction. Su origen se atribuye a evolucion por selection natural en una poblacion pequena, en alopatria.

Se proporcionan comentarios sobre conservacion y manejo tanto de la neuva subespecie como de Cyprinodon macularius en general. Cyprinodon macularius esta en peligro de extincion. En Arizona sobrevive solamente en Organ Pipe Cactus National Monument y ya esta extencta en la major parte de California. Su situation en parte de Mexico es incierta. Se discute la distribution y destruccion del perrito de desierto y se ilustra su distribution geografica. No se acepta Cyprinodon m. californiensis como subespecie valida.

INTRODUCTION

Organ Pipe Cactus National Monument, in Pima County, Southwestern Arizona (Weight and Weight, 1952; Dodge, 1964), is remarkable for its endemic pupfish that inhabits the spring outflows and the pond at Quitobaquito. Two springs, probably the largest in the Papago Indian Country, provide the water for the pond. They are warm springs located about 100 m to the south along the southern border of the pre-Cambrian Quitobaquito Hills. The present pond (Leonard, 1972:26; Bowers, 1980:Fig. 8) was enlarged and deepened in 1962 from a shallow irrigation reservoir (Fig. 1) dug a century earlier (Dodge 1964:79; Gehlbach, 1981:262).

The Quitobaquito fish is assignable to the desert pupfish, Cyprinodon macularius Baird and Girard. This species was once common in cienagas, springs, streams, sloughs, and lakes within the Gila River basin of Arizona and parts of Sonora, Mexico, the Colorado River from near Yuma to its mouth in Mexico, the disjunct Salton Sea and Laguna Salada basins (including springs, wells, and tributaries) in California and Mexico, and the Rio Sonoyta basin of Sonora, Mexico, and adjacent Arizona (Fig. 2). Now threatened with extinction throughout its range (Miller, 1979) and recently formally listed as an endangered species (U. S. Federal Register 4/30/86), the only population of C. macularius still surviving in Arizona (and one of the few surviving anywhere) is the one described herein as a new subspecies. Consequently, it is most important that this fish be perpetuated. Threats to its survival and recommendations for its maintenance are discussed later.

EVIDENCE FOR SUBSPECIFIC RANK

METHODS. We made 26 measurements on specimens from 12 localities in southwestern United States and northwestern Mexico (Fig. 2). The first author measured the samples comprising Group 1 (see Table 4), including 10 males and 10 females from each locality. The second author measured 15 males and 15 females from each population in Group 2, with the exception of the collection from El Doctor (10 individuals of each sex) and the syntypes of Cyprinodon californiensis (2 males only available). Data from the two samples are presented because they show that despite differences in techniques of measuring the results led to the same taxonomic conclusion. We selected individuals to represent uniformly the size range from about 20 to 50 mm SL. Measurements, defined by Miller (1948), were made with dial calipers and recorded to the nearest 0.1 mm.

Trends of morphometric variation among populations were explored through principal components analysis. Sexes were treated separately because of the observable sexual dimorphism in Cyprinodon (Miller, 1948). Since principal components analysis was sensitive enough to detect differences in our measurement techniques, we analyzed Groups 1 and 2 separately.

Principal components (PC1, PC2 and PC3) were calculated on covariance matrices of log $_{0}$ transformed measurements. Effects of size differences among samples were reduced by shearing components (Humphries et al., 1981; Bookstein et al., 1985). Measurements contributing strongly to interpopulational shape differences were identified by the magnitude of their loadings on PC2 (Table 3). The degree of allometry (ontogenetic shape change) in a measurement for a population was estimated by the multivariate allometric coefficient, obtained from the within group PC1 (Humphries et al., 1981). Statistically significant differences in allometric coefficients among populations were determined through analysis of covariance, using a 0.05 level of significance.

RESULTS. The first two principal components account for 93.3% of the total variance in measurements among males from the seven populations in Group 1. The first component, a representation of size, indicates that the sample from Wise Ranch contains individuals larger than other samples (Fig. 5). Many measurements load heavily on the primary shape axis, PC2, which shows that six of the populations are roughly similar. The fish from Quitobaquito are distinct from the others. Those from Rio Sonoyta and Pozo del Tule are most similar to Quitobaquito. Quitobaquito pupfish are broader (see measures of body, head and mouth widths in Tables 1-3), have smaller fins (dorsal, anal and pelvic) and a shorter peduncle. The head tends to be deeper and the jaw longer than in the other populations. shearing of components has little effect on the analysis.

For Group 1 females, PC1 and PC2 account for 94.5% of the morphometric variation. The Quitobaquito fish are distinct from the others, and the Rio sonoyta population forms an intermediate link. Females, like males, are broader, have smaller fins (pelvic, caudal and anal), and a shorter peduncle than the other populations (Tables 1-3).

Among Group 2 males, principal components 1 and 2 account for 94.9% of the total variance in measurements form the eight populations of Cyprinodon macularius. The first component indicates that the El Doctor sample contains smaller individuals than other samples (Fig. 7). Most populations occupy a similar position along the shape axis. Fish from Quitobaquito are quite distinct from the others, and those from Rio Sonoyta have an intermediate shape. As in Group 1, Quitobaquito pupfish are broader (Tables 2-4) and have smaller fins (dorsal, anal, and pelvic), and a smaller eye, but a longer snout than the other populations. Shearing of components has little effect on the analysis.

Components 1 and 2 for Group 2 females describe 94.2% of the total variance. Again, PC2 shows that the Quitobaquito fish are different from the others (Fig. 8), although two specimens from the Salton Sea have a shape similar to the Quitobaquito fish. Features accounting for the separation in females are largely the same as those in males (widths, fin lengths, orbit length; Tables 1-3). Shearing has little effect on the results.

Tables 1 and 2 suggest that Quitobaquito males have a wider mouth and that females have a longer snout, wider head, and broader interorbital region. These apparent differences are allometric, resulting from the larger size of individuals in the Quitobaquito sample.

DISCUSSION. Despite differences between the four analyses (shape among the sexes, groups of populations analyzed together, measurement technique and sample size), results were remarkably consistent. All four analyses described the Quitobaquito population as a distinctively shaped fish. Five characters summarize this shape: body, head and mouth widths, depressed anal-fin length and pelvic-fin length. Additional characters become important in certain comparisons, depending on the sex and populations being compared. Rio Sonoyta fish are most similar morphometrically to those from Quitobaquito and are nearest geographically. Multivariate allometric coefficients for the characters measured are not different for the Quitobaquito and the Rio Sonoyta samples, so none of these differences results from allometry. Principal components analyses (Figs. 5-8) using two sets of populations show that the Quitobaquito pupfish is a distinct form separable from all other populations of C. macularius studied. By assigning it a scientific name this

Figure 1. Pond at Quitobaquito, 14 April 1950

Key to Symbols Used for Pupfish Populations

Symbols for Figure 2 and Figures 5-8

Miller and Fuiman
1986

- ✪ - Quitobaquito, Arizona
- ★ - Rio Sonoyta, Sonora
- ▲ - El Doctor, Sonora
- ● - Wise Ranch, California
- ◇ - Pozo del Tule, Baja California
- ◆ - Rio San Pedro, Sonora*
- ◉ - Monkey Springs, Arizona
- ○ - NE corner Salton Sea, California
- ☆ - Dos Palmas Spr. (1881), California
- ▼ - Harper Well Wash, California
- □ - Cyprinodon californiensis (2 syntypes)

* Rio San Pedro, Arizona, is type locality for C. macularius

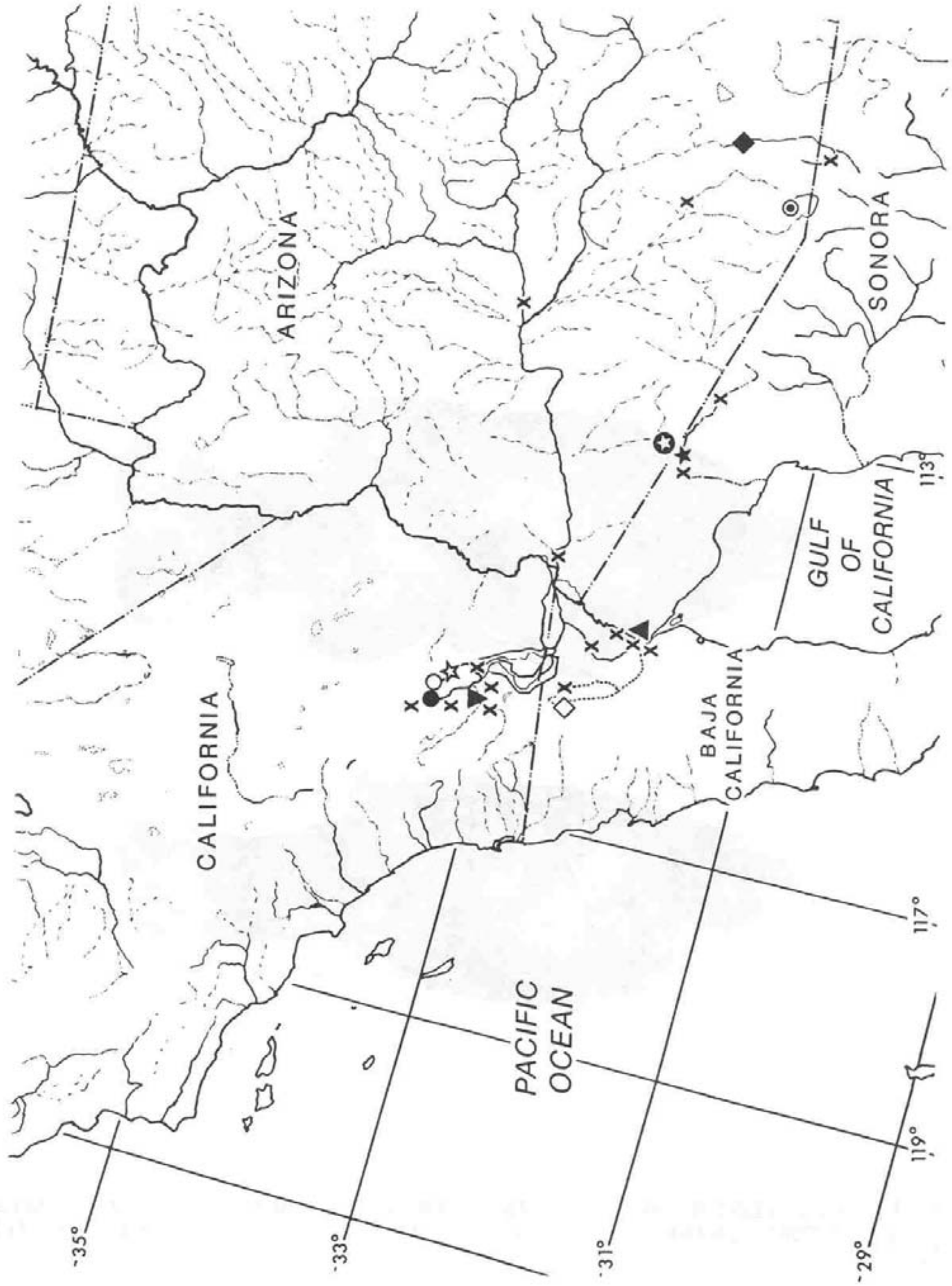


Figure 2. Natural Distribution of <u>Cyprinodon</u> <u>macularius</u>. Records from artesian well at Thermal and wells about Indio, both north of Salton Sea, are given by Jordan (1924). The X symbols are for verified records.

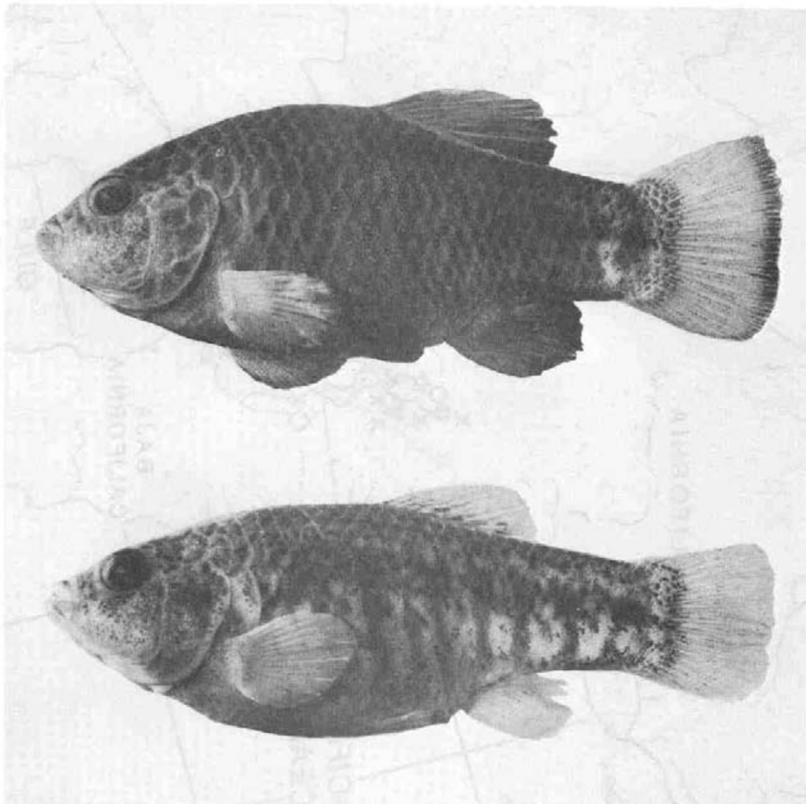


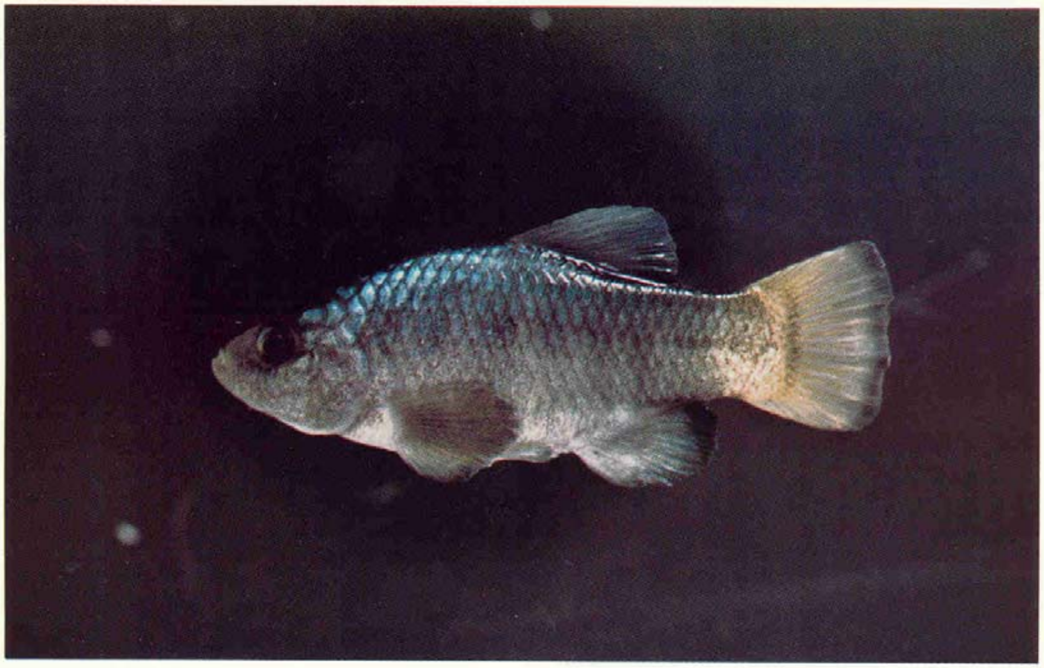
Figure 3. Cyprinodon macularius eremus n. subsp. Above, male holotype (UMMZ 162661), 40 mm SL; below, female paratype (UMMZ 162662), 40 mm SL.

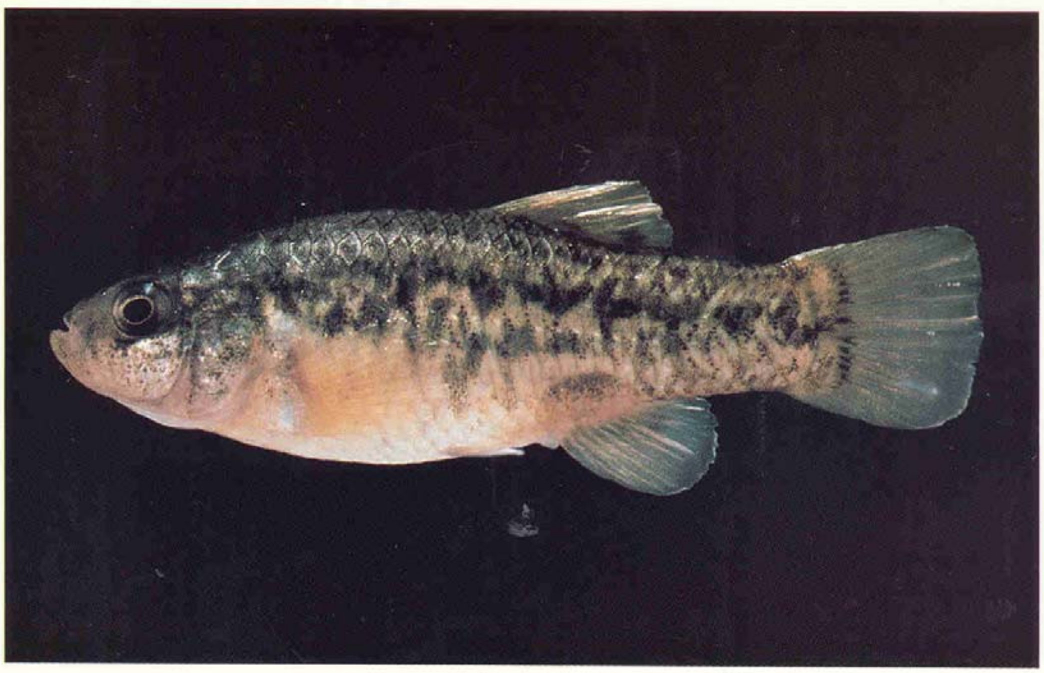
facilitates communication and helps support conservation efforts. We regard this pupfish to be a subspecies because there is too much overlap with other populations to justify naming it as a full species.

Cyprinodon macularius eremus, n. subsp.
Quitobaquito pupfish

Cyprinodon macularius. Huey, 1942:375 (common name, abundant in springs and reservoir, attraction for fish-eating birds); Miller, 1952 (ice-age origin, size, courtship); Cole, 1963 (name misspelled macularis, referred to as distinct subsp., ecology) ; Miller, 1964: Fig. 3 (photo of holotype and paratype); Miller and Lowe, 1964:146 (type loc. mentioned, spelled Quitovaquito); Cole and Whiteside, 1965 (ref. to distinct subsp., ecology of Quitobaquito); Kidd and Wade 1965 (subsp. of C. macularis [sic]) ; Cox, 1966 (endemic morph, behavior, ecology); Lowe et al., 1967 (O_2 tolerance); Lowe and Heath, 1969 (behavioral thermoregulation, max. temp. tol.); Cox, 1972 (food habits); Leonard, 1972 (ref. to unnamed subsp., origin); Minckley,

Figure 4. Cyprinodon macularius eremus n. subsp. (paratypes, UMMZ 211156). Above, male 33.4 mm; below, female, 30.5 mm. Kodachrome by R. R. Miller.





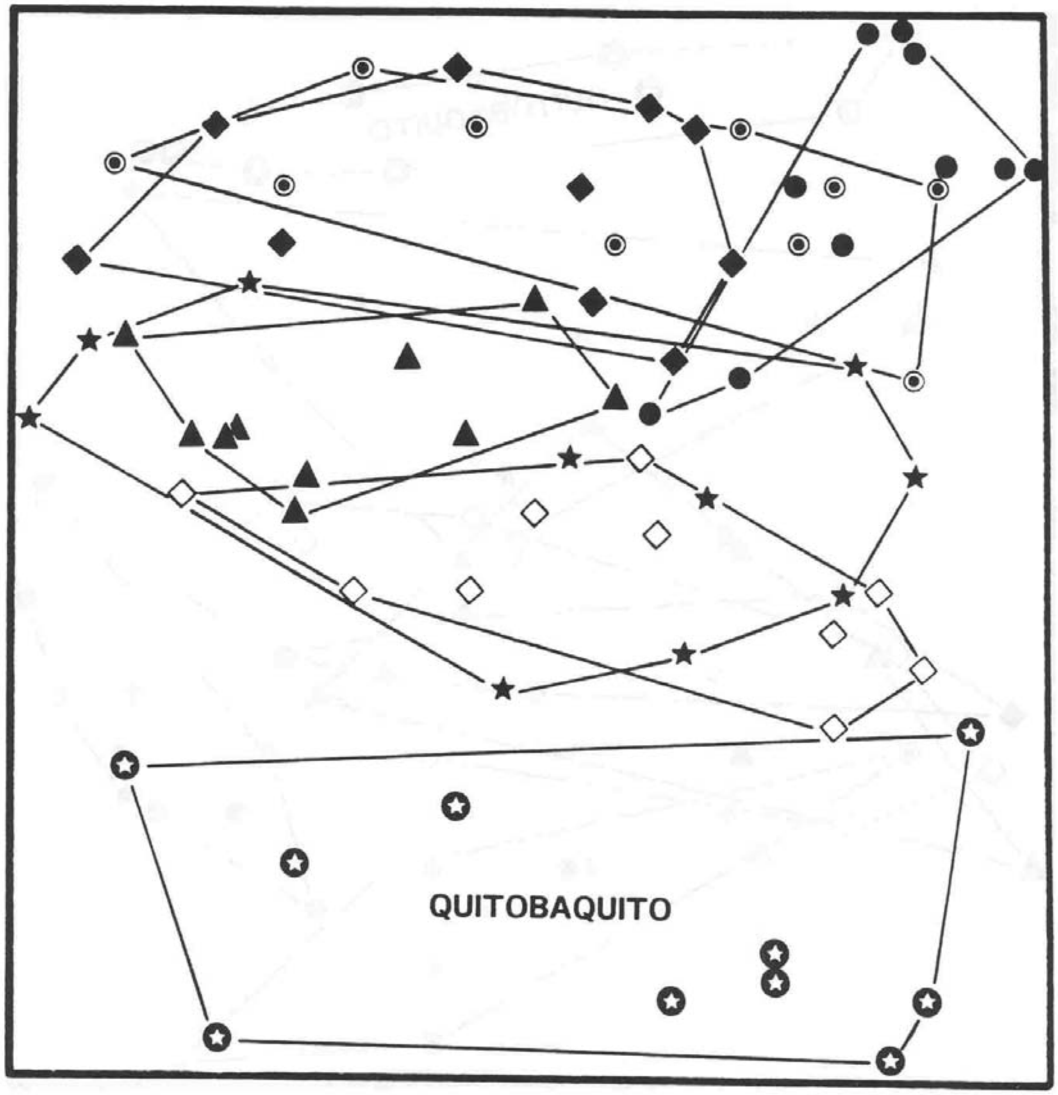


Figure 5. Principal components, Cyprinodon macularius, Group 1, males. Symbols in Figure 5 are as in Figure 2.

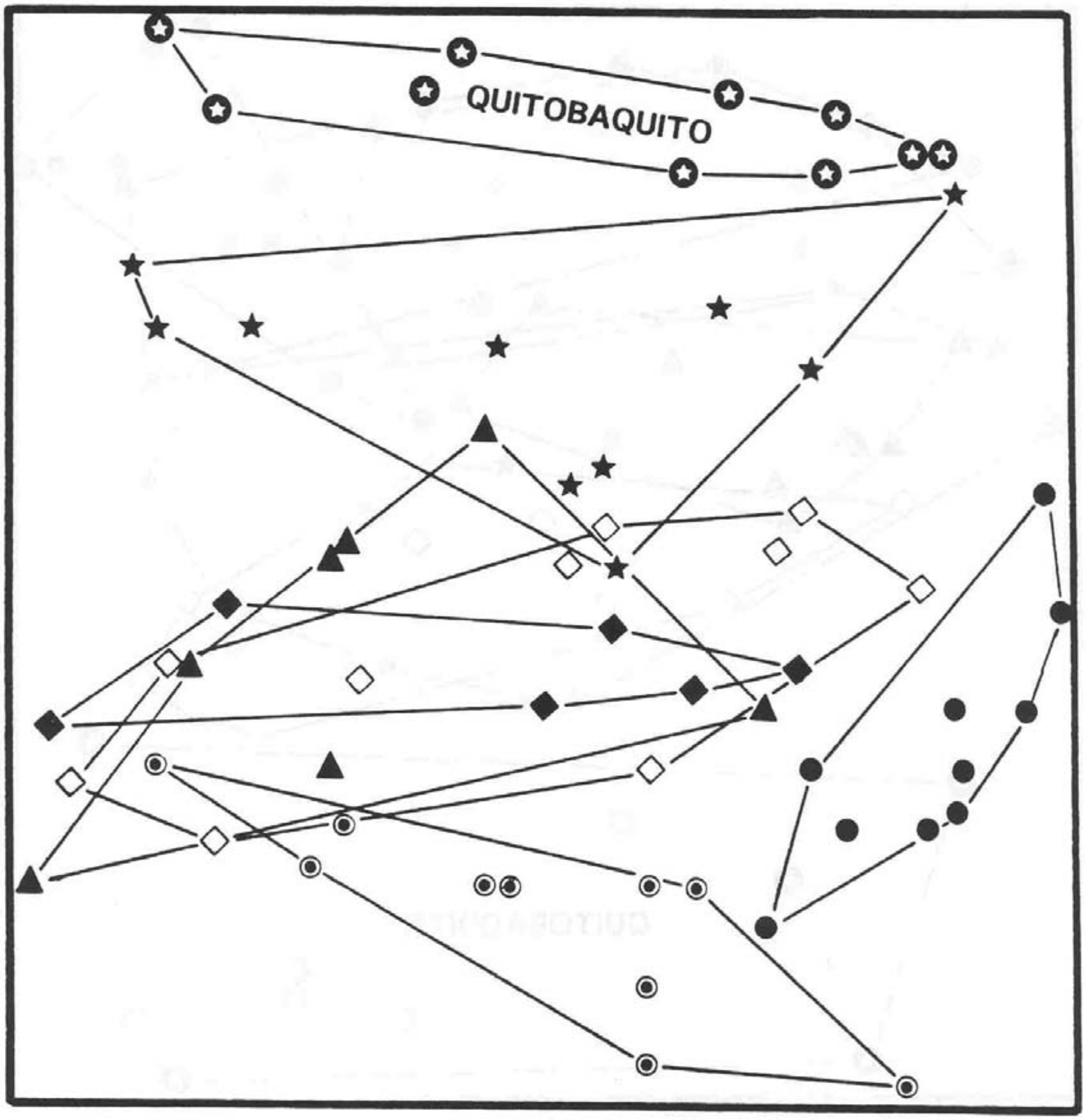


Figure 6. Principal components, Cyprinodon macularius, Group 1, females. Symbols in Figure 6 are same as in Figure 2.

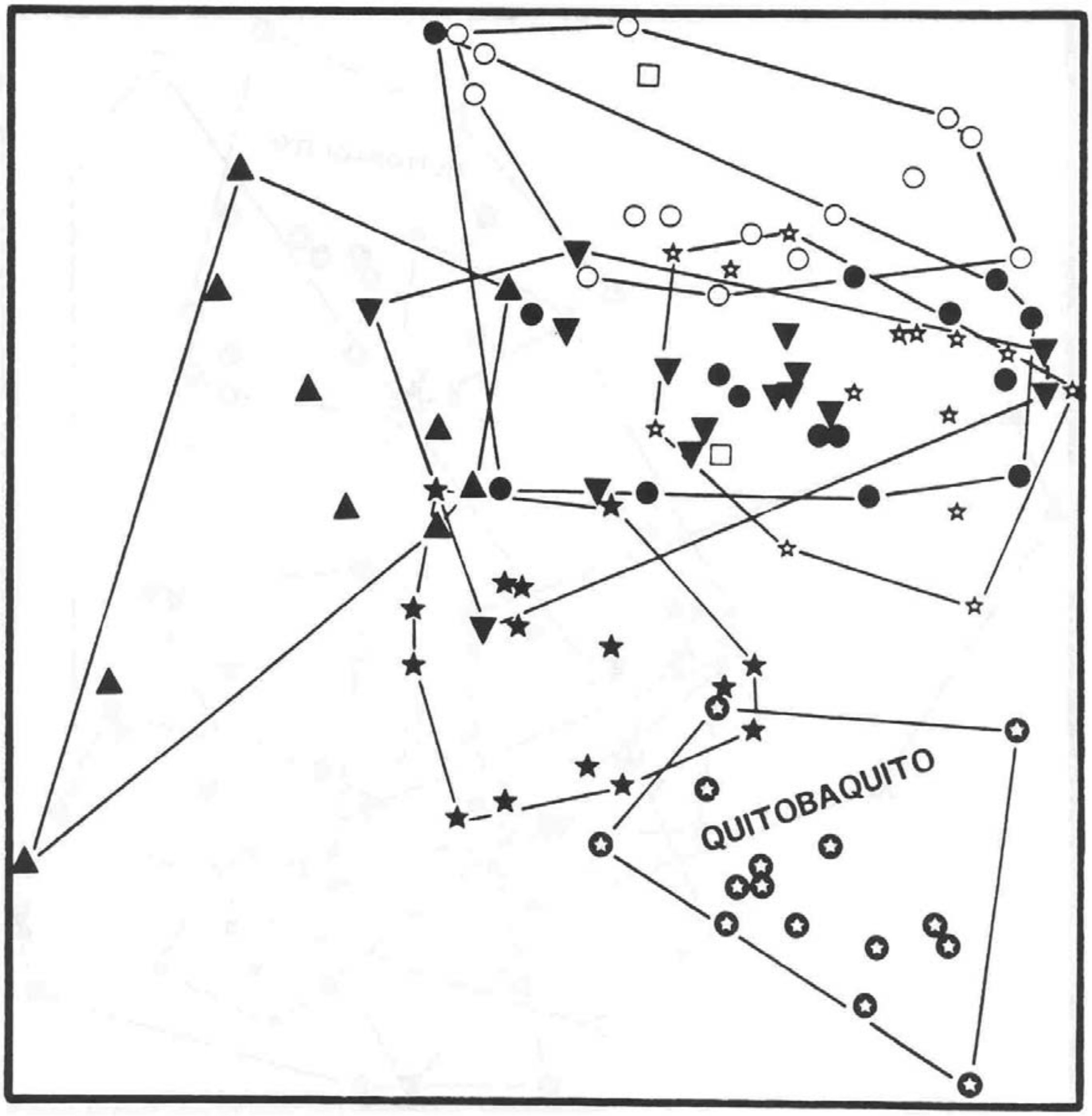


Figure 7. Principal components, Cyprinodon macularius, Group 2, males. Symbols in Figure 7 are same as in Figure 2.

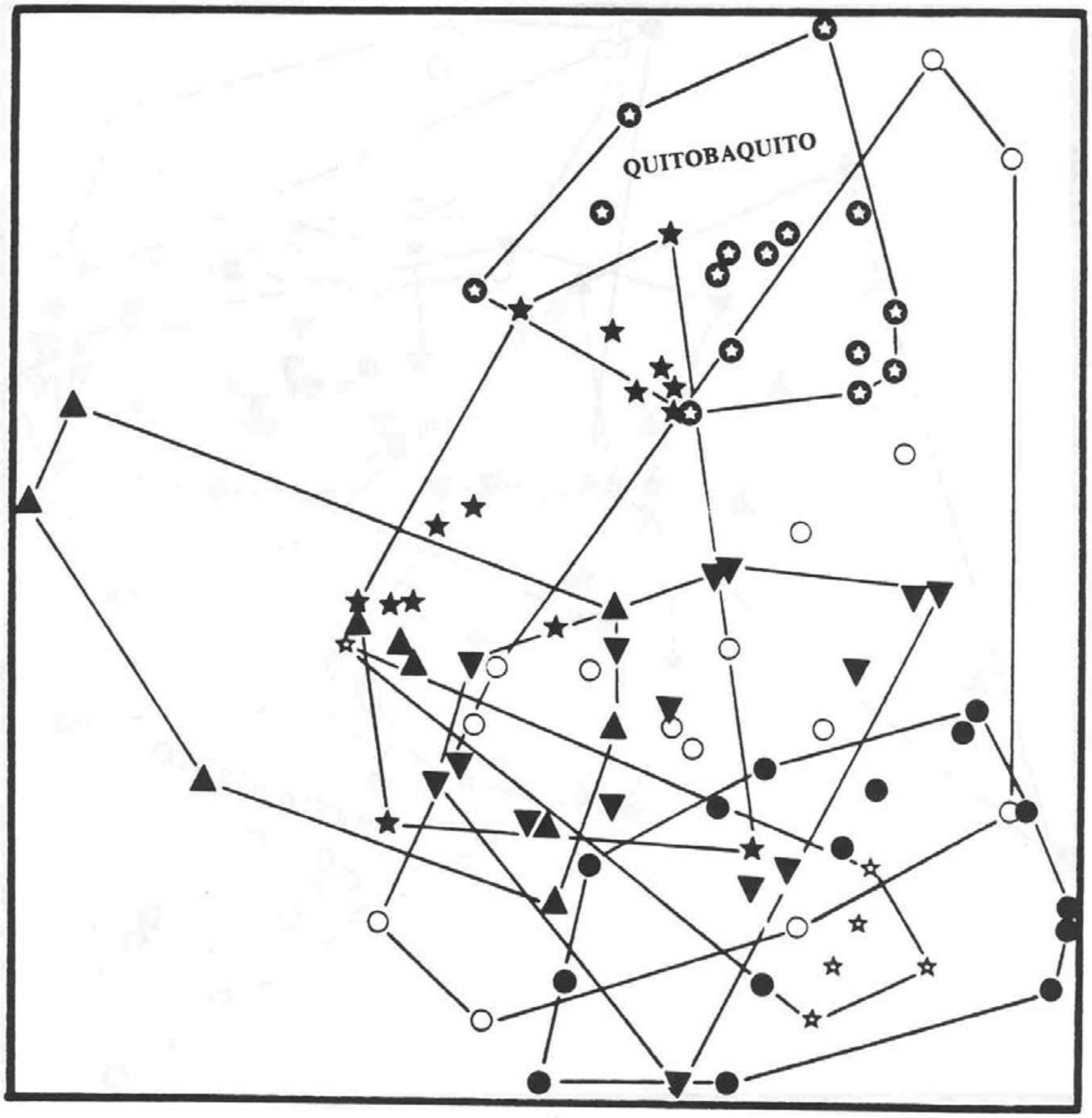


Figure 8. Principal components, Cyprinodon macularius, Group 2, females. Symbols in Figure 8 are same as in Figure 2.

1973:190 (undescribed subsp., introd. and eradication of golden shiner at Quitobaquito); Deacon et al., 1979:41 (listed as of special concern); Kynard and Garrett, 1979 (reproductive ecol., life span); Miller, 1979 (distinctive subsp.); Nabhan et al., 1982:126 (divergence of pupfish at Quitobaquito); Turner, 1983:691 (ref. to Quitobaquito pupfish); McMahon and Miller, 1985 (endemic subsp., threats to survival, habitat modification).

Cyprinodon macularius sonoytae (nomen nudum),. Anonymous, 1977, as cited by Minckley and Brooks (1986:86, ftn. 10).

DIAGNOSIS. A population of Cyprinodon macularius differing from pupfish in the adjacent Rio Sonoyta as follows (see Tables 1-2): males with longer, wider and deeper head, and broader and deeper body. Distances between tip of snout and pelvic-fin insertion and from anal-fin origin to tip of snout greater in males. In females, head deeper, body slightly deeper, dorsal-fin base longer, and depressed anal fin not as long.

TYPES. Holotype, UMMZ 162661, a nuptial males 40.0 mm SL, and 426 yearling to adult paratopotypes, UMMZ 162662 (386), 24-46 mm SL, AMNH 57133 (10), 25.3-36.3, ANSP 158520 (10), 23.7-39.1, FMNH 97069 (10), 25.1-38.8, and USNM 279473 (10), 24.5-36.3, all collected by R. R. and F. H. Miller and H. E. Winn, 14 April 1950, in spring-fed pond at Quitobaquito, Organ Pipe Cactus National Monument, Pima County, Arizona; elevation 332 m. Four paratypes, UMMZ 211156, 2 males and 2 females, 30-36 mm SL, taken from type locality by R. R. Miller, T. E. McMahon, and M. K. Kunzmann, 20 May 1982. S1059-43, 27 juvenile to adult paratypes, 17-33 mm SL, from type locality by E. L. Hubbs and D. S. Jonas, 28 March 1959.

DESCRIPTION. Body form and life colors are shown in Figs. 3-4. Morphometric data appear in Table 2 and are analyzed by principal components in Figs. 5-8. Morphometry has already been discussed. Meristic data for 15 males and 15 females follow, with means after each count. Counts for the holotype are indicated by asterisks. Dorsal-fin rays 9(4), 10*(20), 11(6), 10.07; anal-fin rays 10*(25), 11(5), 10.17; pectoral-fin rays (both fins) 15*(17), 16*(37), 17(6), 15.82; pelvic-fin rays 5(1), 7*(58), 8(1), 6.98; caudal-fin rays 15(1), 16(12), 17(8), 18*(8), 19(1), 16.87. Scales: lateral series 25(18), 26*(12), 25.40; origin of dorsal fin to origin of anal fin 11(3), 12(13), 13*(14), 12.37; around caudal peduncle 16*(29), 17(1), 16.03; around body 30(3), 31(2), 32(12), 33(2), 34*(10), 36(1), 32.60. Gill rakers (total, arch 1) 16(2), 17*(10), 18(9), 19(6), 20(3), 17.93. Vertebrae (incl. hypural as 1): precaudal 11*(5), 12(25); caudal 13(1), 14(20), 15*(9); and total 25(1), 26*(25), 27(4), 26.10. Brachiostegal rays 5(2), 6(18) in 10 males and 10 females. Head pores (both sides counted): mandibular 0(1), 2*(59), 1.97; preopercular 6(1), 7*(54), 8(5), 7.17; preorbital 2(1), 3(10), 4*(49), 3.80.

In 20 males (26.5-41.5 mm SL), dorsal-fin origin is equidistant between caudal-fin base and a point varying from tip to snout to tip of rostrum. This is more posterior than typical for C. macularius. In addition, dorsal-fin position in females is the same as that in males, whereas this trait shows marked sexual dimorphism in most populations of C, macularius (including Rio Sonoyta - compare Tables 1 and 2).

Scale covering Numeral process larger and thicker than adjacent scales (as in C. macularius from Rio San Pedro, Sonora, UMMZ 162680, near type locality), but not as strongly developed as in desert pupfish from saline Salton Sea, California. Scale shape, detailed ornamentation and number of radii match those of Rio Sonoyta pupfish (Miller, 1943:P1. 5).

The tricuspid teeth are very similar to those of C. macularius, as described and illustrated by Miller (1943:4, Fig. 1A).

When distance between posterior margin of humeral scale and snout tip is stepped into predorsal distance, ratios in 20 males varied from 1.4-1.6 and for 20 females from 1.45-1.6 (as in C. macularius, Miller 1943:Table 2).

The first dorsal ray is moderately thickened at base, not strengthened and spine-like as in C. variegatus. Longest pelvic ray of males extends posteriorly to front, center, or posterior edge of vent, only rarely to anal-fin origin (1 in 20 individuals examined). In females this ray reaches from front to center of vent or, occasionally (3 in 20) falls short of front of vent. Pelvic fins are reduced in size in Quitobaquito and Rio Sonoyta fish compared to most populations of C. macularius.

COLORATION. Colors of freshly preserved and live individuals were noted in the field in 1950 and 1982 and are shown in Figure 4. Nuptial males brilliant, dark metallic blue to turquoise over all of body except abdomen; dorsal and anal fins deep chalky blue; caudal fin varies from yellow to olive-yellow, this color just encroaching onto posterior of third caudal peduncle; pectorals and pelvics greyish blue. Interradial membranes of dorsal, anal, and pectoral fins dusky to black; posterior borders of dorsal and anal fins black; caudal fin with black, terminal bar somewhat wider than pupil; tips of pelvic fins black.

Females golden yellow to brownish olive, with lower sides silvery and abdomen white; dorsal and anal fins watery white, caudal pale yellow, and pectorals and pelvics yellowish. Bars on side form a disconnected series of irregularly shaped, dark blotches extending from behind head to base of caudal fin (these become prominent in preservative - see below). When observed in the water, some males showed a similar interrupted lateral stripe.

The color pattern in alcohol varies as follows. In 20 females (28-39.5 mm SL), vertical bars vary from virtually continuous (n=12), to disrupted (3), or intermediate in development (5), thus differing from usual condition in most populations of C. macularius in which bars are generally disrupted.

HABITAT. The following description is based on observations of Quitobaquito Springs and Pond on 14 April 1950. The man-made marshy pond (Fig. 1), fed by the outflow from two springs, supported the bulk of the pupfish population at Quitobaquito. The springs and pond are about 100-200 m north of the U.S.-Mexico boundary. The shallow, open pond was about 70 x 70 m in major dimensions and was frequented by livestock. The border of the pond was nearly surrounded by mesquite, with some willows, and a large cottonwood tree (Populus fremontii) grew at each end. The depth was no greater than 26 cm over most of the pond', its bottom comprising thick mud covered by fine silt. Many large cottonwood leaves lay over 75% of the numerous small holes made by dry cracks when the water level was lower or by cattle tracks; these holes were from 7.6 to 18 cm deep. Where no holes existed the water was only 2.5 to 5 cm deep; in summer this shallow water varied in temperature from 39.6-41.0 C (Lowe and Heath, 1969:58). Much detrital Scripus and algal scum floated on the surface, with concentration around

[1] In 1959 Lowe and Heath (1969) found the maximum depth to be 30-40 cm.

the edges of many small islands of mud. Current in the pond was slight to none and aquatic vegetation was ha a (sparse), Eleocharis, and Scirpus. Water temperature in the pond in mid-morning on 14 April was 26.2 C (as was the air).

Outflow from these two springs, given by Bryan (1925:165) as 43 gallons per minute (gpm), or 27 liters per second (L/s), was impounded about 1860 for primitive irrigation farming. A series of low dikes retained this pond about 1900 (Bryan, 1925:P1. XXIV, Fig. 13). Although Bryan (Op. cit.) claimed that the pond was in Mexico, it actually lies just north of the international boundary. The flow from the springs in recent years has varied from 30 to 35 gpm (= 1.9-2.3 L/s) according to Anderson and Laney (1978), who believed Bryan's estimate was too high.

The Quitobaquito Springs are classified as warm, about 4 C above the mean annual air temperature (Anderson and Laney, 1978:12). On 14 April 1950, the temperature of the eastern springs was 25 C and that of the northern one 26.3 C (given by Bryan, 1925:165, as 80.3 F - 26.8 C). These two springs joined shortly below the eastern one to form a narrow ditch leading to the pond. About 15 m below this junction pupfish were seen under green algae and were common for the next 80 m of the ditch to its mouth in the pond. No fish were seen in either spring source. In and near these springs there is evidence from travertine deposits that more water once flowed from numerous spring seepages arranged in a radial fashion up against the hills.

Sand Papagos, that branch of Papago Indians inhabiting the head of the Gulf of California, used the Quitobaquito oasis, at least seasonally, long before European explorers visited the region (Nabhan et al., 1982). We do not know what the aboriginal conditions at and around Quitobaquito were like, but it is clear that man has modified the area and its plant life. "This was accomplished through the channeling and diking of the spring outflow, woodcutting for shelter and firewood, grazing of livestock, clearing of adjacent areas for agriculture, construction of dwellings, and the introduction of exotic plants for orchards and shade. Even the several large cottonwood trees (Populus fremontii), which are so important as nesting sites for some birds, were probably introduced during this period. After the monument was established in 1937, Papagos continued to live and farm at Quitobaquito. This continued until the 1950's when the National Park Service formally acquired the site" (Johnson et al., 1983:1). Water temperature in Quitobaquito pond on 21 April 1983 was 24 C (air 21.5 C) at 1630 hr, salinity 0.7 ppt, Umhos 1,113. Water analyses of the pond and springs at Quitobaquito and of Rio Sonoyta are given in Table 5.

BIOLOGY. Several studies of the Quitobaquito pupfish provide information on various aspects of its biology that are briefly summarized here. Food habits (Cox, 1972) conform to those for pupfishes in general, which are omnivores. Cyprinodon macularius eremus is unselective, their digestive tracts containing large amounts of detritus. Plants, insect larvae and nymphs, water mites, ostracods, their own eggs and one juvenile, Daphnia, sponge, mollusk eggs and some other organisms were observed by Cox. Like some other desert-spring fishes that can tolerate low oxygen concentrations (Hubbs et al., 1967), this subspecies is able to survive 0.13 mg O=/1 (Lowe et al, 1967), a distinct advantage in its often physiologically stressed habitat. Under laboratory conditions, it can tolerate water temperatures as high as 44.6 C, varying from 44.2 to 45.4 C (Lowe and Heath, 1969). The highest natural temperature tolerated by Cyprinodon, 43.8 C, is evidently that for the pupfish of San Diego, Chihuahua (Smith and Chernoff, 1981), recently described as C. pachycephalus (Hinckley and Hinckley, 1968).

This paragraph summarizes information from Kynard and Garrett (1979). The maximum life span of C. m. eremus appears to be three years, with the age-1 year class averaging 29.6 mm TL, age-2 40.2 mm, and age-3 48 mm. The sex ratio in June 1976 among 154 breeding fish (>32 mm TL) favored females 43:57: in November, however, the sex ratio was approximately equal. The first fry observed in 1975 were seen on 27 April in a shallow cover of the modified pond when air temperature at noon was 24.5 C. One young was seen in the outflow ditch above the marshy pond on 14 April 1950. Thus, breeding may commence in April or May. In 1975, breeding ceased between 14 July and 28 August; and in 1976 a few fish were still breeding on 5 August, with none observed doing so on 9 September. Males prefer to breed in water less than 15 cm deep over solid substrates.

Population size estimates were 7,986 on 22 October 1975, 3,592 on 10 June 1976, and 4,558 on 10 November 1976 (Kynard and Garrett, 1979); an estimate for the fall of 1980 was 3,143 (Robert L. Hall in letter to James E. Johnson 28 August 1981).

Adult pupfish remain active in the spring outflows during all seasons, but become dormant in the pond during winter, when air temperatures may fall to 10 C or lower. The mean temperature for January at Sonoyta, Sonora, about 60 m higher than Quitobaquito, is 11.2 C, according to Hastings and Humphrey (1969). As soon as the water temperature exceeds 20 C (usually in April), they become active. Territorial and breeding behavior peak early (May - early June), tapering off and ceasing completely in August. A nematode parasite was present in 13 of 58 fish (22%); it resembles one found in wading birds and may have gained access to the pond by them (Cox, 1966).

ORIGIN. The original assumption (by RRM) that the pupfish inhabiting the Rio Sonoyta would be the same as the one at Quitobaquito was based on direct water connection within the past 100 years (Lumholz, 1912:199; Ives, 1936:351) between Quitobaquito and Rio Sonoyta, which lies less than 2 km to the south. Field reconnaissance of the Quitobaquito area, however, does not indicate a historical water connection from the present springs, or from their ponded portion, to the Rio Sonoyta. Fossil spring deposits to the west of the springs indicate that, during floods or in times of greater natural flow (perhaps Pleistocene), water filled an adjacent wash and established such a connection (field study with Peter Bennett, 6 May 1986). Permanent contact between the two probably occurred at some time in the Holocene and certainly during the Pleistocene and earlier times.

Rio Sonoyta clearly received its pupfish from the region about the Colorado River delta before blockage of the Sonoyta's original westward course by the eruptions of the Pinacate Volcanic Field (Ives, 1936, 1964) - a date probably within the past 100,000 years (Donnelly, 1974; see comments in Turner, 1983). This, of course, is a minimum invasion date, for Cyprinodon has plausibly inhabited the Rio Sonoyta basin at least since the Pliocene (Miller, 1981:71, Fig. 5).

There is no information on the pristine pupfish habitat at Quitobaquito, but at times it may have been so spatially restricted that the fish population, especially the minimum effective reproductive numbers, fell to very low levels. Differentiation of this pupfish by selection for the particular habitat at Quitobaquito, aided by chance fixation from random drift of a few genes (the Sewall Wright effect) in a small, closely inbreeding population, could be responsible for its evolution. That such a small pupfish population can maintain itself for millennia is well demonstrated by the Devils Hole pupfish, Cyprinodon diabolis (Deacon and Deacon, 1979).

Aquatic habitats suitable for endemic fishes and snails (Tryponia) have had a long history in the Quitobaquito area (J. J. Landye, pers. comm., 1986).

ETYMOLOGY. Latinized from the Greet word eremos, meaning solitary or lonely, reflecting the fact that this isolated population may eventually be the only surviving natural stock of Cyprinodon macularius.

CONSERVATION. Although the Quitobaquito pupfish lives within a national monument and a Man and the Biosphere Reserve, and is, thus, presumed to be protected, its survival there has been threatened by (1) the introduction of an exotic species, the golden shiner (Notemigonus crysoleucas); (2) drastic modification of its habitat by man; (3) potential loss of habitat from mining of water in the Mexican part of the Rio Sonoyta basin; and (4) contamination from airborne pesticides from agricultural practices in Mexico just south of its habitat. The golden shiner was eliminated on 18 December 1969, the pond the pupfish now inhabits has yet to be made more suitable for them, pumping in Mexico seems not yet to be affecting the water supply at Quitobaguito, and the pesticide contamination is being monitored. According to a letter from Boyd Kynard to James E. Johnson dated 27 September 1978, a fish kill during the summer of 1976 reduced the pupfish population to fewer than 3000 individuals by fall and less than 1800 the next spring. Analysis of fish tissue revealed lethal levels of m-parathion.

Refuges developed on the monument for the Quitobaquito pupfish were established at Bates Well tank (distant from airborne pesticides) and at Rincon (=Williams) Spring but have since been abandoned. A stock was also sent to the Arizona Sonora Desert Museum and the Arizona Historical Museum in Tucson (according to the above letter). Unfortunately, the purity of these stocks is uncertain. In cooperation with the Arizona Game and Fish Department, stocks were transferred to their care and also held at Arizona State University, Tempe (Minckley, 1973:191). The 1958 record from near Tempe was the result of introduction of the Quitobaquito pupfish into the Salt River channel by the State of Arizona (Minckley and Brooks, 1986:81). The subspecies did not become established there, however, and cultured stocks survive today in Arizona only at Arizona State University (Minckley, pers. comm. 1986).

In comparing the allozymes of five natural and four artificial (refugia) populations of C. macularius, Turner (1984) showed that levels of polymorphism and heterozygosity are essentially identical between the natural and cultured stocks. Thus, utilization of refugia can be at least a temporary expedient in management and conservation of such endangered species.

Considering the species throughout its range, the prospect for continued survival of C. macularius in any part of its original distribution (other than at Quitobaquito) is bleak (see review by Black, 1980 and Turner, 1983). Once abundant in Salton Sea (a single shoreline pool was estimated by Barlow (1960:351353] to contain 10,000 juveniles during 1954-56, and another pool 150 adults/°'2), this species is now scarce there, is gone from all wells and springs in which it formerly occurred around and north of the Salton Sea, and is apparently barely surviving in Salt Creek and San Felipe Creek where it was common as recently as 1983 (Schoenherr, pers. comm., 1986). The Salton Sea populations contracted greatly in the late 1960's (R. K. Liu and B. J. Turner, field observations 1967, 1968; Crear and Haydock, 1971). Introductions of exotic fishes into Salton Sea are believed to be the major cause of the elimination of Cyprinodon macularius (Schoenherr, 1981, 1985, pers. comm. 1986).

In the Colorado Delta the species is known to survive in Baja California along the edge of the Santa Clara Slough (see Rinne and Guenther, 1980) and in saline pools at the south end of the Cocopah Mts., Dec. 1985 (W. L. Minckley, pers. comm. 1986), but all populations in the Laguna Salada basin were extirpated by 1970 (observation by Richard P. Phillips, San Diego State College, received by C. L. Hubbs). However, high-water levels of the Colorado River since 1983 have flooded the delta region (for the first time in more than 20 years) and filled Laguna Salada. Consequently, the current status of the desert pupfish in the Mexican portion of its range is uncertain. Unlike conditions that prevailed in the pristine delta, however, this area is now probably infested with exotic species. At least 44 are known from the lower Colorado (Minckley 1982). Tilapia, in particular, impacts the pupfish.

Artificial refugia for the desert pupfish have been established in Arizona at Boyce Thompson Arboretum of the University of Arizona (see Minckley and Brooks, 1986), Arizona State University, and Deer Valley High School Natural Area (West Phoenix); in California in Anza-Borrego Desert State Park (San Diego Co., three ponds), Butte County Mosquito Abatement District (Butte Co.), Living Desert Reserve (Riverside Co.), Salt Creek State Recreation Area (Imperial Co.), and Oasis Spring Refuge upstream on Salt Creek (Riverside Co.); and in New Mexico at Dexter National Fish Hatchery. Refugia are a temporary expedient only (see Turner, 1984), wild populations under natural field conditions being essential in the long run to maintain local genomes.

MANAGEMENT OPTIONS. The survival of the Quitobaquito pupfish would be greatly enhanced if its pond were modified to provide a more suitable habitat for reproduction and natural life style. A section of the pond should be filled in so that the water depth is no more than six inches (ca. 15 cm), preferably shallower in places: areas with depths three times this now provide suitable refuges from temperature extremes. Pupfishes have a very broad physiological amplitude, as compared to most other fishes, and have been described as "stress "tolerant," eurythermohaline species, thriving in habitats that provide severe physiological problems (see papers in Naiman and Soltz, 1981). Exceptional hardiness is a hallmark of this genus. The pond at Quitobaquito should not be managed solely as a bird-watching site (Nabhan et al., 1982:126).

DISTRIBUTION OF CYPRINODON MACULARIUS

The historical and present natural distribution of the desert pupfish (Fig. 2) is indicated by specimens examined or unquestionable literature and written or verbal reports. As Turner (1983) postulated, this species probably once occurred farther up the Colorado River than the vicinity of Yuma because suitable, though transitory, habitats (oxbows, marshes, backwaters) formerly existed upstream at least as far as the vicinity of Needles (Ohmart et al., 1975). However, there are no voucher specimens of desert pupfish from the U.S. section of the Colorado River, and the great fluctuations of the pristine river channel (Grinnell, 1914) argue against establishment of long-term populations.

In Sonora, except for records along and near the Colorado River and its delta and the upper San Pedro River, C. macularius is native only in the basin of Rio Sonoyta, a flood tributary to the Gulf of California (McMahon and Miller, 1985). The belief that it was endemic to an isolated, endorheic lake, Laguna Prieta, is here shown to be erroneous. This laguna, 27 airline km (or about 40 km by road) ESE of San Luis, Sonora (114 33`30"N long., 32 18'40"W lat.), constitutes an interior marshland habitat in extensive, hard sand dunes (Minckley and Brown, 1982:226, 230, Fig. 151) ; the sand-dune rim surrounding the lake likes below 50 m elevation and the water surface at 28 m elevation (see Map NI 11-12, El Centro, Ser. F501, 1:250,000, Army Map Service). Laguna Prieta is about 1000 x 700 m in major dimensions. Cyprinodon macularius was recorded without comment from this marshy lagoon by May (1976:150), and its extirpation was reported by Kynard and Garrett (1984) who regarded it to be native. On 25 May 1938, Samuel b. Ward and one of us (RRM) made a thorough exploration of Laguna Prieta because the police chief of Yuma had told Carl Hubbs that there were tiny fish in this lagoon. Its main part appeared to have a salinity comparable to that of Great Salt Lake, since our bodies floated without sinking. The "tiny fish" turned out to be brine shrimp (Artemia) that swarmed in the lagoon, but no fish life was seen there or in any of the pools (some of potable water) surrounding it. Lumholz (1912) also visited Laguna prieta and made no mention of fish life there although he noted the fish at Quitobaquito and in Rio Sonoyta. Thus, the pupfish observed by May were introduced; unfortunately none was collected, so their possible source is unknown.

The desert pupfish is now nearing extinction. Habitat destruction from marsh drainage, groundwater mining, deforestation, overgrazing, agricultural use of water, dam building, and real estate development attendant upon burgeoning populations of man (especially since World War II), and perhaps most important, the serious impact from introduction of vast numbers of exotic predators and competitors, have eliminated the species over almost all of its range. These factors, singly or in combination, eliminated Cyprinodon macularius from the entire Gila river basin and from all of Arizona except Quitobaquito, destroyed most of its habitat in the Colorado River Delta (by preventing the river from reaching the Gulf of California), and so drastically reduced its populations in the Salton Sea that it is approaching extinction there today.

In the Salton Sea basin, California, 1986 surveys by California Department of fish and Game personnel revealed juvenile pupfish in San Felipe Creek, Imperial county (16-18 April), and 70 individuals were captured (29 April-1 May) in upper Salt Creek, Riverside County (memos of 16 May 1986, issued by Kimberly Nicol, kindly provided by Darlene McGriff). Thus the species is still surviving, although precariously, in these two tributaries to the Salton Sea and in the artificial refuges cited above.

High population variability of fishes is typical for the harsh environments encountered in desert arroyos (Constantz, 1981). The monsoon climate in the Rio Sonoyta basin is characterized by torrential summer rains and sporadic catastrophic flooding (McMahon and Miller, 1985). this river was drastically changed in August, 1981, when a major flood deeply entrenched the drainage, destroyed the headwater cienegas, and forced resettlement of Sonoyta downstream (Gehlbach, 1981:262). Major floods in Rio Sonoyta during 1982 scoured the channel and obviously swept the desert pupfish to the end of permanent flow near Agua Salada (McMahon and Miller, 1985:Fig. 1). In November, 1982, McMahon was able to collect only one adult female pupfish in a long stretch of the river above Agua Salada. Prior to these floods, in May, 1982, pupfish and dace were common in the permanent stretch of river that rises 17.6 km west of Sonoyta and 1.6 km south of Hwy. 2. But on 20 April 1983 a three-hour examination of some 5 km of this area revealed only swarms of Gambusia and Agosia. Not a pupfish was seen or collected. At that time, however, Aqua Salada was not visited. Salinity in this flow on 20 April 1983 was 1.8 ppt. Umhos 2,450, air 17 and water 21 C at 1500 hrs.

Reexamination of the permanent part of Rio Sonoyta on 5 and 7 May 1986 revealed that pupfish had repopulated the stream in large numbers (over 100 were easily caught in three short hauls of a small seine); at least 5-6 km stretch of the river contained Cyprinodon macularius, from just west-southwest of El Papalote to the vicinity of Agua Salada; the latter lies at 113 08'N long., 31 55`W lat. (see Carta Topografica H12A13, 1:50,000, El Papalote). Elevations in the permanent section of the river vary from about 310 to 265 m.

Large, healthy, natural populations of desert pupfish that can be expected to provide long-term survival may now be virtually restricted to the one at Quitobaquito.

The history of the basins of Salton Sea and Laguna Salada (Baja California), has been one of recurring filling by overflow of the Colorado River meandering over its delta, followed by desiccation. There is ample evidence to indicate that lakes of variable sizes occurred in the Salton Sink between about 300 and 1600 years before present (Hubbs et al., 1960:215-217; Waters, 1982). From 1840 to 1907, the river overflowed into Salton Sink seven times (Caplan, 1961). Thus, pupfishes surviving in desert springs following desiccation of these lake stages were not long isolated from other lower Colorado River stocks of C. macularius carried into Salton Sink with each incursion. Such repeated mixing of stocks helps to explain why we found no compelling evidence for taxonomic recognition of C. macularius californiensis (recognized by Hubbs et al., 1979:41; Loiselle, 1980, 1982) or the Le Conte desert pupfish (Deacon et al., 1979:41), within the Salton Sink, or any populating from Laguna Salada.

Table 1. **Chemical constituents in Water at Quitobaquito, Arizona, and Rio Sonoyta, Mexico**[1].

Sample	TDS	TSS	pH	HCO_3	F	Cl	PO_4	NO_3	SO_4	Na	K
Quitobaquito pond											
Cole & Whitehead (1965)	....	....	....	411	5.3	383	....	....	100	350	7.0
Kunzman (1982)	820	<10	9.22	220	4.9	190	<0.50	<0.50	110	230	3.1
Quitobaquito Spring											
Cole & Whitehead (1965)	....	....	....	316-402	4.3	148-318	....	....	71-91	191-284	4.5-6.0
Kunzman (1982)	670	<10	8.07	300	4.1	150	<0.50	9.9	95	188	2.7
Rio Sonoyta											
Kunzman (1982)	1640	<10	7.60	820	7.8	370	4.0	1.3	240	550	5.2

[1]**Cole & Whitehead** sampled the spring in June, 1963 and May, 1964. **Mike Kunzmann** kindly **provided the 1982** analysis. The analyses by Bryan (1925:167) show similar contrasts between water chemistry at Quitobaquito Spring and Rio Sonoyta.

Table 2. **Measurements in thousandths of standard length of** _Cyprinodon_ _macularius_ _eremus_. **Based on the type series. Holotype included with males.**

Measurement	15 Males			15 Females	
	Holotype	Range	Avg.	Range	Avg.
Standard length, mm	39.7	29.5-41.5	35.1	27.9-39.0	34.9
Predorsal length	597	554-604	584	552-602	583
Prepelvic length	577	557-588	573	545-602	579
Preanal length	698	676-704	693	667-728	699
Anal origin to caudal base	378	366-407	386	340-377	359
Dorsal origin to caudal base	504	483-535	503	463-497	484
Body depth	441	393-449	427	369-421	396
Body width	277	235-285	262	239-292	263
Head length	330	322-353	336	310-339	325
Head depth	287	278-317	292	265-297	285
Head width	292	246-292	262	237-279	257
Caudal-peduncle length	252	231-275	257	235-268	252
Caudal-peduncle depth	204	190-217	205	172-203	186
Interorbital width	133	112-140	123	115-129	123
Snout length	103	85-111	100	86-103	95
Orbit length	78	78-94	85	74-86	81
Mouth width	131	115-131	122	101-126	113
Mandible length	101	81-111	102	82-109	101
Dorsal fin, basal length	212	168-224	202	168-195	183
Dorsal fin, depressed length	315	289-330	305	227-279	252
Anal fin, basal length	131	123-148	134	92-129	112
Anal fin, depressed length	242	235-274	254	181-208	196
Caudal-fin length, middle rays	234	221-251	235	193-239	215
Pectoral fin, basal length	98	86-99	93	77-99	88
Pectoral-fin length	265	234-276	254	203-249	230
Pelvic-fin length	111	99-126	115	92-107	101

Table 3. Measurements in thousandths of standard length of <u>Cyprinodon</u> <u>macularius</u> from Rio Sonoyta, Mexico. Based on UMMZ 211155.

Measurement	15 Males		15 Females	
	Range	Avg.	Range	Avg.
Standard length, mm	25.5-34.5	29.3	25.4-34.4	29.9
Predorsal length	540-580	562	562-601	583
Prepelvic length	497-557	530	517-585	553
Preanal length	625-673	655	639-712	681
Anal origin to caudal base	385-433	407	349-391	369
Dorsal origin to caudal base	479-527	502	445-500	475
Body depth	323-391	355	322-399	357
Body width	213-251	228	213-278	245
Head length	303-330	317	294-329	309
Head depth	246-277	262	238-282	254
Head width	213-248	230	213-269	236
Caudal-peduncle length	254-293	275	238-279	257
Caudal-peduncle depth	179-206	190	162-189	173
Interorbital width	102-122	113	94-123	111
Snout length	81-100	89	76-90	84
Orbit length	77-91	83	74-88	81
Mouth width	102-115	109	97-123	108
Mandible length	95-104	99	86-108	96
Dorsal fin, basal length	162-204	181	146-183	162
Dorsal fin, depressed length	252-298	279	235-285	248
Anal fin, basal length	120-151	136	100-120	113
Anal fin, depressed length	249-299	269	201-271	221
Caudal-fin length, middle rays	225-255	239	201-256	230
Pectoral fin, basal length	75-98	87	71-101	86
Pectoral-fin length	225-263	248	218-254	237
Pelvic-fin length	105-127	116	90-119	105

Table 4. **Loadings on unsheared principal components for populations of** *Cyprinodon macularius*. **Characters (and loadings) important to separation of populations are given in boldface type.**

Character	Group 1				Group 2			
	Males		Females		Males		Females	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Standard length, mm	.18	.05	.19	.01	.17	.00	.18	.04
Predorsal length	.19	-.08	.20	.09	.18	-.10	.19	.08
Prepelvic length	.19	-.05	.20	.10	.19	-.04	.19	.05
Preanal length	.19	-.06	.19	.11	.19	-.04	.19	.08
Anal origin to caudal base	.18	.25	.18	-.22	.17	.15	.18	-.12
Dorsal origin to caudal base	.19	.13	.18	-.07	.18	.14	.20	.02
Body depth	.27	.03	.23	.05	.26	.12	.23	.00
Body width	.21	-.37	.21	.34	.23	-.36	.22	.30
Head length	.17	-.04	.19	.01	.18	.00	.18	-.03
Head depth	.18	-.29	.20	.08	.22	.05	.22	.01
Head width	.19	-.32	.20	.30	.22	-.28	.21	.19
Caudal-peduncle length	.19	.33	.18	-.34	.17	.16	.19	-.09
Caudal-peduncle depth	.22	-.01	.22	.02	.22	.00	.21	.04
Interorbital width	.20	-.04	.21	-.09	.22	-.07	.22	.14
Snout length	.24	-.07	.23	.09	.23	-.23	.23	.13
Orbit length	.14	.03	.16	-.13	.14	.22	.15	-.24
Mouth width	.21	-.35	.21	.28	.21	-.48	.21	.26
Mandible length	.19	-.20	.21	.11	.19	-.07	.21	.19
Dorsal fin, basal length	.22	.09	.20	-.03	.21	.18	.22	.00
Dorsal fin, depressed length	.24	.19	.22	-.09	.22	.21	.19	-.09
Anal fin, basal length	.17	.13	.20	.02	.18	.12	.17	-.12
Anal fin, depressed length	.14	.28	.17	-.19	.13	.29	.14	-.22
Caudal-fin length, middle rays	.14	.14	.15	-.28	.15	.01	.13	-.30
Pectoral fin, basal length	.19	-.04	.19	.17	.21	-.09	.22	.20
Pectoral-fin length	.18	.05	.17	-.11	.19	-.05	.18	-.31
Pelvic-fin length	.21	.37	.18	-.55	.21	.40	.20	-.58

Table 5. Measured samples of Cyprinodon belonging to Groups 1 and 2. Catalog Numbers are UMMZ except as noted.

Locality and Cat. No.	Group 1 (Measured by RRM)	Group 2 (Measured by LAF)
Pozo del Tule, Baja Calif. (133074)	X	-
El Doctor, Sonora (138919)	X	-
(212313)	-	X
Rio Sonoyta, Sonora (162664)	X	-
(211155)	-	X
Rio San Pedro, Sonora (162680)	X	-
Monkey Sprs., Arizona (125050, 162700)	X	-
Quitobaquito, Arizona (162661-62)	X	X
Wise Ranch, California (133172)	X	X
Dos Palmas Spr. (USNM 43061)	-	X
Date Palm Beach, Salton Sea (133169)	-	X
Harper Well Wash, Calif. (132924)	-	X
Syntypes (2), C. californiensis (ANSP 7220; USNM ----)	-	X

All but the sample from Monkey Springs (Minckley, 1973:192-194) represent C. macularius.

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MATERIAL EXAMINED

Specimens studied prior to 1943 are listed in Miller (1943); subsequent material is recorded below. all are UMMZ catalogue numbers unless noted otherwise. To locate Figtree John Spring, Fish Springs, and Dos Palmas Spring (Miller, 1943, all near Salton Sea), see Brown (1923: Pl. II).

Arizona: USNM 126810, near Land's Station, Cochise Co., P.H. Kirsch, 23 May 1899.

California**:** In or near Salton Sea: 162636, SIO 58-73, SIO 61496, SIO 62-158 & 161, SIO 70-58; SIO H45-72, hot artesian well, 8 km E Pope; SIO 69-166, 8 km S Mecca; 162626, USNM 43061, Dos Palmas Spr.; 200711, Whitefield Cr., near NE shore Salton Sea; M50-13, Mouth Alamo R.; ANSP 7220 & MCZ 1314, 2 syntypes, C. californiensis, "salt springs in the desert," San Diego Co. The syntypes of C. macularius, USNM 992, have been lost (Susan Jewett pers. comm., 1986).

Mexico. Baja California: USNM 57838 (holotype, Lucania browni), hot spr., NE side Laguna Salada; CAS-SU 20176, paratypes of same.

Mexico, Sonora: 162664, 164758, USNM 45420 & 45426, Rio Sonoyta at Sonoyta; 162680, Rio San Pedro, ca. 25 km SSW U.S.-Mexico border; 211155, Rio Sonoyta, 18 km W, 1.6 km S Sonoyta; 212313, spring SW El Doctor.

LITERATURE CITED

ANDERSON, T.W., AND R. L. LANEY. 1978. Reconnaissance of ground-water conditions in the Quitobaquito Spring and La Abra Plan area, Organ Pipe Cactus National Monument, Arizona. Admin. Rpt., U. S. Geol. Surv. In coop. with Nat. Park Serv., Tucson, Arizona, 20 pp. (unpublished).

BARLOW, G. W. 1961. Social behavior of the desert pupfish, Cyprinodon macularius, in the field and in the aquarium. Amer. Midl. Nat. 65:339-359.

BLACK, G. F. 1980. Status of the desert pupfish, Cyprinodon macularius (Baird and Girard), in California. California Dept. Fish and Game, Spec. Publ. 80-1:i-vi, 1-42.

BOOKSTEIN, F. L., B. CHERNOFF, R. L. ELDER, J. M. HUMPHRIES, JR., G. R. SMITH, AND R. E. STRAUSS. 1985. Morphometrics in Evolutionary Biology. Acad. Nat. Sci. Phila., Spec. Publ. 15:i-xvii, 1-277.

BOWERS, J. E. 1980. Flora of Organ Pipe Cactus National Monument. Jour. Ariz.-Nev. Acad. Sci. 15:1-11.

BROWN, J. S. 1923. Salton Sea region, California. U. S. Geol. Surv. Water-Supply Pap. 499:i-xviii, 1-436.

CAPLAN, L. 1961. History of the Salton Sea, pp. 9-15. In: The Ecology of the Salton Sea, California, in relation to the sportfishery, B. W. Walker, ed. California Dept. Fish & Game, Fish Bull. 113.

COLE, G. A. 1963. The American Southwest and Middle America, pp. 393-434. In: Limnology in North America, D. G. Frey, ed. The Univ. Wisconsin Press, Madison.

_________, AND M. C. WHITESIDE. 1965. An ecological reconnaissance of Quitobaquito Spring, Arizona. Jour. Ariz. Acad. Sci. 3:159-163.

CONSTANTZ, G. D. 1981. Life history patterns of desert fishes, pp. 237-290. In: Fishes in North American Deserts, R. J. Naiman and D. L. Soltz, eds. John Wiley & Sons, New York.

COX, T. J. 1966. A behavioral and ecological study of the desert pupfish (Cyprinodon macularius) in Quitobaquito Springs, Organ Pipe Cactus National Monument, Arizona. PhD dissertation, Univ. of Arizona, 102 pp.

_________. 1972. The food habits of the desert pupfish (Cyprinodon macularius) in Quitobaquito Springs, Organ Pipe Cactus National Monument, Arizona. Jour. Ariz. Acad. Sci. 7:25-27.

CREAR, D., AND I. HAYDOCK. 1971. Laboratory rearing of the desert pupfish, Cyprinodon macularius. U. S. Fish & Wildlife Serv., Fish. Bull. 69:151-156.

DEACON, J. E., AND M. S. DEACON. 1979. Research on endangered fishes in the National Parks with special emphasis on the Devil's Hole pupfish, pp. 9-19. In: Proc. First Conf. Sci. Res. Nat. Parks, 1, R. M. Linn, ed. U. S. Dept. Int. NPS Trans. & Proc. Ser., No. 5, Washington, D. C.

_________, G. KOBETICH, J. D. WILLIAMS, AND S. CONTRERAS. 1970. Fishes of North America endangered, threatened or of special concern: 1979. Fisheries (Bull. Amer. Fish. Soc.) 4:29-44.

DODGE, N. N. 1964. Organ Pipe Cactus National Monument, Arizona. U. S. Dept. Int. Nat. Park Serv., Nat Hist. Handbook Ser., No. 6, Washington, D. C. 91 pp.

DONNELLY, M. F. 1974. Geology of the Sierra de Pinacate volcanic field, northern Sonora, Mexico, and southern Arizona, U.S.A. PhD dissertation, Stanford Univ., 722 pp. [not seen]

GEHLBACH, F. H. 1981. Mountain Islands and Desert Seas. Texas A & M Univ. Press, College Station, 298 pp.

GRINNELL, J. 1914. An account of the mammals and birds of the lower Colorado River Valley. Univ. California Publ. Zool. 12:51-294.

HASTINGS, J. R., AND R. R. HUMPHREY (eds.). 1969. Climatological data and statistics for Sonora and northern Sinaloa. Univ. Arizona Inst. Atmos Physics, Tech. Rept. 19:iv+1-76.

HUBBS, C. L., G. S. BIEN, AND H. E. SUESS. 1960. La Jolla natural radiocarbon measurements. Amer. Jour. Sci. Radiocarbon Suppl. 2:197-223.

_________, W. I. FOLLETT, AND L. J. DEMPSTER. 1979. List of the fishes of California. Occ. Pap. California Acad. Sci. 133:151.

HUBBS, C., R. C. BAIRD, AND J. W. GERALD. 1967. Effects of dissolved oxygen concentration and light intensity on activity cycles of fishes inhabiting warm springs. Amer. Midl. Nat. 77:104-115.

HUEY, L. M. 1942. A vertebrate faunal survey of the Organ Pipe Cactus National Monument, Arizona. Trans. San Diego Soc. Nat. Hist. 9:353-376.

HUMPHRIES, J. M., F. L. BOOKSTEIN, B. CHERNOFF, G. R. SMITH, R. L. ELDER, AND S. G. POSS. 1981. Multivariate discrimination by shape and relation to size. Syst. Zool. 30:291-308.

IVES, R. L. 1936. Desert floods in the Sonoyta Valley. Amer. Jour. Sci. (ser. 5) 32-349-360.

_________. 1964. The Pinacate region, Sonora, Mexico. Occ. Pap. California Acad. Sci. 47:co1. frontis. + 1-43.

JOHNSON, R. R., B. T. BROWN, AND S. GOLDWASSER. 1983. Avian use of Quitobaquito Springs oasis, Organ Pipe Cactus National Monument, Arizona. Coop. Nat. Park Res. Stud. Unit, Arizona, Tech. Rept. 13:i-iv, 1-16.

JORDAN, D. S. 1924. A top minnow (Cyprinodon browni) from an artesian well in California. Proc. Acad. Nat. Sci. 76:23-24.

KIDD, D. E., AND W. E. WADE. 1965. Algae of Quitobaquito: a springfed impoundment in Organ Pipe Cactus National Monument. Southwestern Nat., 10:227-233.

KYNARD, B., AND R. GARRETT. 1979. Reproductive ecology of the Quitobaquito pupfish from Organ Pipe Cactus National Monument, Arizona. Pp. 625-629. In: Proc. First Conf. Sci. Res. Nat. Parks, 1, R. M. Linn, ed. U. S. NPS Trans. & Proc. Ser., No. 5, Washington, D. C.

_________, AND ________. 1984. The extirpation of endemic pupfish from Laguna Prieta, Sonora, Mexico. 8th Ann. Symp. Desert Fishes Council 1976 (1983):269.

LEONARD, P. G. 1972. The pupfish of Quitobaquito. Nat. Parks and Conser. Mag. 46:24-26.

LOISELLE, P. V. 1980. Spawn recognition by male Cyprinodon macularius californiensis. Proc. Desert Fishes Council, 11(1979):46 (abstract).

________. 1982. Male spawning partner preference in an arena-breeding teleost Cyprinodon macularius californiensis Girard (Atherinomorpha: Cyprinodontidae). Amer. Nat. 120:121-132.

LUMHOLZ, C. 1912. New Trails in Mexico. An account of one year's exploration in the northwestern Sonora, Mexico, and southwestern Arizona 1909-1910. Charles Scribner's Sons, New York, i-xxv + 1-411 pp.

MAY, L. A. 1976. Fauna de vertebrados de la region del gran desierto, Sonora, Mexico. An Inst. Biol. Univ. Nat. Auton. Mexico, ser. Zool. 47:143-182.

McMAHON, T. E., AND R. R. MILLER. 1985. Status of the fishes of the Rio Sonoyta basin, Arizona and Sonora, Mexico. Proc. Desert Fishes Council 14(1982):237-245.

MILLER, R. R. 1943. The status of Cyprinodon macularius and Cyprinodon nevadensis, two desert fishes of western North America. Occ. Pap. Mus. Zool. Univ. Michigan 473:1-25.

_________. 1948. The cyprinodont fishes of the Death Valley system of eastern California and southwestern Nevada. Misc. Publ. Mus. Zool. Univ. Michigan 68:1-155.

_________. 1952. Ice age fish in Arizona. Nat. Hist. 61-173.

_________. 1964. Extinct, rare and endangered American freshwater fishes. Proc. XVI Intl. Cong. Zool. 8(1963):4-16.

_________. 1979. Freshwater fishes. Red Data book, vol. 4:Pisces, rev. ed. IUCN, Morges, Switzerland, 1977 (=1979):16 pp., 194 sheets.

_________. 1981. Coevolution of deserts and pupfishes (genus Cyprinodon) in the American Southwest, pp. 39-94. In: Fishes in North American Deserts, R. J. Naiman and D. L. Soltz, eds. John Wiley & Sons, New York.

_________. and C. H. LOWE. 1964. Annotated check list of the fishes of Arizona, pp. 133-151. In: The Vertebrates of Arizona, C. H. Lowe, ed. Univ. Arizona Press, Tucson.

MINCKLEY, W L. 1973. Fishes of Arizona. Arizona Game and Fish Dept., Phoenix, 293 pp.

_________. 1982. Trophic interrelations among introduced fishes in the lower Colorado River, southwestern United States. California Fish and Game 68:78-89.

________, and J. E. BROOKS. 1986. Transplantation of native Arizona fishes: records through 1980. Jour. Arizona Nevada Acad. Sci. 20 (1985):73-89.

________, and D. E. BROWN. 1982. Wetlands, pp. 222 (col frontis.)-287. In: Biotic Communities of the American Southwest - United States and Mexico, D. E. Brown, ed. Desert Plants 4, Univ. Arizona Press, Tucson.

_________, and C. O. MINKLEY. 1986. Cyprinodon pachycephalus, a new species of pupfish (Cyprinodontidae) from the Chihuahuan Desert of northern Mexico. Copeia 1986:184-192.

NABHAN, G.P., A. M. REA, K. L. REICHARDT, E. MELLINK, AND C. F. HUTCHINSON. 1982. Papago influence on habitat and biotic diversity: Quitovac oasis ethno-ecology. Jour. Ethnobiol. 2:124-143.

NAIMAN, R. J., AND D. L. SOLTZ, eds. 1981. Fishes in North American Deserts. John Wiley & Sons, New York, 552 pp.

OHMART R. O., W. O. DEASON, AND S. J. FREELAND. 1975. Dynamics of marsh land formation and succession along the lower Colorado River and their importance and management problems as related to wildlife in the arid Southwest. Trans. 40th N. Amer. Wildlife and Nat. Res. Conf. 1975:240-254.

RINNE, W. E., AND H. R. GUENTHER. 1980. Recent changes in habitat characteristics of the Santa Clara Slough, Sonora. Proc. Desert Fishes Council 11(1979):44.

SCHOENHERR, A. A. 1981. The role of competition in the replacement of native fishes by introduced species, pp. 183203. In: Fishes in North American Deserts, R. J. Naiman and D. L. Soltz, eds. John Wiley & sons, New York.

_________. 1985. Replacement of Cyprinodon macularius by Tilapia zillii in an irrigation drain near the Salton Sea. Proc. Desert Fishes council, 13(1981):65-66.

SMITH, M. L., AND B. CHERNOFF. 1981. Breeding populations of cyprnodontoid fishes in a thermal stream. Copeia 1981:701-702.

TURNER, B. J. 1983. Genic variation and differentiation of remnant natural populations of the desert pupfish, Cyprinodon macularius. Evol. 37:690-700.

_________. 1984. Evolutionary genetics of artificial refugium populations of an endangered species, the desert pupfish. Copeia, 1984:364-369.

WATERS, M. R. 1982. Late Quaternary lacustrine chronology and archaeology of ancient Lake Cahuilla, California, p. 176. In: Program and Abstracts, 7th Bien. Conf., Amer. Quaternary Assoc., Univ. Washington, Seattle.

WEIGHT, L. AND H. WEIGHT. 1952. Virgin desert wonderlands. Nat. Hist. 61:120-127.