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# Late Pleistocene Large Mammalian Herbivores: Implications for Early Human Hunting Patterns in Southern California

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*Abstract.*—The paleogeographic distribution of large herbivorous mammals and their inferred migratory and behavioral patterns may be critical in reconstructing the scheduling and procurement strategies of early human hunters in the southwestern United States. During Rancholabrean time there were provincial differences in faunal composition between the southwestern Great Basin and Mojave Desert, intermontane southern California, and coastal southern California. Such provinciality is not unexpected, especially in view of ecological differences between continental and maritime conditions during the late Pleistocene. Although many large mammalian herbivores ranged widely throughout this region, the distribution of rare or provincially endemic taxa (such as *Tapirus*) and the relative abundance of common taxa (e.g., species of *Equus, Camelops, Hemiauchenia,* and *Bison*), reflect local paleoecological conditions and habitat patterns. These data suggest that if human hunters were present in the region, their procurement strategies should reflect faunal provinciality and would have been adjusted to local mammalian distributions and conditions.

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Provincial paleoecologic conditions suggested by the late Pleistocene record of mammalian faunas in the southern Great Basin, Mojave Desert, and coastal southern California may provide a framework for the analysis of early human adaptive systems in the far southwest. If large herbivorous mammals were preferred game, then their paleogeographic distribution and inferred migratory and behavioral patterns may be critical to the reconstruction of the scheduling and procurement strategies of early human hunters in the region (Reher 1974).

Provincial mammalian faunal patterns are not unexpected given the differences in maritime and continental conditions in this region during the late Pleistocene. A paleogeographic cross-section of Rancholabrean age fossil assemblages from coastal southern California, through intermontane southern California and the southwestern Great Basin and Mojave Desert exhibits distinctive provincial faunal compositions with respect to the relative abundances of large to medium-sized herbivores. Most large mammalian herbivores are known to have ranged through all provinces in the region. However, the distribution of rare forms and the relative abundance of more common species reflects provincial ecologic conditions and habitats within the region.

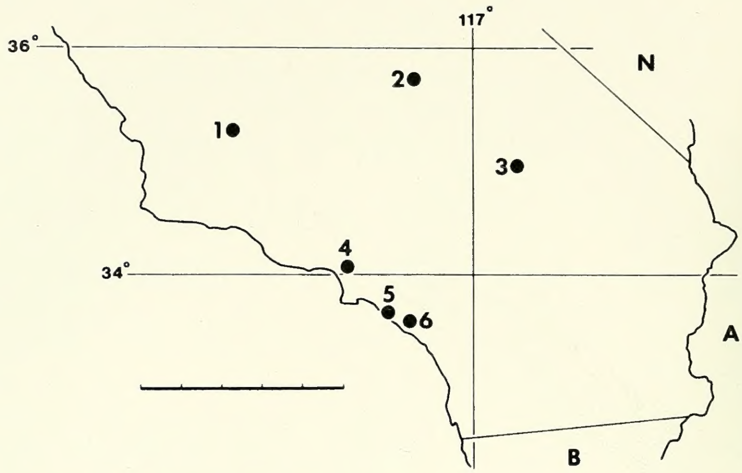



Fig. 1. Locations of Major Late Pleistocene Vertebrate Assemblages in Southern California. Explanation: A = Arizona; B = Baja California del Norte; N = Nevada; 1, McKittrick, Kern County; 2, China Lake, Inyo County; 3, Camp Cady/Manix, San Bernardino County; 4, Rancho La Brea, Los Angeles County; 5, Newport Bay Mesa, Orange County; and 6, Costeau Pit, Orange County; scale bar is 200 kilometers.

## Data Base and Methods

Although few Rancholabrean age fossil localities from provinces in this region (Fig. 1) have produced sufficient numbers of large mammalian specimens to allow a determination of relative taxonomic abundances, six large, temporally comparable assemblages (Table 1) have been recovered and studied. Within the southern Great Basin and Mojave Desert province, these include the Camp Cady local fauna from the Manix Formation, San Bernardino County (Fig. 1, no. 3), and the China Lake faunule, Inyo County, California (Fig. 1, no. 2). Intermontane southern California is represented by a large assemblage from McKittrick in the southern San Joaquin Valley, Kern County, California (Fig. 1, no. 1). Collections from the coastal southern California province include Costeau Pit, Orange County (Fig. 1, no. 6), Rancho La Brea, Los Angeles County (Fig. 1, no. 4) and Newport Bay Mesa, Orange County (Fig. 1, no. 5).

### *Age*

Relative temporal synchroneity of fossil assemblages is an essential prerequisite to the regional analysis of mammalian paleofaunal composition. Three of these six assemblages are temporal correlatives which range in age from about 10 to 11 thousand years (kyr) to a maximum of about 40 kyr BP (before present). The others are comparable but older.

The China Lake faunule (Fortsch 1972, 1978; Davis 1978, 1986; Davis *et al.* 1981) is approximately 10 kyr to 42 kyr BP in age. The Camp Cady local fauna (Jefferson 1968, 1985a, b) from the Manix Formation, ranges in age from about 20 kyr BP to greater than 350 kyr BP (Bassett and Jefferson 1971; Bischoff pers. comm. 1984; Jefferson 1985a), and overlaps with the ages of younger assemblages between 20 and 40 kyr BP.

The Costeau Pit assemblage has a maximum age of greater than 40 kyr BP but

Table 1. Southern California Late Pleistocene Taxonomic List. Localities are arranged from west to east. Abbreviations: C = coast, CC = Camp Cady, CL = China Lake, CP = Costeau Pit, D = desert interior, I = intermontane, MB = McKittrick Brea, NM = Newport Bay Mesa, *P.* = *Preptoceras*, RB = Rancho La Brea. Data from personal observations and: Schultz 1938; Jefferson 1968, 1985a; Miller 1971; Fortsch 1978; Davis 1986.

| | C | | | I | D | |
|---|---|---|---|---|---|---|
| Taxa | CP | RB | NM | MB | CC | CL |
| *Megalonyx jeffersonii* | | X | | | | |
| *M.* cf. *M. jeffersonii* | | | X | | | |
| *M.* sp. | | | | X | X | |
| *Nothrotheriops shastense* | | X | X | | X | |
| *Glossotherium harlani* | | X | | X | | |
| *G.* cf. *G. harlani* | X | | | | | |
| *G.* sp. | | | | | X | |
| Edentata | | | | | | X |
| *Mammut americanum* | | X | X | X | | |
| *Mammuthus columbi* | X | | X | X | | |
| *M. imperator* | | X | | | | |
| *M.* sp. | | | | | X | X |
| *Equus conversidens* ? | | | | | X | |
| *E.* cf. *E. conversidens* | | | | | | X |
| *E. occidentalis* | | X | X | X | | |
| *E.* cf. *E. occidentalis* | | | | | | X |
| *E.* sp. (large) | X | | | | X | |
| *E.* sp. (small) | | | X | | | |
| cf. *E.* sp. (small) | X | | | | | |
| *Tapirus* cf. *T. californicus* | | X | | | | |
| *T.* sp. (small) | | | X | | | |
| *Platygonus compressus* | | X | | | | |
| *P.* nr. *P. compressus* | | | | X | | |
| *Camelops hesternus* | | X | | X | | |
| *C.* cf. *C. hesternus* | X | | | | X | X |
| *C.* aff. *C. minedokae* ? | | | | | X | |
| *C.* sp. | | | X | | | |
| *Hemiauchenia macrocephala* | | | | X | X | |
| *H.* cf. *H. macrocephala* | | X | | | | |
| *H.* sp. | X | | X | | | X |
| Lamini gen. sp. nov. | | | | | X | |
| Cervidae | X | | | | | |
| *Cervus* cf. *C. elaphus* | | | X | X | | |
| *Odocoileus hemionus* | | X | | | | |
| *O.* cf. *O. hemionus* | | | X | X | | |
| *O.* sp. | | | | | | X |
| *Antilocapra americana* | | X | X | X | | |
| *A.* sp. | | | | | X | |
| *Capromeryx* (*Breameryx*) *minor* | | X | X | X | | |
| *C.* sp. | X | | | | | |
| *Ovis canadensis* | | | | | X | |
| *Euceratherium* cf. *E.* (*P.*) *collinum* | | | | X | | |
| *E.* (*P.*) sp. | | X | | | | |
| *Bison latifrons* | X | X | | X | | |
| *B.* cf. *B. latifrons* | | | X | | | |
| *B. antiquus* | X | X | | X | X | |
| *B.* cf. *B. antiquus* | | | | | | X |
| *B.* sp. (large) | | | | | | X |

is probably less than 100 kyr BP (Miller 1971). Late Pleistocene, littoral sandy sediments that produce the Newport Bay Mesa collections are estimated to be between 100 and 130 kyr BP in age (Fanale and Schaeffer 1965; Miller 1971). Although this assemblage is older and deposited entirely during interglacial conditions, it is generally typically of later coastal provincial mammalian frequencies.

The maximum age of the Rancho La Brea assemblage is approximately 38 kyr BP (Marcus and Berger 1984). The assemblage from McKittrick is of similar age (Berger and Libby 1966).

Although the record primarily represents Wisconsinan age deposits, the apparent relative abundance and provincial distribution of late Rancholabrean large mammalian herbivores did not change significantly until the latest Pleistocene or earliest Holocene (Martin 1967, 1973; Grayson 1982); this follows documented human occupation of the region. Because the provincial composition of paleofaunas appears to have been relatively stable, either a very early (Budinger 1983; Simpson *et al.* 1986) or late (Martin 1973) initial occupation by humans is not relevant to the hypothetical reconstruction of potential procurement strategies if large mammalian herbivores are the economically significant game.

### *Taphonomy*

The relative abundance of a particular species in these assemblages is based on the number and type of separate osteologic elements or portions of skeletons recovered. This should directly reflect the population density or number of individuals of each taxon which originally inhabited the local area. However, the numbers of skeletal elements recovered may also reflect a variety of taphonomic factors that include the sedimentary processes involved in the formation of a deposit, the nature of preservation of skeletal elements and various sampling or collecting biases.

The relative abundance of a taxon in a fossil assemblage can be expressed as a percentage of the total number of identified osteologic elements (NISP) or as a percentage of the total minimum number of individuals (MNI) in the assemblage (Horton 1984). The MNI of a taxon is based on the total number of the most frequently represented skeletal element. Interpretation of either expression of abundance must be made with an understanding of the taphonomic factors which influence the composition of the assemblage (Badgley 1986). These analyses allow the comparison of faunal composition between assemblages that have accumulated under different depositional conditions.

Large mammalian vertebrate fossils from the southern Great Basin and Mojave Desert have been recovered mainly from eroded exposures of pluvial, paralimnetic, and associated fluviatile deposits. Although the remains of small verebrates may be locally abundant, with respect to medium and large-sized animals, conditions of sedimentary transport and burial favor the preservation of scattered, isolated osteologic elements and fragments of elements. Articulated specimens are rarely encountered. Given these taphonomic factors, relative taxonomic abundances in the Camp Cady local fauna and China Lake faunule are calculated on the basis of the total NISP rather than on total MNI (Fig. 2).

The unique conditions of asphalt entrapment are clearly responsible for the unusually high percentage of carnivores relative to herbivores at McKittrick (Schultz 1938) and Rancho La Brea (Akersten 1985). Although the remains of carnivores are far more abundant than herbivores, the relative numbers of the larger mammalian herbivores alone from these assemblages approximate the paleofaunal composition at other sites. Apparently, these concentrated accumulations of disarticulated elements are not otherwise significantly biased taphonomically. Here, the most numerous single osteologic element from each taxon has been used to calculate an MNI (Schultz 1938; Marcus 1960), and relative abundance is expressed as a percentage of total MNI (Fig. 2).

The depositional conditions at Costeau Pit were dominantly fluviatile. Miller (1971:4–7) states that most fossil remains have undergone some stream transport. He reported no articulated materials. Given these factors, although MNI are listed by Miller (1971), the relative percentages of taxa are based on the total NISP (Fig. 2). Miller (1971) also presents MNI for taxa in the Newport Bay Mesa assemblage. However, a calculation of relative percentages based on the total NISP (Fig. 2) is reasonable when the high energy conditions of littoral depositional environments are considered.

### *Behavior and Diet*

Inferences about the habits of extinct taxa including herding behavior, migrational patterns, or seasonal changes in distribution, are based largely on the diet and behavior of their closest extant relatives and modern analogous species. The available information on size, weight, and probable behavior of the principal late Pleistocene taxa is summarized in Table 2. However, when a single species of a diverse lineage survives, the inferred habitat and behavior of the related extinct form(s) must be tentative. For example, the current habitat of three of the four living species of *Tapirus* (tapir) is mainly tropical forest. *Ovibos* (musk ox) habitat is artic tundra. Extinct relatives of these animals are found together in Rancholabrean age coastal California assemblages.

## Provincial Paleofaunas

The character of the provincial paleofauna from southern California coastal areas (Fig. 2) appears to have been influenced by marine conditions. Extinct species of *Bison* (bison) and *Equus* (horse) are the dominant large herbivores. Large ground sloths are abundant, and *Camelops* (extinct large camel) is relatively rare. Few *Hemiauchenia* (extinct long-limbed llama) specimens have been recovered and the occurrence of a small species of *Equus* is questionable. *Mammut* (mastodon) and an extinct species of *Tapirus* (tapir) are present.

The frequency of *Bison* at Rancho La Brea is relatively high in comparison to Costeau Pit and Newport Bay Mesa where the taxon is only moderately well represented (Fig. 2). Juvenile *Bison* comprise a significant portion of the sample from Rancho La Brea. Apparently, young animals were seasonally entraped during the late spring portion of a local migration (Goldin 1979). This recurrent event accounts for their increased representation in Rancho La Brea deposits.

The provincial paleofauna from intermontane southern California appears intermediate in composition, containing taxa represented in both the inland and coastal environments (Fig. 2). A large species of *Equus* and *Hemiauchenia* are both abundant. *Antilocapra* (pronghorn) is common and *Bison,* which is not well represented, outnumbers *Camelops*. *Mammut* is also present.

Mammalian faunal assemblages from pluvial lacustrine and related deposits in

Fig. 2. Histograms of Taxa from Major Late Pleistocene Assemblages. Abbreviations: A = Antilocapridae and Cervidae, B = Bovidae, C = Camelops, E = *Equus,* G = Edentata, H = *Hemiauchenia,* M = Mammutidae and Elephantidae.

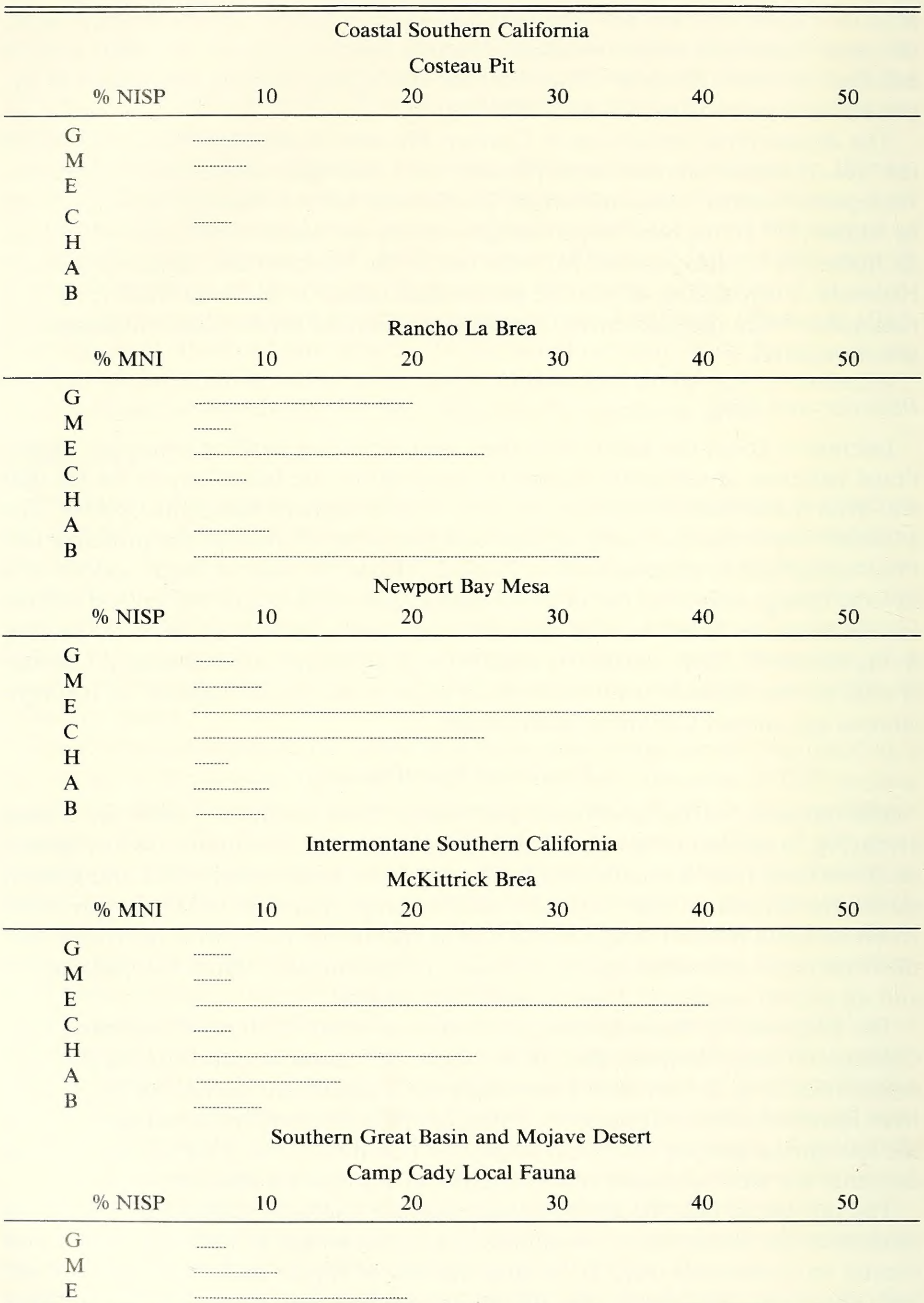
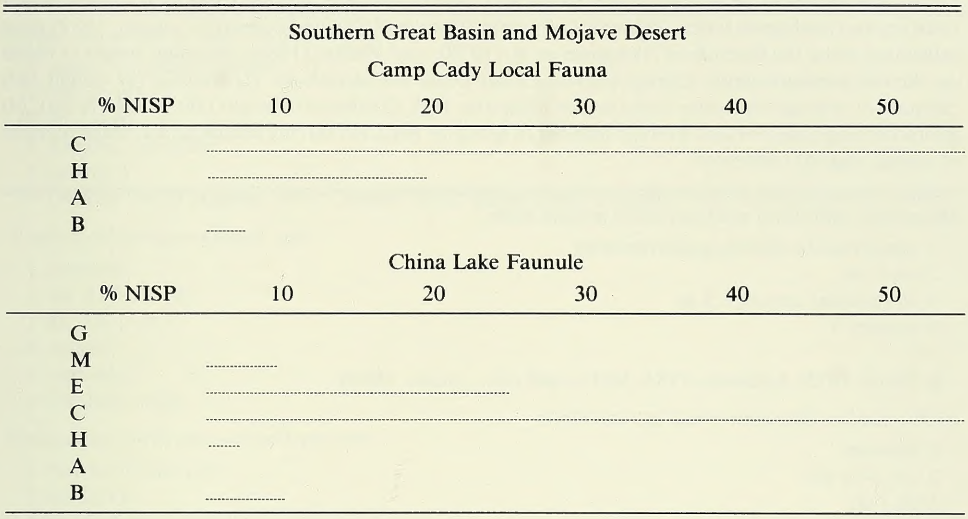


Fig. 2. Continued.




the southern Great Basin and Mojave Desert (Fig. 2) document a continental environment. The paleofauna of this province is typified by an abundance of *Camelops.* In the Mojave Desert a large extinct species of *Equus* and *Hemiauchenia* are well represented. A small extinct species of *Equus* is common, and *Bison* is rare in most assemblages. *Bison* is moderately well represented in the China Lake assemblage where *Hemiauchenia* is relatively rare. Throughout the province, all ground sloth taxa are very rare. *Tapirus* is absent.

*Mammuthus* (mammoth) is widespread throughout the region but not abundant in any province. Relative numbers of this taxon exhibit much intra-provincial variation between assemblages. Apparently, taphonomic factors of the local depositional environment (Conybeare and Haynes 1984) control the observed abundance of these very large mammals.

Some minor intra-provincial differences in faunal composition between assemblages may result from glacial or interglacial environmental conditions. For example the apparently anomalous abundance of *Camelops,* a typical inland taxon, in the coastal Newport Bay Mesa assemblage (Fig. 2) in comparison to Costeau Pit or Rancho La Brea, may reflect an interglacial habitat. Furthermore, the frequency of Cervidae and Antilocapridae from this assemblage resembles the paleofauna from the southern San Joaquin Valley. Local environmental factors may also account for some intra-provincial variation between assemblages. The proximity of seasonally favorable montane habitats to China Lake may account for the larger number of *Bison* there in comparison to sites in the Mojave Desert.

## Discussion

These data suggest that if human groups in the region hunted large mammals, their prey should reflect provincial faunal distributions. Procurement strategies and scheduling would have been adjusted to local environmental conditions such as the population density and seasonal availability of preferred game species and botanical resources (Spaulding *et al.* 1984). An understanding of paleogeographic

Table 2. Characteristics of the Principal Late Pleistocene Large Herbivores from Southern California. The probable behavioral characteristics of extinct taxa are inferred from their closest extant relatives and analogous forms. Estimates of weight (Shaw and Tejada-Flores pers. comm. 1982) were calculated using the formula of Alexander et al. (1979), and Walker (1968). Shoulder height is based on skeletal measurements. Entries following each taxon are as follows: (1) feeding, (2) weight (wt) estimate or average in metric tons (mt) or kilograms (kg), (3) shoulder height (sh) in meters (m), (4) group/herding behavior and average number in group or herd, (5) calving season and average number of young, and (6) references.

*Megalonyx jeffersonii* medium-sized ground sloth

1 opportunistic feeder, grazer/browser
2 wt 1 mt
3 sh (bipedal stance) 1.5 m
4 solitary ?
5 ?
6 (Stock 1925; Anderson 1984; McDonald pers. comm. 1985)

*Nothrotheriops shastense* small ground sloth

1 browser
2 wt .5–.6 mt
3 sh 1 m
4 solitary ?
5 ?
6 (Martin *et al.* 1961; Hansen 1978; Anderson 1984)

*Glossotherium* (*Paramylodon*) *harlani* large ground sloth

1 opportunistic feeder, grazer or grazer/browser
2 wt 1.5 mt
3 sh (bipedal stance) 1.8 m
4 solitary ?
5 ?
6 (Stock 1925; Kurtén and Anderson 1980; McDonald pers. comm. 1985)

*Mammut americanum* mastodon

1 browser
2 wt 4–5 mt
3 sh 2.1 m
4 ?
5 ?
6 (Whitehead *et al.* 1982; Peterson *et al.* 1983; Hallen pers. comm. 1984)

*Mammuthus* sp. (*M. columbi*/*M. imperator*/*M. jeffersonii* group) mammoth

1 opportunistic feeder, grazer/browser
2 wt 5–6 mt
3 sh 3.6–4.0 m
4 herding, 11
5 late spring, 1
6 (Eltringham 1982; Agenbroad 1984; Conybeare and Haynes 1984; Davis *et al.* 1984; Davis *et al.* 1985)

*Equus occidentalis* large extinct horse

1 grazer or grazer/browser
2 wt .35 mt
3 sh 1.5 m
4 herding, variable
5 spring, 1
6 (Walker 1968; Hansen 1976; Ginnett 1982; Ginnett and Douglas 1982; Akersten *et al.* 1984)

Table 2. Continued.

*Equus conversidens* small extinct horse
1 grazer or grazer/browser
2 wt .26 mt
3 sh 1.4 m
4 herding, variable
5 spring, 1
6 (Walker 1968; Hansen 1976; Ginnett 1982; Ginnett and Douglas 1982; Akersten *et al.* 1984)

*Tapirus californicus* extinct tapir
1 browser
2 wt .225–.30 mt
3 sh .75–1 m
4 solitary
5 variable, 1
6 (Walker 1968)

*Platygonus compressus* extinct peccary
1 browser/omnivore
2 wt 35 kg
3 sh .6–.7 m
4 groups/herds, 4.6
5 late fall, 2.7
6 (Hall and Kelson 1959; Walker 1968; Wetzel *et al.* 1975; Kurtén and Anderson 1980; Mayr and Brandt 1981)

*Camelops hesternus* extinct camel
1 opportunistic feeder, browser
2 wt .843 mt
3 sh 2.3 m
4 herding, 10–30
5 winter–early spring, 1
6 (Gauther-Pilters 1981; Akersten *et al.* 1984; Anderson 1984; Harris 1985)

*Hemiauchenia macrocephala* extinct llama
1 opportunistic feeder, browser
2 wt .22 mt
3 sh 1.5 m
4 groups ?
5 ?
6 (Walker 1968; Franklin 1981; Anderson 1984)

*Odocoileus hemionus* deer
1 browser
2 wt 48–145 kg
3 sh .8–1 m
4 solitary
5 late spring–early summer, 2
6 (Walker 1968)

*Cervus elaphus* elk
1 browser/grazer
2 wt .2–.35 mt
3 sh 1.4–1.5 m
4 herding, 30–40
5 spring, 1
6 (Walker 1968; McCullough 1969)

Table 2. Continued.

*Antilocapra americana* pronghorn

1 browser
2 wt 36–60 kg
3 sh .8–1 m
4 herding, variable
5 late spring, 1.5
6 (Hall and Kelson 1959; Walker 1968; Johnston 1962)

*Capromeryx minor* small extinct pronghorn

1 browser
2 wt 19 kg
3 sh .5 m
4 solitary ?
5 ?
6 (Walker 1968; Anderson 1984)

*Ovis canadensis* mountain sheep

1 opportunistic feeder, browser/grazer
2 wt 47–74 kg
3 sh .7–1 m
4 family groups
5 variable, 1–2
6 (Hall and Kelson 1959; Wells and Wells 1961; Geist 1971)

*Euceratherium* (*Preptoceras*) *collinum* extinct musk ox

1 grazer/browser
2 wt .5 mt
3 sh .6 m
4 herding ?
5 ?
6 (Anderson 1984; Reynolds pers. comm. 1984; Harris 1985)

*Bison antiquus* extinct bison

1 grazer or grazer/browser
2 wt .733 mt
3 sh 2.2 m
4 herding, variable
5 spring, 1
6 (Bailey 1931; Peden 1976; McHugh 1972; Meagher 1973; Goldin 1979; McDonald 1981; Akersten et al. 1984)

*Bison latifrons* large extinct bison

1 browser/grazer
2 wt .988 mt
3 sh 2.4 m
4 herding ?
5 ?
6 (McDonald 1981)

and seasonal distribution of potential game species and provincial paleobotanical associations may contribute to hypotheses concerning subsistance activities that can be tested in local paleontologic and archaeologic records.

Many archaeologic sites within the region have been considered late Pleistocene in age (Moratto 1984). The actual age or validity of many of these sites has not been confirmed (Moratto 1984; Taylor *et al.* 1984; Waters 1985). Some well documented late Pleistocene sites contain human remains, artifacts or both in association with fossil vertebrates. However, apparent evidence of hunting, butchering, or utilization of extinct large mammalian remains has been presented for only a few locations within the region. They include China Lake (Davis 1978, 1982, 1986; Davis *et al.* 1981), the Manix Formation (Miller 1975), and Tule Springs (Schutler 1967) in the southern Great Basin and Mojave Desert province. Presently, there is no evidence of a direct association of humans with the paleofauna from the southern San Joaquin Valley. For coastal southern California, only two such sites exist, Santa Rosa Island (Orr 1968; Berger 1982) and Rancho La Brea (Miller 1969).

The predator/prey relationship between humans and extinct mammals at each of these localities has been examined and questioned (Grayson 1984; Haynes and Stanford 1984; Moratto 1984). The natural or cultural origin of mammoth remains on Santa Rosa Island that appear to have been burned has not been resolved and requires further investigation (Moratto 1984; Reeves 1985). Preliminary investigations by Cushing *et al.* (1986) suggest that surrounding soil colorations may be a result of groundwater conditions. *Smilodon* (sabercat) limb bones from Rancho La Brea that exhibit parallel incised grooves (Miller 1969) are now known to have been formed by natural taphonomic processes called pit wear (Reynolds 1985).

Artifacts including Clovis-like projectile points have been found in close spacial and temporal association with vertebrate fossil remains at China Lake (Davis et *al.* 1981; Reeves 1985). Here, a single specimen of mammoth bone exhibited post mortem/preburial flaking (Davis 1982). However, clear evidence of predation, carcass dismemberment, or other human bone modification or utilization has not been described. Several specimens of *Equus* and *Camelops* from the Manix Formation show post mortem/preburial modification including polish and abrasion, scratches, punctures, and "cut marks" (Miller 1975; Bonnichsen pers. comm. 1982). A possible bone tool was recovered from Tule Springs (Tuohy 1967). To date, the origin of every example of post mortem/preburial modified bone found from these localities may be explained through non-human processes.

## Concluding Remarks

Any assemblage of fossil mammals that exhibits relative taxonomic abundances which are unexpected, given the composition of the provincial paleofauna, probably reflects anomalous taphonomic conditions which may include human predator/prey activities. An intensification of predation rates with respect to a particular taxon is an obvious example.

However, conclusive evidence of hunting or butchering of extinct large mammals is yet to be found in the southern Great Basin, Mojave Desert, or coastal southern California region. This apparent lack of evidence would suggest that a big game hunting pattern, like that expressed in the early archaeologic record of the Great Plains (Frison 1978), may not have been a frequently or intensively practiced subsistence strategy. A short lived event, like the "overkill" described by Mosimann and Martin (1975), remains undetected. Although compelling circumstantial evidence exists at localities like China Lake, Manix, and Santa Rosa Island, cooperative seasonal hunting of late Pleistocene large herding animals is not confirmed in the archaeologic record of the region.

The inferred behavior of extinct taxa and the paleofaunal composition of provincial areas in the southwestern United States must be considered in any reconstruction of early human subsistance patterns, especially where the hunting of large game species is suspected.

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# A Review of the Life History and Status of the Desert Pupfish, *Cyprinodon macularius*

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*Abstract.*—The desert pupfish, *Cyprinodon macularius,* and its allies were formerly common in sloughs and backwaters of the Gila River in Arizona, and the lower Colorado River in the United States and Mexico. They also were common in shoreline pools and irrigation drains of the Salton Sea in California. In spite of their remarkable tolerance for environmental extremes and high reproductive rate, details of which are summarized herein, the species has undergone a serious decline in numbers. Since the late 1800s fish have disappeared in association with activities of humans such as dam building, diversions of water, ground-water pumping, and pesticides. They have been further threatened by encroachment of non-native vegetation such as tamarisk, *Tamarix* spp. The most rapid decline has occurred in recent years in association with introduced fishes. Through predation, aggression, and various behavioral activities that interfere with reproduction, introduced species have driven pupfish to the brink of extinction. A natural population of reasonable size occurs today only at Quitobaquito Spring in Organ Pipe Cactus National Monument in Arizona. Populations of insecure status, subject to wide fluctuations in density, occur south of Quitobaquito in Rio Sonoyta, Sonora, Mexico, and in San Sebastian Marsh and Salt Creek near the Salton Sea in California. On 31 March 1986 a final rule was published in the Federal Register listing *Cyprinodon macularis* as an endangered species. Designated critical habitat at San Sebastian Marsh, Imperial County, California at best contains an unstable population of desert pupfish.

## Introduction

In 1977 a group of us, including representatives from academia and various state and federal agencies, got together to begin the laborious process of preparing a listing package to get *Cyprinodon macularius* placed by the Federal Government on the list of endangered species. As of early 1986, during preparation of this manuscript, that goal had yet to be accomplished. The original intent of this paper was to bring together everything known about the desert pupfish and to call attention to its precarious status. It was hoped that this effort somehow would help to hasten the process of getting the species listed. On 31 March 1986, nine years after our efforts began, a final rule was published in the Federal Register listing *Cyprinodon macularius* as endangered. The listing became official on 30 April 1986, two days before the symposium at which this paper was presented. It is hoped now, that the information compiled herein will be useful for government management plans and a program of recovery for the desert pupfish.

At the turn of the century, the desert pupfish, *Cyprinodon macularius* enjoyed widespread distribution. It occurred in sloughs and marshes along the lower Colorado as far north as Blythe, California (Turner 1982), and as far east as the San

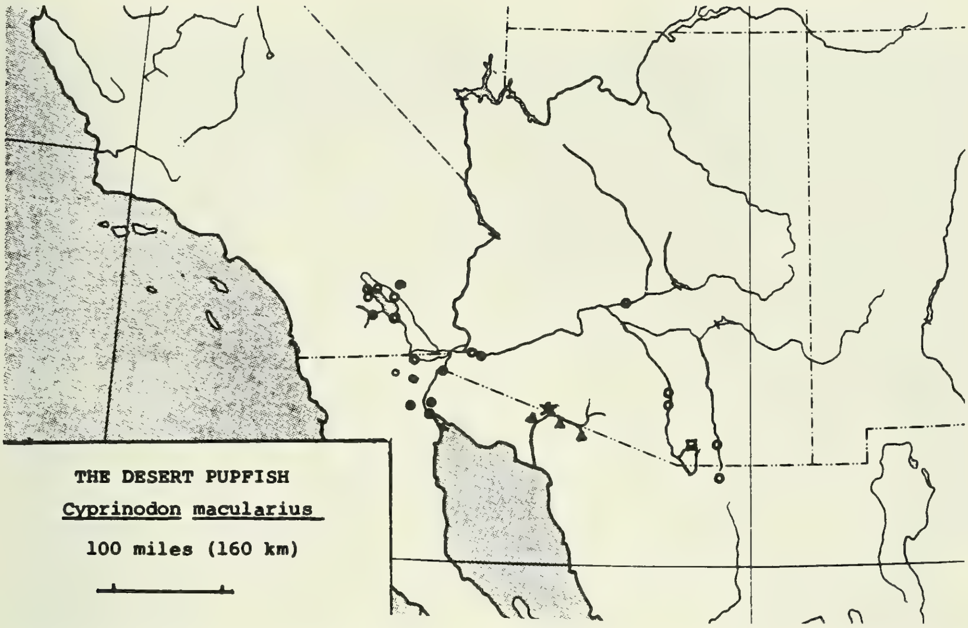


Fig. 1. Distribution of *Cyprinodon macularius.* Closed figures indicate present distribution. Open figures indicate former distribution. Monkey Spring pupfish indicated by a square, Sonoyta Creek pupfish by triangles, Quitobaquito pupfish by a star, and Salton Sea pupfish by circles.

Pedro and Santa Cruz Rivers, tributaries of the Gila River in Arizona (Minckley 1973). In the Salton Sea region, Riverside and Imperial Counties, California, pupfish occurred in isolated springs (Miller 1943). These populations were remnants of those that inhabited Lake Cahuilla that had dried about A.D. 1500. At the turn of the century there was no Salton Sea. In 1905 flooding of an irrigation system carrying Colorado River water began forming a new Salton Sea (Aleshire 1981). Apparently, this event reintroduced the desert pupfish to a portion of its former range in the Salon Trough. By the 1960s they were very common in shoreline pools of the Salton Sea (Barlow 1961).

Over the years, activities of humans have diminished distribution of the desert pupfish. As of this writing, the fish primarily occur in small refugia. The only healthy natural populations of reasonable size occur at Quitobaquito Spring in Pima County, Arizona in Organ Pipe Cactus National Monument, and in Santa Clara Slough, Sonora, Mexico, near the mouth of the Colorado River. Fig. 1 is an updated distribution map revised from those published by Minckley (1973); Lee et al. (1980); Turner (1982); and Miller and Fuiman (1987).

## Taxonomy

*Cyprinodon macularius* is the only species of desert pupfish that has been named officially. The Monkey Spring Pupfish, a separate species, has yet to be named (Minckley 1973). *Cyprinodon macularius* was described from a population that occurred in the headwaters of the San Pedro River near the Arizona–Mexico border. This was the form that occurred most widely throughout the natural range of the species.

Fig. 2. San Sebastian Marsh, Imperial County, California (4 January 1986). Small backwater to right center is favored habitat.

A description adapted from Moyle (1976) and Minckley (1973) is as follows: Males are larger than females, up to 75 mm total length (TL). The body is thickened, chubby, or markedly compressed laterally. The dorsal profile is smoothly rounded, not markedly concave posterior to the origin of the dorsal fin. There is a single series of incisor-like tricuspid teeth on each jaw. The middle cusp of each tooth is spatulate. Scales are large and rectangular, usually numbering 26 along the lateral line. Circuli on the scales have spinelike projections, and the interspaces are regular, without reticulations. Fin rays are 9–12 in the dorsal and anal fins, 14–18 in the pectoral fins, 14–20 in the caudal fin, and 2–8 (usually 7) in the pelvic fins. During the breeding season dominant males become dark blue with lemon yellow tails and caudal peduncles. The tail usually has a dark terminal band. Females and juvenile males look alike. They are tan to olive, with a lateral band of 5–8 disrupted vertical bars.

Hubbs et al. (1979) recognized the California populations living in the vicinity of the Salton Sea as *Cyprinodon macularius californiensis.* Miller and Fuiman (1987) disputed this designation. Therefore, populations in California and the lower Colorado River should be referred to as *Cyprinodon macularius macularius.* In California, two natural habitats are occupied by this subspecies. One of these, in San Sebastian Marsh, Imperial County is a spring-fed stretch of flowing water on San Felipe Creek (Fig. 2). This area has been designated critical habitat for the species by the federal government. It is administered by the Bureau of Land Management. A complete description of the management plan was prepared in 1986 in conjunction with the California Department of Fish and Game (USDI,

Fig. 3. Salton Sea shoreline pool near North Shore airport, Riverside County, California (18 July 1978).

BLM and CRA, DFG 1986). The other natural population is in a similar habitat on the eastern side of the Salton Sea, on upper Salt Creek, Riverside County. Historically, other populations occurred in shoreline pools (Fig. 3) and irrigation drains (Fig. 4) of the Salton Sea (Barlow 1961). Electrophoretic studies showed minor genetic differences between these populations (Turner 1982). For the purposes of this paper, fish from these populations shall be referred to as Salton Sea fish.

Pupfish that occur in the Santa Clara Slough near the mouth of the Colorado River in Sonora, Mexico have been assigned to the same taxon as Salton Sea fish. Electrophoretic analysis showed some differences between the present Salton Sea and Santa Clara Slough fish (Turner 1982). Differences were not great. Genetic distance values of 0.014 were calculated. This difference is considered normal for within-drainage variation. Even though the actual genetic analysis was conducted on Santa Clara fish taken from a refugium at the Boyce Thompson Arboretum in Arizona, there is some talk of assigning subspecific status to fish from the Santa Clara Slough (Johnson pers. comm.). Presumably there are morphological differences as well.

The Quitobaquito pupfish has been considered a distinct entity for quite some time (Miller 1943; Hubbs and Miller 1948; Cole 1963; Cole and Whiteside 1965; Minckley 1973). Recently, Miller and Fuiman (1987) described it as a new subspecies, *Cyprinodon macularius eremus.* At the present time, the population at Quitobaquito Spring in Organ Pipe Cactus National Monument may be the only natural population in existence. The habitat at Quitobaquito includes a short

Fig. 4. Pupfish habitat in irrigation drain, King Street canal, Riverside County, California (3 March 1977).

spring-fed stretch that runs into a one-half acre pond (Fig. 5). This pond is not natural. It was enlarged by the National Park Service about 1965. Water is now impounded by an earthen dam. According to Turner (1982) the genetic distance between the Quitobaquito and Salton Sea fish is 0.042. Morphologically, these two populations differ as well. Among other things, coloration of Quitobaquito males is less intense. They are paler blue, and the yellow of the tail is pale. Pelvic fins are smaller, and the dorsal fin is more posterior. Males have a longer, wider, and deeper head, and the body is broader and deeper (Miller 1943; Minckley 1973; Miller and Fuiman 1987).

In Rio Sonoyta, near Sonoyta, Sonora, Mexico there are pupfish that are similar to, but not the same as those in Quitobaquito Spring. They are intermediate in shape between the Quitobaquito fish and those from Santa Clara Slough (Miller and Fuiman 1987). It appears that they are different enough to be described as a distinct subspecies (McMahon and Miller 1982). It is possible, however, that the fish occurring in Rio Sonoyta today are not exactly the same as those that occurred there formerly (Minckley pers. comm.). It may be that fish occurring there today were influenced by hybridization from fish transplanted from nearby Quitobaquito Spring. Apparently Quitobaquito fish have been transplanted to various points throughout Arizona; some of them in localities far outside their native range (Minckley pers. comm.).

The Monkey Spring pupfish has been determined to be a separate species, but

Fig. 5. Pond at Quitobaquito Spring, Organ Pipe Cactus National Monument, Pima County, Arizona (4 April 1985).

it remains unnamed (Minckley 1973). It differs from *Cyprinodon macularius* by having a thicker anterior body and a concave profile posterior to the origin of the dorsal fin. Breeding males lacked yellow coloration on the tail. This species occupied waters fed by Monkey Spring, a few miles NNE of Patagonia, Santa Cruz County, Arizona (Fig. 6). Apparently the species is extinct (Minckley 1973).

A problem associated with pupfish taxonomy is that genetic distance determined from electrophoretic data implies less divergence than do morphological data (Soltz and Hirshfield 1981). Turner (1982) contended that the effect of geographic isolation has been overestimated. The ease with which hybridization occurs also attests to the close relationship of forms with different morphology (Turner and Liu 1977). Also, it has been determined that *C. macularius* eggs raised under different combinations of temperature and salinity develop into adults with significant differences in body shape (Sweet and Kinne 1964).

## History of the Desert Pupfish

The Bouse Embayment was a Mio-Pliocene extension of the Gulf of California. It covered what is today the lower Colorado River and Salton Trough (Miller 1981; Smith 1981). It appears that *Cyprinodon macularius* descended from fish that occupied that estuary. Furthermore, it appears that all the other pupfishes that occur in the Death Valley area probably descended from *Cyprinodon macularius* or a *C. macularius*-like ancestor (Miller 1981). Through the 1800s the species occupied mostly quiet water habitats, particularly sloughs and backwaters along major drainages such as the Gila and lower Colorado Rivers (Miller 1961; Minckley and Deacon 1968).

The origin of Rio Sonoyta fish clearly was the Colorado River Delta (Miller and Fuiman 1987). Sometime within the past 100,000 years, eruptions of the Pinacate Volcanic Fields blocked the original westward course of the river and isolated the fish. The present population at Quitobaquito Spring has been isolated probably since Pleistocene. There is no evidence of a historical connection to Rio Sonoyta although fossil springs west of Quitobaquito probably overflowed to Rio Sonoyta during times of high water flow, presumably at some time in Holocene or Pleistocene (Miller and Fuiman 1987).

Drying of Lake Cahuilla about A.D. 1500 eliminated from the Salton Basin what was essentially a Colorado River fauna. Old fish traps and middens bear witness that Cahuilla Indians used these fishes, including the desert pupfish as food (Wilke 1979). Natural rerouting of the Colorado River about 600 yr ago diverted water away from Lake Cahuilla and into the Gulf of California. Estimates imply that it took about 55 to 60 yr for the lake to dry completely (Wilke 1979), leaving the desert pupfish isolated in certain springs of the Salton Basin.

In the early 1900s a period of arroyo cutting associated with cattle grazing and compaction began (Hastings 1959; Hastings and Turner 1965; Miller 1961). Drying of wetlands and diversion of water for agricuture led to a decline of pupfish habitat. Nevertheless, pupfish flourished locally until about the 1930s (Deacon and Minckley 1974). At about that time, native fishes began to be replaced by introduced species. Through various interactions such as aggression and predation, these introduced species began to cause native fish populations to become reduced to locally isolated entities (Schoenherr 1981b).

The 1905 flooding that refilled the Salton Sea fortuitously reintroduced the

Fig. 6. Monkey Spring, Santa Cruz County, Arizona (4 February 1970).

Table 1. Number of populations of pupfish in the *Cyprinodon macularius* complex known to exist as of May, 1986. Numbers represent minimal estimates because unreported populations on private property are suspected to exist.

| Native population | Natural | Introduced |
|---|---|---|
| Salton Sea | 2 | 7 |
| Santa Clara Slough | 5 | 6 |
| Quitobaquito Spring | 1 | 4 |
| Rio Sonoyta | 3? | 1 |
| Monkey Spring | 0 | 0 |

desert pupfish. In the early 1960s, shoreline pools contained thousands of them (Barlow 1961).

Since the 1960s, activities of humans have steadily decimated stocks of the desert pupfish. In the early 1960s pupfish were localized in four different regions (Miller 1979): 1. Springs and sloughs along the lower Colorado River in Mexico; 2. Waters associated with Monkey Spring in Arizona; 3. Quitobaquito Spring in Organ Pipe Cactus National Monument and adjacent Rio Sonoyta; and 4. Shoreline pools and irrigation drains of the Salton Sea in California. At the present time, the only large natural populations of the species are located in Mexico near the mouth of the Colorado River. All other populations are in unstable streams or small refugia. Most of them are in artificial impoundments managed by federal and state government agencies.

## Current Status

The number of known populations in the *Cyprinodon macularius* complex is summarized in Table 1. A brief summary of the status of recent and historic populations is listed in Table 2.

*Salton Sea populations.*—These pupfish are located primarily in California refugia. Refugia are located as follows: 1. Palm Spring, Anza Borrego Desert State Park, San Diego County (Fig. 7); 2. Palm Canyon trailhead, Anza Borrego Desert State Park, San Diego County; 3. Visitor Center, Park Headquarters, Anza Borrego Desert State Park, San Diego County; 4. Living Desert Reserve, Palm Desert, Riverside County; 5. Salton Sea State Recreation Area, Riverside County; and 6. Oasis Spring, near Salt Creek, Riverside County. Two future refugia are planned; one at the State Department of Fish and Game Warmwater Fish Hatchery, near Niland, Imperial County, and another at Thousand Palms Oasis, Riverside County.

The only natural populations are at San Sebastian Marsh, a spring-fed stretch of permanent water on BLM land in Imperial County and upper Salt Creek in Riverside County. San Sebastian Marsh (Fig. 2) on San Felipe Creek is a tamarisk-lined, interrupted stream. The population here is in precarious condition. Population numbers fluctuate widely. Very little is known about the hydrology of the aquifer. Sometimes the stream flows vigorously, maintaining permanent water for nearly 16 km. Other times flow becomes reduced to a few pools. Since 1978 there is no known record of it drying completely (Black pers. comm.). Between 1983 and 1986 no pupfish were observed in the marsh.

Because of the apparent absence of desert pupfish in San Sebastian Marsh, in 1985, the California Department of Fish and Game attempted to reintroduce fish

Table 2. Brief summary of the status of recent and historic populations of the desert pupfish, *Cyprinodon macularius* and its allies. See text for explanation of threats.

| Locality | Threats | Status |
|---|---|---|
| Gila River, Ariz. | Habitat destruction<br>Introduced fishes<br>Tamarisk<br>Dewatering | Extirpated |
| San Pedro River, Ariz. | Dewatering | Extirpated |
| Santa Cruz River, Ariz. | Dewatering | Extirpated |
| Colorado River, (USA) | Habitat destruction<br>Introduced fishes | Extirpated |
| Santa Clara Slough, Mex. | Introduced fishes<br>Increased salinity | Poor |
| Salton Sea shoreline | Introduced fishes | Nearly extirpated |
| Salton Sea drains | Introduced fishes<br>Aquatic weeds | Extirpated |
| Salt Creek, Calif. | Introduced species<br>Tamarisk | Unstable |
| San Sebastian Marsh, Calif. | Introduced species<br>Groundwater pumping<br>Pesticides<br>Tamarisk | Unstable |
| Quitobaquito Spring, Ariz. | Introduced fishes<br>Pesticides<br>Groundwater pumping | Good |
| Rio Sonoyta, Mex. | Introduced fishes<br>Pesticides<br>Groundwater pumping | Unstable |
| Monkey Spring, Ariz. | Habitat destruction<br>Introduced fishes | Extinct |

during late May of that year. Stream flow was 4.4 CFS (Nicol pers. comm.). Fishes released at that time behaved aberrantly, becoming disoriented by the current. They appeared to be washed helplessly downstream (St. Amant pers. comm.). A short time thereafter a major storm caused San Felipe Creek to flood. It was feared that the entire effort may have been for naught.

In January and March 1986, I conducted surveys of a 5 km portion of the habitat in the vicinity of Harper's well. Using seines and fish traps baited with bread and canned cat food I sampled the stream and its backwaters. No fish of any kind were captured or observed. Stream flow at the time was high, perhaps five CFS. Quiet water was minimal. No good pupfish habitat was observed. In January, water temperature at the surface was 24°C. During two days in March, water temperature at the same point on the surface varied from 30°C to 21°C. The latter reading was taken on an overcast day with threatening rain.

The next month, in April 1986, the California Department of Fish and Game using fish traps, conducted a three-day survey, sampling most of the flow. No fishes of any kind were trapped, but at two locations in drying backwaters, small fish less than 20 mm TL were observed (Black pers. comm.). They were tentatively

Fig. 7. Palm Spring refugium, Anza Borrego Desert State Park, San Diego County, California (12 March 1983).

identified by California Fish and Game personnel as desert pupfish. By June 1986, however, swarms of pupfish could be observed. One month later a flood seemed to wash out the entire population. Once again, in June 1987, the pupfish reappeared (Nicol pers. comm.).

Although the pupfish population seems always to return, it is disconcerting that the designated critical habitat is subject to such severe perturbations, and now at least two species of non-native fishes share the habitat with pupfish. Since the winter of 1986, flow in San Felipe Creek usually has been uninterrupted from San Sebastian Marsh to the Salton Sea. In May and June 1987 beneath the Highway 86 Bridge over San Felipe Creek pupfish shared a pool with *Gambusia affinis, Poecilia latipinna,* and *Tilapia mossambica.*

The population in Salt Creek on the east side of the Salton Sea was thought to be extirpated as of May 1986. The lower portion of the drainage in Salt Creek State Recreation Area, Imperial County, was totally overtaken by introduced fishes. However, in June 1986, a population occupying approximately 150 m of slow moving water was found by California Fish and Game personnel in upper Salt Creek, Riverside County. Subsequent visits by me and Kim Nicol of the Department of Fish and Game have found fish in that area as recently as October 1987. Source of this water is unknown, but it may be seepage from the nearby Coachella Canal. If that portion of the canal is lined with concrete, as is proposed, it may eliminate permanent water in upper Salt Creek.

Populations in the shoreline pools and drains (Figs. 3, 4) are all but gone. They were very common in the 1960s (Barlow 1961; Walker 1961). An extensive survey conducted by the California Department of Fish and Game showed that in 1979 desert pupfish represented less than 5% of the fishes captured (Black 1980). A similar survey in 1983 revealed that pupfish had declined to 0.2% of the population (Moore 1983). Of 40 irrigation drains that were sampled a total of 6 pupfish were captured. During April, May, and June 1987, S. J. Montgomery conducted surveys in the drains on the southeastern corner of the Salton Sea near Niland, Imperial County. Of 1128 fish captured, three were desert pupfish. It is heartening that at least a small number of pupfish may be holding on in one or more drains.

*Santa Clara slough populations.*—W. L. Minckley of Arizona State University conducted a survey of the Santa Clara Slough region during spring 1985. This was followed up in autumn 1987 by Dean Hendrickson of the Arizona Game and Fish Department. Floods of 1983 and 1984 have added much water to the habitat. At a point approximately 40 km above Montague Island, Minckley (pers. comm.) estimated the flow to be 300 m wide and 30,000 CFS. A strong flow into Laguna Salada was observed. A large population of introduced fishes, those associated with the lower Colorado River, was observed. In particular, *Tilapia aurea* was "everywhere." They appeared to have replaced other species of *Tilapia* as well. Minckley (1982) reported that at least 44 species of introduced fishes were known to occur in the lower Colorado River. Pupfish were observed at three localities: 1. East of the highway south of Sierra Cucapa fish were rare, but present; 2. West of the Colorado River in a small saline pool that may be reached by crossing a causeway; and 3. East of the road, 1–2 km north of the salinity canal inflow. All pupfish observed appeared to be in good shape. Where they occurred, there were no other fishes present. For the time being, the populations were judged "safe" but the hot spring near El Doctor was converted to a *Tilapia* rearing pond. Dean Hendrickson (pers. comm.) reported that fish were present in habitats near El Doctor in September, 1987.

The future for Santa Clara Slough pupfish is uncertain. For obvious reasons, there is no assurance that populations within Mexico will be protected. The recent input of fresh water has enlarged the habitat to the degree that the traditional boundaries of the region known as Santa Clara Slough have become obscure (Minckley pers. comm.). Future increase in salinity due to brine from the Yuma desalination plant also remains a threat.

Six refugia for fish from Santa Clara Slough are known to exist. these occur at the following localities: 1. Arizona State University, Tempe, Maricopa County, Arizona; 2. Boyce Thompson Arboretum, Pinal County, Arizona (Fathead minnows, *Pimapheles promelas,* of unknown origin now share this refuge with pupfish; Brooks, pers. comm.); 3. Dexter U.S. Fish and Wildlife hatchery, Chavez County, New Mexico; 4. Howard Well on BLM land near Safford, Graham County, Arizona (Johnson pers. comm.); 5. Deer Valley High School, West Phoenix, Maricopa County, Arizona. (Fish from this population may have been transplanted to other high school campuses. It has been reported that at least one high school in Phoenix and another in Tucson has such populations; Hendrickson pers. comm.); 6. Centro Ecologico de Sonora, Hermosillo, Sonora, Mexico. A seventh refuge at Fort Huachuca, Cochise County, Arizona, may have been contaminated with a later introduction of Quitobaquito fish (Hendrickson pers. comm.). Attempted introductions into refugia on BLM land in the Bill Williams drainage, Mohave County, and Mesquite Spring in the Gila River drainage, Pinal County, Arizona have failed because fish are not reproducing (Brooks pers. comm.).

*Quitobaquito populations.*—The population at Quitobaquito Spring in Organ Pipe Cactus National Monument (Fig. 5) is the only native population of these pupfish. Two other small refugia within the national monument recently have been eliminated (Miller and Fuiman 1987). Two refugia for this species are known to occur. One is at Arizona State University. The other is at the Arizona–Sonora Desert Museum in Pima County, Arizona. Fish at the desert museum were introduced in 1982 or 1983 and appear to be doing well (Brooks pers. comm.). Purity of this stock may be questionable. Unauthorized introductions may have placed Quitobaquito pupfish outside of their natural range. A record for *C. macularius* reported by Minckley and Deacon (1968) was actually an introduction of Quitobaquito fish. This introduction, by the State of Arizona, in the Salt River channel near Tempe, Maricopa County, Arizona put the Quitobaquito form into a former locality for a different subspecies (Minckley and Brooks 1986). Two other such introductions are known. Origin and/or purity of these stocks is uncertain (Minckley pers. comm.). One is at Bog Hole near the head of the Santa Cruz River, Santa Cruz County, Arizona. Recently some of the fish escaped into the River proper (Brooks pers. comm.). The other is in Finley Tank at the Audubon Society Research Ranch near Elgin, Santa Cruz County, Arizona. These two populations will be renovated in the future (Brooks pers. comm.).

*Rio Sonoyta populations.*—Three populations of fish have been known to occur in Rio Sonoyta, Sonora, Mexico. This drainage is immediately south of Organ Pipe Cactus National Monument, but lies in Mexico. History of this population shows a pattern of flooding and recovery similar to that at San Sebastian Marsh. Floods in 1981 and 1982 drastically changed the river, carrying pupfish to the end of permanent flow near Agua Salada (McMahon and Miller 1982).Between 1983 and 1986 pupfish were not officially observed in Sonoyta Creek. The only known refugium for Rio Sonoyta fish is at Centro Ecologico de Sonora, Hermosillo, Sonora, Mexico (Hendrickson pers. comm.). Status of pupfish populations in the area has been inconsistent. A bleak picture appeared in early 1986, but visits by Robert R. Miller of the University of Michigan in May 1986 and Dean Hendrickson in September 1987, indicated that the fishes were abundant, and stream flow was good.

*Monkey Spring population.*—This fish, considered by Minckley (1973) to be a distinct species, slipped into oblivion about 1971. Populations existed in waters fed by Monkey Spring, Santa Cruz County, Arizona (Fig. 6). These populations were on the Rail-X Ranch near Patagonia. The headspring has remained a protected habitat. In the headspring today is a population of the rare and endangered Gila topminnow, *Poeciliopsis occidentalis.* Although Gila topminnows and pupfish shared the same habitat in sloughs and backwaters, pupfish seem not to be able to reproduce in the headspring (Minckley 1973; Schoenherr 1974). Downstream from the spring was a pond where pupfish abounded (Minckley 1969). In the late 1800s, prior to manipulation by humans, pupfish shared a marsh habitat in the area with the Gila topminnow and the Gila chub, *Gila intermedia* (Minckley 1973). Pupfish maintained a breeding population in the pond until 1969 when they were extirpated by unauthorized stockings of largemouth bass. Attempts to

Table 3. A summary of life history data for desert pupfish, *Cyprinodon macularis.* See text for discussion and references.

| | | |
|---|---|---|
| Environmental tolerances: | | |
| Minimum dissolved oxygen, 0.13 mg/liter | | |
| Temperature extremes, 7°–44.6°C | | |
| Temperature preference, 36°C (Salton Sea) | | |
| Salinity (TDS) extremes: | Eggs, 0–70 g/liter | |
| | Juveniles, 0–90 g/liter | |
| | Adults, 0–70 g/liter | |
| Food preferences: | Aquatic insect larvae | |
| | Detritus | |
| | Algae | |
| | Snails | |
| Reproduction: | | |
| Breeding season: | Variable temperature, April–October | |
| | Constant warm temperature, year-round | |
| Fertility-Fecundity: | Number of eggs laid at a time, 1–4 | |
| | Number of eggs per female, 50–800 | |
| | Number of eggs laid per day, 20 | |
| Growth and Development: | | |
| Egg size, 1 mm | | |
| Size at hatching, 4–5 mm TL | | |
| Hatching time, 10 days at 20°C | | |
| Size at sexual maturity, 15 mm SL | | |
| Age at sexual maturity: | Variable temperature, 1 yr | |
| | Constant warm temperature, 2–3 months | |
| Optimum growth: | Fresh water at 15–20°C | |
| | Sea water at 25–35°C | |

keep them in captivity at Arizona State University and by the Arizona Game and Fish Department failed in 1971 (Minckley 1973).

In summary, the only truly viable populations of these pupfishes in the United States are in habitats managed by various state and federal agencies. As will be discussed below, even in refugia, these fishes may be subject to perturbations that threaten their existence. The healthiest natural populations appear to be in Mexico. For obvious reasons we cannot expect that they will be protected there.

## Life History

If a recovery program for *Cyprinodon macularius* is to be effective, details of its natural history must be assembled. A compilation of what is known about the life history of *Cyprinodon macularius* is included here. Table 3 is a summary.

Breeding activity for fish from the Salton Sea has been described by Cowles (1934) and Barlow (1961). Kynard and Garrett (1979) summarized breeding for Quitobaquito fish.

Liu (1969) has pointed out the importance of visual stimuli during courtship. Males become brightly colored in the spring when water temperature rises. Breeding usually commences in April or May and continues into August. In constant temperature warm habitats it continues year-round. They will spawn from 13°C to 44°C, but they seem to prefer spawning at 28°C. A dominant male patrols a territory from which he chases intruders. Cox (1972b) pointed out that at Quitobaquito this includes females in the early part of the season. The male contacts the female with the lower part of his head. The female nips the substrate and spits a piece of it. She may repeat this procedure several times. The male swims to the female, positioning his body parallel to hers. The male wraps his anal fin around the underside of the female in the region of her vent. She trembles and lays from one to four eggs. Crear and Haydock (1970) calculated that a single female may lay from 50 to 800 eggs during a season. Females may lay up to 20 eggs a day (Cortois and Hino 1979). Eggs may be laid on a sandy or muddy substrate, but Cortois and Hino (1979) using wool yarn to simulate spawning substrate, discovered that desert pupfish prefer to spawn on green substrate. This preference presumably indicates a preference for spawning in algal mats.

Young of the year begin to appear soon after breeding commences in April or May. Sex ratios seem to remain about 50:50, although only a small proportion of males attain full sexual coloration. To determine true sex ratios requires dissection.

Kodric-Brown (1977, 1978, 1981) studied the adaptive significance of several breeding systems in pupfish. She concluded that the territorial breeding system described above was optimally successful in large habitats. In smaller habitats, a dominance hierarchy becomes more successful. In large habitats with low population density a consort pair system is preferred. In this system observed by Barlow (1961) for Salton Sea fish in aquaria, a gravid female is followed closely by one or more males. The males are nonaggressive toward each other. Periodically, a mating pair will descend to the substrate and spawn. The male consort may block the approach of another male by placing his body between the female and the approaching male. In this system, where population density is low, there is less stress, and there are more males participating in mating. Greater heterogeneity is maintained in this way.

Another aspect of mating behavior was described by Loiselle (1979). He pointed out that males recognize their own spawn by its odor.While males are patrolling a territory they are protecting their spawn. They will eat the spawn of another male that appears on the territory. Sub-dominant males resemble females. they move on to the spawning ground with females. When the dominant male is occupied mating with a female, or chasing another male, a subdominant male attempts to fertilize the eggs of one of the females. The subdominant male also will prey upon the spawn of the dominant male. This is known as sneak mating. Its importance is that it introduces variation into a system where territoriality would favor propagation by a small number of males. Loiselle (1982) also reported that males maximize reproductive effort and survival of eggs by chasing small females from the territory. By preferentially courting large females, theoretically more and larger eggs will be fertilized.

Eggs hatch in about a week. Crear and Haydock (1970) reported that it takes 10 days at 20°C. The rate of growth and development is strongly influenced by the environment (Soltz and Hirshfield 1981). In the laboratory, hatchlings were 4–5 mm TL and doubled their size in less than eight weeks. Kinne (1960) showed the interactive effect of temperature and salinity on development. Juveniles grow faster in freshwater than in sea water at temperatures of 15° and 20°C. At higher temperatures (25°, 30°, 35°C) fish grow faster in sea water. Eggs from Salton Sea fish develop normally and produce greater than 50% hatch at temperatures between 17° and 34°C with salinity at 35 g/liter (ppt) (Kinne and Kinne 1962).

*Cyprinodon macularius* that live in constant warm water become mature and reproduce at 2–3 months of age. In variable environments they mature in about a year (Constantz 1981). McGinnis (1984) specified that breeding in variable temperature environments occurred in the second year of life. Males mature at about 15 mm SL (Constantz 1981). Maximum size reported by McGinnis (1984) for breeding males was 75 mm.

Desert pupfish usually have a long gut. This implies their diet consists largely of detritus or algae. In general, however, feeding is opportunistic. Pupfish eat what is available. Detritus and algae are often available. Minckley and Arnold (1969) described "pit digging" behavior in which pits hollowed in soft or sandy substrate become detrital traps. Male pupfish will defend these traps along with their spawn.

Walters and Legner (1980) studied food habits of *Cyprinodon macularius* in shallow ponds. They found that pupfish foraged mostly on the bottom, consuming chironomid (=tendipedid) midge larvae, detritus, aquatic vegetation, and snails. They also found that in rice fields, pupfish forage on littoral Cladocera, Coleopterous larvae, and mosquitoes, suggesting that pupfish might be an effective aid in mosquito control in the southwestern United States. Studies on mosquito predation by *Cyprinodon macularius* indicated that the pupfish are superior to *Gambusia affinis* for mosquito control because they forage throughout the entire water mass, including emergent vegetation and floating algal mats (Legner and Medved 1974; Legner et al. 1975).

In studies of Salton Sea fish, Naiman (1979) found that the diet varies seasonally, with detritus and algae making up variable components of the diet. Animal composition of gut contents varied from 30% to 56%. Of the animals consumed they preferred chironomid larvae and diptera pupae. Cox (1972a) reported similar findings for fish at Quitobaquito Spring. He further reported that they occasionally eat their own eggs and young.

High water temperatures may create exceptional nutritional problems for fishes (Deacon and Minckley 1974). Lowe and Heath (1969) indicated for Quitobaquito fish that maximum intake of food occurred at 35°C but maximum conversion efficiency was at 20°C. Kinne (1960) documented more than a 24-fold increase in food intake as temperature was increased from 15° to 30°C. Interestingly, however, maximum rate of growth with unlimited food occurred at 30°C. It appears that in fluctuating temperature environnents, maximum intake of food during the day when temperatures are high is compensated for by digestion and absorption of food later, when the temperature drops. Barlow's (1958a) observation of daily movement into and out of shallows, coincident with a preference for water at 36°C, might be explained by the temperature effect on feeding and assimilation. Pupfish frequently rest on the bottom, particularly at night (Deacon and Minckley 1974). Presumably this sedentary behavior reduces metabolic demand, thus maximizing feeding efficiency. Feldmeth (pers. comm.) indicated that compared to patrolling a territory, metabolic demand while resting was reduced over three-fold.

Tolerance for environmental extremes is a notable feature of *Cyprinodon macularius.* Records for highest temperature and lowest oxygen are held by this species.

Their tolerance for salniity is no less remarkable. The lowest tolerated minimum for dissolved oxygen ever recorded, at 0.13 mg/liter was attributed to *Cyprinodon macularius* (Lowe et al. 1967). These fish dive into reducing, odoriferous mud which is devoid of oxygen and high in hydrogen sulfide (Lowe and Heath 1969; Deacon and Minckley 1974). This behavior is probably a form of thermoregulation which minimizes metabolic rate, but it would not be possible if the fish were not remarkably tolerant to low concentrations of dissolved oxygen.

Lowe and Heath (1969) reported for Quitobaquito pupfish a critical thermal maximum (CTM) of 44.6°C. This is the highest CTM ever reported for a fish. They also reported finding the fish in nature at Quitobaquito Spring in water at 41°C. Barlow (1961) reported pupfish at the Salton Sea holding territories at 38.3°C. I observed the same phenomenon in water at 39°C in the King Street Irrigation drain, Riverside County, California (Schoenherr 1979). Of greater interest, perhaps, is an early report of *Lucania browni* (=*Cyprinodon macularius*) taken from a spring in northeastern Baja California. Jordan and Richardson (1907) reported that the water temperature taken by trained personnel was 48.9°C. This may be the highest known temperature of water from which living fish were obtained.

The CTM of a fish depends on the temperature to which it was acclimated. Lowe and Heath (1969) found a seasonal periodicity in CTM for *Cyprinodon macularius* regardless of acclimation temperature. Winter acclimated fish could not tolerate normal summer field temperature. In other species of pupfish it has been determined that smaller fish had consistently higher CTMs than older fish (Shrode 1975). This observation may help to explain Barlow's (1958a) observation at the Salton Sea that juveniles consistently occupied warmer, shallow water than adults. Temperature preferences must be related to a complex of factors involving age, metabolism, and mating behavior.

Tolerance for low temperatures is also important. A thermal minimum of 7°C is recorded for *Cyprinodon macularius* (Lowe and Heath 1969). Deacon and Minckley (1974) reported that pupfish from the spring source at Quitobaquito were able to tolerate short periods of time under ice if they were raised in the experimental ponds at Arizona State University.

Temperature extremes in the desert are the rule. The same holds true for shallow water desert habitats. Daily fluctuations may reach 15°C (Naiman et al. 1973). It is logical that fish will move from place to place to minimize stress. Barlow (1958a, 1961) described daily movements in the shoreline pools at the Salton Sea. Typically, they move into shallow water where they feed in the early morning. As the temperature rises they move into deeper water (ca. 40 cm deep). In the deeper water they remain motionless, perhaps minimizing metabolic demand as food is processed. In afternoon they move back to the shallows and feed again. After dark they once again remain motionless. An exception to this pattern is that breeding males may remain on the spawning grounds day and night, although they do become inactive after dark (Deacon and Minckley 1974). This behavior is probably necessary to protect the spawn.

Tolerance for variation in salinity or total dissolved solids (TDS) is also impressive in pupfish. *Cyprinodon milleri* from Cottonball Marsh in Death Valley has been found in pools with salinities ranging from 14 to 160 g/liter (LaBounty and Deacon 1972). The latter value, at nearly five times the concentration of sea water, is the highest salinity known for a fish. For pupfish at the Salton Sea, Barlow (1958b) found 90 g/liter to be about the maximum tolerated. This value is nearly three times the concentration of sea water, which is also remarkable. Another impressive early record was that of Coleman (1926) who reported that *Cyprinodon macularius* can tolerate salinities up to 200 g/liter.

The ability of pupfishes to tolerate rapid changes in salinity is an adaptive feature related to its origin in an estuarine environment (Miller 1981). Miller (1981) reported that at his lab in Berkeley, *Cyprinodon macularius* could adjust rapidly to direct transfer back and forth from fresh to full sea water. This ability is certainly related to the notable ability of desert pupfish to invade newly inundated terrain or temporary ponds and establish breeding populations. The last time reasonable numbers of pupfish were found in shoreline pools at the Salton Sea was following the heavy rains that broke the drought in 1978 (Black 1980).

Tolerances for different salinities may not be equivalent at all stages of development. Kinne and Kinne (1962) found that some eggs of *Cyprinodon macularius* will hatch and develop in ranges of salinity from distilled water to 70 g/liter. Barlow (1958b) found that juveniles have the highest tolerance for salinity. The 90 g/liter value mentioned above was for juvenile fish. Adults appear not to be able to tolerate salinities in excess of 70 g/liter.

There is an adaptive interaction between tolerance for these extreme physical parameters (Hilliard 1981). It has been reported that only fishes acclimated to high temperature are able to tolerate the metabolic demand that goes with osmoregulation in hypersaline waters (Stuenkel and Hilliard 1980). Only at higher temperatures is metabolic rate high enough to provide the energy it takes to excrete salt by active transport over gill membranes. Hilliard (1981) reported that desert fishes are most likely to encounter the combination of hypersaline water and high temperature in the summer. This ability coupled with their tolerance for low dissolved oxygen makes them the only fishes to inhabit many desert localities.

## Factors Leading to the Decline of the Desert Pupfish

Simplistic cause and effect relationships are seldom adequate to explain the decline of what was once a widespread species complex. Many factors contributed to the demise of the desert pupfish and its allies. Listing the factors and discussing them here is an attempt to document what has happened, and what might happen again, so that in our attempt to protect these fish and construct a recovery program, old pitfalls might be avoided. Table 2, mentioned above, includes a brief summary of past, present, and future threats to the well being of desert pupfish.

*Natural phenomena.*—Two natural phenomena frequently are implicated in the demise of pupfish populations; flooding and drying. For millions of years pupfish have been living with natural cycles of flooding and drying. Their short life span, high reproductive rate, and high tolerance for environmental extremes makes them particularly well suited to natural fluctuations in habit, size and quality. They often endure adversity and prosper in its absence.

I know of no natural situation where a population of pupfish was eliminated by flooding, but the possibility cannot be ignored. Flooding is more likely to eradicate non-native fishes, while leaving native forms to prosper in the aftermath

(Minckley 1973; Meffee 1984). Pupfish are able to bury themselves in the substrate (Lowe and Heath 1969). In this way, they may be able to tolerate a flood better than other fishes in the same water.

Some examples in San Felipe Creek may serve to illustrate the remarkable tolerance of pupfish populations to flooding. In June 1978, I visited San Sebastian Marsh. Pupfish were common in backwaters adjacent to the main flow. I also observed mosquito fish, *Gambusia affinis,* and sailfin mollies, *Poecilia latipinna.* A survey by the California Department of Fish and Game two months later showed a similar assemblage (Black pers. comm.). Shortly thereafter, there began a series of storms. For the first time in many years water flowed all the way to the Salton Sea. Sailfin mollies were eliminated but no new species was introduced. In 1979, *Gambusia affinis* returned along with the pupfish. To my knowledge, sailfin mollies have not been recorded in San Sebastian Marsh since, although they have been observed with pupfish and *Tilapia* in a pool under the Highway 86 bridge (Nicol pers. comm.). In March 1979, Glenn Black of the California Department of Fish and Game surveyed the lower portion of San Sebastian Marsh. He reported capturing pupfish in fish traps and observing mosquitofish. Flooding occurred again that year after which mosquitofish did not return. The winter of 1980–81 was comparatively dry. A pupfish survey by Glenn Black in August 1981, found pupfish relatively common in interrupted flow about one kilometer above Harper's Well. No other species was observed. Total habitat reduction was estimated to be about 60% from previous years, but pupfish were abundant. A major flood in July 1986, once again appeared to obliterate a sizeable pupfish population. From that time until the present, water has flowed without interruption all the way to the Salton Sea. A survey by Kim Nicol of California Department of Fish and Game in the summer of 1987 revealed that pupfish had returned to San Sebastian Marsh in sizeable numbers but they had been joined by *Gambusia affinis* and *Tilapia mossambica.* This is the first record for *Tilapia* in San Sebastian Marsh. It appears that they moved up San Felipe Creek from the Salton Sea.

Since the flooding, appropriate backwater habit also is lacking. The abundant water in San Felipe Creek at the present time is of mysterious origin. The winter of 1986–87 was unusually dry. Water may be coming from irrigation upstream, or surface flow may be apparent because several years of flooding have scoured the streambed to levels that are lower than usual.

Flooding in the late 1970s also washed out non-native species. The red shiner, *Notropis lutrensis* was formerly one of the most common fishes in the Avenue 81 drain (Soltz pers. comm.). Flooding apparently eliminated red shiners, but not sailfin mollies or pupfish. Why were mollies not eliminated, too? Minckley (1973) reported that sailfin mollies were the only species extirpated from the Salt River near Tempe, Arizona during flooding in the winter of 1970. It is likely that euryhaline mollies found temporary refuge in the salty water and simply returned after flooding subsided. Red shiners probably were not able to tolerate the salt water.

A similar pattern of flooding, apparent extirpation, and reestablishment has been documented for the pupfish population at Rio Sonoyta (Miller and Fuiman 1987). In that system, however, native minnows such as longfin dace, *Agosia chrysogaster* and mosquitofish recolonized more quickly than pupfish.

In contrast to flooding, drying of a habitat can be devastating to fishes. All it takes is a few minutes without water and the habitat can become fishless. On the other hand, pupfish, more than any other fishes of the southwest are able to cope with the events that accompany drying of a habitat. Their tolerance for high temperature, low dissolved oxygen, and high salinity make them uniquely able to tolerate dewatering during evaporation. If some water remains, pupfish probably will maintain low population density in proportion to habitat size. They have been doing this sort of thing for millions of years. It might even be possible for a pupfish population to return after a short period of time with no standing water. Deacon and Minckley (1974) described a situation where pupfish eggs hatched within a few hours from muds of dried experimental ponds after resting there for about a week. They concluded that pupfish have a remarkable colonizing ability following almost-terminal drying of water courses.

*Habitat destruction.*—Destruction of fish habitats by the activities of humans is a well documented story (Miller 1961; Minckley and Deacon 1968; Pister 1974). Dimunition of pupfish habitat in the early part of this century occurred in association with habitat destruction. Hastings (1959) and Hastings and Turner (1966) described a period of arroyo cutting in association with increased runoff, aggravated by soil compaction and overgrazing by cattle. Diversion of water for agriculture and dam building contributed further to dewatering of habitats along the Gila and Colorado Rivers. Roosevelt Dam blocked the Salt River, a major tributary of the Gila, in 1910. Headwaters of the Gila River were blocked by Coolidge Dam in 1929. The river is now a dry wash throughout most of its lower course (Minckley and Deacon 1968). At the present time the lower 700 km of the Colorado River are dammed, regulated, channeled, and diked. Beginning with Hoover (Boulder) Dam in 1936, followed by Parker and Imperial Dams in the early 1940s, the lower Colorado River began to lose its sloughs and backwaters. Now there are nine major reservoirs on the river. Downstream flow has decreased, temperature regimes have become monotonized, silt loads have decreased, and salinity has increased (Pillsbury 1981).

In the Salton Sea area, physical habitat changes have been commonplace. Irrigation drains represented the major habitat for desert pupfish in the late 1970s. The Coachella Valley Water District and the Imperial Valley Irrigation District reconstructed canals and altered flow without concern for the aquatic biota. Drains were bulldozed and scraped free of emergent vegetation. Some were lined with concrete. From 1977 to 1981 I was attempting to study a pupfish population in the King Street irrigation drain. During the time of my attempted study, the habitat was flooded and reconstructed completely. Hot water from a nearby thermal spring was impounded for bathing and washing clothes. Finally, runoff was redirected and flow reduced to a trickle (Schoenherr 1979, 1981a, b). Irrigation districts have a right to regulate their drains, but it is possible to proceed with some concern for endangered native species.

Groundwater pumping is a major concern for continued flow in desert springs (Minckley and Deacon 1968; Pister 1974). In 1981 a jojoba (*Simondsia chinensis*) farm was proposed for BLM land, upflow from San Sebastian Marsh. Development of this facility would have involved groundwater pumping from the aquifer that supplies water for the marsh. No one knows the details of the aquifer, or what impact groundwater pumping would have. Fortunately, at this time plans for the jojoba enterprise have been abandoned, but it was not because there were pupfish in San Sebastian Marsh.

Groundwater pumping for agricultural purposes is also a potential threat for populations at Quitobaquito Spring and nearby Rio Sonoyta. Agricultural activities in Mexico have expanded greatly since the 1970s as part of a government-sponsored land settlement program. Large tracts of land have been cleared and groundwater pumps installed on ejidos throughout the Sonoyta Valley (McMahon and Miller 1982). The extent of groundwater pumping is unknown, but drying of a stream near Ejido Santo Domingo may be due to activities of new groundwater pumps in the area (McMahon and Miller 1982). Recent visits to the region by R. R. Miller (1986) and D. Hendrickson (1987) verify that new agricultural activity could be a serious problem to these populations.

*Chemical changes.*—The most significant of the chemical changes that occurred in the first half of the century was increasing salinity associated with agricultural runoff. Although that took its toll of some native species it seemed to have little effect on pupfish. The loss of only one pupfish population has been attributed to increasing salinity. The Salton Sea U.S. Fish and Wildlife pupfish refuge near Niland, Imperial County, California, experienced an increase in salinity associated with lowering of the water table. Salinity in the refuge rose to nearly 100 g/liter. The fish died in 1981 (Black pers. comm.).

Since 1977 the Santa Clara Slough popuation has received additional water through a drain that brings bypass water from the Gila Valley, Arizona. This water flowing into the slough with a salinity of 52 g/liter actually had a freshening effect. The added water helped expand the slough from about 75 acres in 1974 to 1000s of acres of open water (Rinne pers. comm.). Flooding of the Colorado River in 1983 and 1984 provided a new influx of fresh water. Pupfish habitat apparently has expanded. In the future, however, reject water from the desalinization plant at Yuma, Arizona is predicted to raise salinity of the slough from its present 32 g/liter to about 90 g/liter (Rinne pers. comm.). The effect of this influx remains to be seen. It will bear watching.

Pesticides or other agricultural chemicals have been suspected of causing fish deaths, but nothing is certain. One theory about periodic scarcity of fishes in San Sebastian Marsh is that pesticides from a ranch upflow from the marsh may have contaminated the habitat. Thirteen different pesticides apparently have been authorized for use in the area (Black pers. comm.). Possible chemical contamination is also feared if either geothermal or oil and gas development occur on federal land adjacent to the marsh.

At Quitobaquito Spring, studies in the late 1970s showed that fishes contained detectable levels of parathion and DDT (Kynard 1981). Fish kills in 1976 were attributed to lethal levels of m-parathion. The population there is located downwind from farms in Mexico where chlorinated hydrocarbons and organophosphates are in use. Although no detectable effect has been shown to occur recently, this too will bear watching. This is the only population of Quitobaquito fish where it is certain that the strain is pure. An increase in pesticide in the area, either due to blow-over, or an accidental spill, could have a devastating effect. The same concerns apply to the populations in nearby Rio Sonoyta.

In March, 1976, I was studying *Cyprinodon macularius* densities in algal mats.

One study population was in the Johnston Street drain on the east side of the Salton Sea, near Mecca, Riverside County. I arrived at the site to discover the water covered with an oily film. It appeared to be kerosene or diesel fuel. It could have been an accidental spill from the nearby highway or railroad, or it may have been an application to kill mosquito larvae. Fortunately, no dead fishes were observed, but rather than foul my seine, I abandoned the study for that day. Whatever the case, it further illustrated that aquatic habitats are never safe from the unexpected.

*Aquatic vegetation.*—An aquatic weed, *Hydrilla verticillata,* has been introduced into the All American Canal in the Imperial Valley, California.There is valid concern that it may escape, and move into pupfish habitats. The chemical, mechanical, and biological means required to eradicate it could endanger pupfish. Introduction of another "weed eating" fish, such as grass carp, *Ctenopharyngodon idellus,* in order to control weeds could be another stress on pupfish populations.

Other examples of aquatic vegetation encroaching upon pupfish habitat have been observed. Cattails (*Typha* sp.) have invaded most of the surface water in several drains around the Salton Sea. After reconstruction of the King Street canal in 1978, complete encroachment of surface water took place in a little over two years (Schoenherr 1981a). Personnel from the U.S. Fish and Wildlife service flew over Santa Clara Slough during winter 1986. They reported a severe invasion of cattails, no doubt associated with the large input of fresh water (Brooks pers. comm.). Also, cattails have invaded many marsh areas along the lower Colorado River. Regulated flow has allowed this to happen. In the years before damming, periodic flooding would scour out the aquatic vegetation nearly every year.

In a small spring habitat, invasion of aquatic vegetation can have a rapid, profound effect. Such an invasion nearly overtook the open water at Palm Spring, a refuge for desert pupfish in Anza Borrego Desert State Park. Total surface area of the refuge (Fig. 7) is about sixteen square meters. All but about one meter of surface was impacted by rhizomes and emergent growth of bulrushes (*Scirpus* sp.). In March 1985, a volunteer crew of students and faculty from Fullerton College assisted a state park ranger in clearing the refuge. Four full truck-loads of vegetation were carried away by a small stake-bed truck. As of March 1986, the refuge appeared to be clear of encroaching vegetation and contained a healthy population of pupfish.

Of perhaps greatest concern is the tamarisk (*Tamarix* spp.) invasion of desert riparian areas. Tamarisk was imported originally from the eastern Mediterranean and east Asian regions (Munz 1974). Tamarisk was first noted in 1916 growing in the wild along the upper Gila River following a flood (Robinson 1965; Turner 1974; Neill 1983). It spread rapidly to become the dominant riparian tree species by the 1940s (Gatewood et al. 1950; Turner 1974). The prolific nature of tamarisk and its high transpiration rate make it one of the most formidable threats to fish habitats. Tamarisk has been reported to have the highest transpiration rate of all known preatophytes (Van Hylckama 1980).

A showcase for the effect of Tamarisk eradication is at Eagle Borax Spring in Death Valley National Monument (Pister pers. comm.). Tamarisk had dewatered the habitat. A ten-year project of tamarisk removal restored the water. The habitat is once again used by migratory birds.

The tamarisk invasion certainly had an influence on dewatering of the Gila

River (Gatewood et al. 1950). It must have helped lead to the demise of desert pupfish there. In the Salton Sea area at the present time, tamarisk is abundant in Salt Creek and San Sebastian Marsh. Reckoning with tamarisk may become one of the most difficult parts of maintaining San Sebastian Marsh as critical habitat for the desert pupfish. If a tamarisk eradication project is undertaken, extreme caution must be taken to make certain that no 2,4D or other herbicides enter the water.

*Introduced species.*—The replacement of native fishes by introduced non-native species has been documented many times (Miller 1961; Minckley and Deacon 1968; Schoenherr 1974, 1977, 1981a, b; Meffee 1982; Meffee et al. 1983; Meffee 1985). Of the 65 fishes in North American deserts that may be considered desert species (Deacon et al. 1979), more than two-thirds have been reduced in number while interacting with introduced species (Schoenherr 1981b). Often these interactions have been coupled with habitat degradation, but the influence of non-native species must not be ignored. The exact mechanism by which this replacement occurs is not always demonstrable, but three kinds of interactions are often mentioned; predation, competition, and hybridization.

Neary 50% of introduced southwestern fishes are piscivores (Meffe 1982). It seems logical that predation is one of the major mechanisms responsible for native fish extirpation, particularly where large game fishes are involved. For example, predation by largemouth bass, *Micropterus salmoides,* is considered to be the major mechanism leading to the extinction of the Monkey Spring pupfish. Factors leading to demise of that population were recorded by Minckley (1973). The original marsh was impounded by a dam in the late 1800s. Attempts to deepen the impoundment at a later date failed, and water drained completely. Water was then diverted to another pond where pupfish persisted until 1968. During that year unauthorized stocking of largemouth bass was discovered. The bass were removed by gill netting. During spring 1969, largemouth bass were introduced again. In a very short time, they multiplied and decimated the pupfish population, taking a toll on the Gila topminnow as well (Schoenherr 1974). Repeated introductions of pupfish into the protected spring source (Fig. 4) by W. L. Minckley and me failed to establish a breeding population there. For unknown reasons, populations maintained by the Arizona Game and Fish Department and Arizona State University failed in 1971 (Minckley 1973). The species is presumed extinct.

Predation by game fish is assumed to be the major mechanism that finally eliminated pupfish from the lower Colorado River in the United States. After dams altered flow and backwaters disappeared, pupfish were forced into the main stream. It is believed that predation in deeper water finished them off. The question arises, "What will be the influence of recent flooding and the influx of some 44 non-native species into Santa Clara Slough (Miller, pers. comm.)?"

Predation is not always an obvious phenomenon. Mosquitofish, *Gambusia affinis,* have been implicated in the decline of over 20 species of fishes on a world wide basis (Schoenherr 1974, 1981b). One of the mechanisms by which the mosquitofish does this is through predation on juvenile fishes (Schoenherr 1974, 1981b; Meffee 1982, 1984, 1985). Everman and Clark (1931) expressed concern that mosquitofish might influence pupfish populations in the Salton Sea. My studies, however, seem to indicate that pupfish and mosquitofish in the Salton Sea and its drains are able to coexist (Schoenherr 1979). Of all the introduced species that are found in pupfish habitat in the Salton Sea area (Table 4), it seems that mosquitofish are one of the lesser threats. Nevertheless, mosquitofish are known to prey on juvenile fishes. It is disconcerting that the most visible pupfish refuge in Anza Borrego Desert State Park, at the trailhead to Palm Canyon, repeatedly contains more mosquitofish than pupfish. Once, when I asked the attendant ranger why there were mosquitofish in the pond, his response was, "Who can tell the difference?"

Competition is often noted as the mechanism by which non-native species eliminate native species. This term is a convenient catchall, but competition seldom can be proved (Schoenherr 1981b). By most definitions, competition implies that two forms compete for a common resource such as food (Weatherly 1972). Competition for food is seldom demonstrated. Rather, it is often discovered that behavioral phenomena are the cause of the problem (Schoenherr 1981b). Aggression may cause stress, and stress may be associated with a decline in reproduction. My data suggested that this was one of the mechanisms by which *Gambusia affinis* eliminated *Poeciliopsis occidentalis* in Arizona (Schoenherr 1974, 1977, 1981b).

At the Salton Sea, pupfish were common in shoreline pools (Fig. 3) until they were replaced by sailfin mollies, *Poecilia latipinna,* which were introduced about 1964. In 1979 these euryhaline fishes were the most common fish. They represented 98% of those trapped along the shoreline, and 70% of those trapped in the drains (Black 1980). At that time, desert pupfish represented less than 5% of the fish sampled. Under pressure of interaction with sailfin mollies, pupfish apparently moved farther up the drains. In 1973, in an attempt to control aquatic weeds, Zill's cichlid, *Tilapia zilli,* was introduced by the local water district. It was thought that they would not reproduce in the cool water of the drains, but they flourished. After that, pupfish moved into shallow water, less than 10 cm deep (Fig. 4). This shallow water proved not to be a refuge either, as juvenile *Tilapia* began to replace them there, too. During 1983, the California Department of Fish and Game, in two surveys, sampled 40 drains. They trapped only 6 pupfish (Moore 1983).

A total of 29 fish species have been recorded from drains and canals in the Salton Sea area (Table 4). All of these species, at one time or another, could have reacted with *Cyprinodon macularius.* Of primary concern, however, are *Poecilia latipinna* and *Tilapia zilli.* They have replaced pupfish in all habitats. The mechanism of this replacement is not thoroughly understood, but replacement by behavioral interaction appears to be important.

Margaret Matsui (pers. comm.) described behavioral interactions by sailfin mollies and Zill's cichlid that interfere with reproduction of desert pupfish. Males of *Poecilia latipinna* court both male and female pupfish. In so doing, they directly interfere with courtship and reproduction. Adult *Tilapia* are too large (ca. 12 cm SL) to interfere with pupfish in shallow water. Pupfish are able to feed and breed in water less than 3 cm deep. Juvenile *Tilapia,* however, invade the shallow water. Matsui described passive interference with pupfish by juvenile *Tilapia.* Male pupfish, in patrolling their spawning sites vigorously chased away intruders including juvenile *Tilapia.* It was suspected the male *Cyprinodon* might spend too much time chasing, and not enough time spawning. Another factor was suggested by Loiselle (1979). He observed that males eat each other's spawn. If the dominant male is busy chasing away juvenile *Tilapia,* could not subdominant males move

Table 4. Fishes recorded from irrigation canals and waterways in the vicinity of the Salton Sea, Riverside and Imperial Counties, California.

| Species | Reference |
|---|---|
| Dorosomidae | |
| *Dorosoma petenense* | Black 1980 |
| Cyprinidae | |
| *Carassius auratus* | Schoenherr 1979 |
| *Cyprinus carpio* | Mearns 1975 |
| *Ctenopharyngodon idellus* | St. Amant pers. comm. |
| *Notropis lutrensis* | Schoenherr 1979 |
| *Notemigonus chrysoleucus* | Soltz, pers. comm. |
| Cyprinodontidae | |
| *Cyprinodon macularius* | Walker 1961 |
| *Rivulus harti* | St. Amant 1970 |
| Poeciliidae | |
| *Gambusia affinis* | Schoenherr 1979 |
| *Poecilia latipinna* | Schoenherr 1979 |
| *Poecilia mexicana* | Schoenherr 1979 |
| *Poecilia sphenops* | Schoenherr 1979 |
| *Poeciliopsis gracilis* | Mearns 1975 |
| *Xiphophorus helleri* | Mearns 1975 |
| *Xiphophorus variatus* | St. Amant and Sharp 1971 |
| Percichthyidae | |
| *Morone saxatilis* | St. Amant pers. comm. |
| Centrarchidae | |
| *Micropterus salmoides* | Soltz pers. comm. |
| *Lepomis cyanellus* | Schoenherr 1979 |
| Ictaluridae | |
| *Pylodictis olivaris* | Bottroff et al. 1969 |
| *Ictalurus nebulosus* | Schoenherr 1979 |
| *Ictalurus punctutatus* | Soltz pers. comm. |
| *Ictalurus natalis* | Black 1980 |
| Pomadasyidae | |
| *Anisotremus davidsoni* | Black 1980 |
| Sciaenidae | |
| *Bairdiella icistia* | Black 1980 |
| *Cynoscion nobilis* | Black 1980 |
| Cichlidae | |
| *Tilapia mossambica* | St. Amant 1966 |
| *Tilapia zilli* | Schoenherr 1979 |
| Gobiidae | |
| *Gillichthyes mirabilis* | Schoenherr 1979 |

on to the spawning ground and prey upon the spawn? Similarly, when the sneak males are successful in fertilizing some eggs, the dominant male eats their spawn.

In an attempt to determine if males eat other's spawn in nature, I watched the behavior of a patrolling male in shallow water in the King Street Canal. The time-consuming part of the project was finding a dominant male among the swarms of juvenile *Tilapia*. By the summer of 1980 pupfish had become rare in the areas where they formerly were common (Schoenherr 1979, 1981a). Several hours of seining yielded only four pupfish, taken from among the roots of cattails. When I spotted a patrolling male *Cyprinodon,* I sat on the edge of the canal and watched with binoculars while he vigorously chased away intruders. I estimated that nearly 80% of his time was spent chasing juvenile *Tilapia.* I observed only three *Cyprinodon.* I could not tell if they were females or subdominant males. They moved on to the spawning ground and pecked at the substrate. This behavior could have been an example of female courtship, or it could have been feeding. I was unable to determine if they spit out the substrate after picking it up. It may be that subdominant males were eating the spawn. The dominant male seemed to ignore them. Whatever the case, pupfish were nearly absent where they formerly were common. By the winter of 1981, cattails covered the entire habitat, and it had been dewatered. Neither *Cyprinodon* nor *Tilapia* was observed.

A potential threat in the near future is grass carp, *Ctenopharyngodon idellus.* In order to head off a possible *Hydrilla* invasion, in 1985, the California Department of Fish and Game approved introduction of "weed eating" grass carp. In October 1985, the Imperial and Coachella Irrigation Districts introduced sterile, triploid grass carp to golf courses, and all the canals and laterals in the area (Nicol pers. comm.). The assumption is that they will not invade the drains or Salt Creek, because they will have to navigate through hypersaline waters of the Salton Sea in order to do so. Pupfish habitat is presumed "safe" from grass carp. Skeptics look with doubt on the prospect that these meter-long fish remain in the habitat to which they were introduced. If they do invade pupfish habitat, similar to *Tilapia zilli,* they are likely to eat pupfish eggs along with vegetation. Furthermore, Minckley (1973) suspected that, on the basis of their morphology, grass carp were omnivorous and could easily shift to a diet of animal material if a favored plant species became reduced in abundance.

The appearance of introduced species is often inexplicable. Two particular unexplained introductions illustrate that desert pupfish are not even safe from non-native species within their refugia. In the first case, in 1968 or 1969, someone introduced golden shiners, *Notemigonus crysoleucus,* to the pool fed by Quitobaquito Spring in Organ Pipe Cactus National Monument (Minckley 1973). Golden shiners are popular bait fish used by anglers along the Colorado River. Their native range is in the eastern United States. They have been implicated as being associated with reduction of two native Arizona spinedace (*Lepidomeda*). Eradication of the introduced shiner and re-establishment of the native pupfish was costly in time and money (Minckley 1973).

The second case of an unauthorized introduction in a refugium involves the population at the Palm Canyon trailhead in Anza Borrego Desert State Park. As indicated above, *Gambusia affinis* got into the refuge sometime around 1981. There was an apparent eradication effort. Either it failed or the mosquitofish were introduced again. As of January 1986 they were still there, outnumbering the pupfish.

Another form of interaction that can occur between two species is hybridization. Because of geographic isolation, different forms of the desert pupfish are not likely to interact in nature. Unauthorized introductions, on the other hand, particularly outside of a native range, are likely to bring together two distinct forms that might hybridize. Hybridization can swamp distinctive genomes. Miller (1981) pointed out that there is extensive genetic compatibility between allopatric morphotypes. For example, if Quitobaquito pupfish became introduced to Rio Sonoyta it could cause swamping of the distinctive genome of Rio Sonoyta pupfish. That would represent extirpation of a subspecies. Great care must be taken to ensure that any future introductions are from known genetic stock, and they occur within the native range of the taxon.

*Pathogens.*—The possibility of epidemic disease must always be considered. Crowded or otherwise stressed populations are more likely to be affected by such a phenomenon. An epidemic in a small population could be a disaster. One may never know the cause of an epidemic, but unauthorized introduction of any aquatic animal could be the source of a pathogen.

Pathogens in pupfish populations seldom have been reported in the literature. My collections in irrigation drains have revealed fungus infections, tail rot, and parasitic protozoa such as *Ichthyophthirius* (Ich) in the introduced fishes, but I have not seen such infections on *Cyprinodon macularius.* Similar observations have been made by Department of Fish and Game personnel (Black and Nicol pers. comm.).

Cox (1966) reported a nematode parasite that was found in 13 of 58 fish examined from Quitobaquito Spring. The parasite resembled one that was found in wading birds, and it may have been introduced by them. This number may not seem significant, but a similar infection rate (22%) of a lethal pathogen in a small refugium would be cause for alarm.

In May 1987, there was a small fish kill in the pupfish refuge at the Salton Sea State Recreation Area (Nicol pers. comm.). Suspecting a possible toxin or pathogen, park service personnel had the dead fish analyzed by a Fish and Game pathologist. The cause of the deaths was diagnosed as "gas bubble disease" or nitrogen embolism. The problem was attributed to a leaky pump that supersaturated the water with dissolved gases prior to entering the pond. The problem was remedied by passing the water over rocks before it entered the pupfish pool. This form of agitation caused the gas to escape before it entered the pool. Prompt attention by State employees solved this problem.

In June 1987, an outbreak of enteric septicemia of unknown origin forced the destruction of nearly 850,000 channel catfish in the Department of Fish and Game's Imperial Valley Warmwater Fish Hatchery near Niland (Black pers. comm.). This is the same site for which there is proposed a desert pupfish refugium. It is apparently unlikely that the same disease could affect pupfish, but the distinct possibility of something unexpected is ample reason to insist that we have as many buffers against extinction as possible.

## Conclusion

Rise and fall of the desert pupfish has been associated with activities of humans. Habitat detruction, chemical degradation, encroachment by noxious weeds, and introduction of non-native species have cooperated in bringing these fishes to the brink of extinction. Distribution of the species has declined to the point that it exists naturally in only three localities in the United States. The habitat at Quitobaquito Spring in Organ Pipe Cactus National Monument in Arizona is a modified spring system potentially threatened by groundwater pumping and pesticides. The natural populations at San Felipe Creek and Salt Creek in California are subject to disturbing fluctuations in flow and unpredictable appearances of non-native species. Hydrology of these drainages is not known. Whether habitats could become dry during a drought is also unknown. Further threats include introduced fishes, possible pathogens, groundwater pumping, pesticides, and/or a tamarisk invasion. In Mexico, at Santa Clara Slough, the largest natural population, could be threatened by introduced fishes, encroachment by cattails, and/or a predicted increase in salinity. Our buffer against extinction lies in a series of small refugia operated by a variety of state and federal agencies. An effective recovery program must be implemented soon.

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