7-19-1999

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ECOLOGICAL REVIEW AND MANAGEMENT RECOMMENDATIONS FOR RECOVERY OF THE ENDANGERED GILA TOPMINNOW

W.L. Minckley

ABSTRACT.—Ecology of the endangered Gila topminnow is reviewed, described, and reconstructed; natural conditions are placed in perspective with human-altered habitats of today. In the natural state of waxing and waning of habitat size as a function of precipitation patterns and catastrophic events such as severe winter cold, the species in the past likely underwent dramatic expansions and contractions in population size and geographic range. Today, population expansions are unlikely because of constraints imposed by human activities. The original patterns of dispersal from refugia in "good" times and retreat in "bad" times, if they are to occur, must be re-created through human translocation. Further, most refugia now are destroyed or inaccessible to recolonization, so remnant, natural populations, along with established, transplanted stocks of appropriate size and genetic quality, need protection. Populations also must be established and maintained in artificial refugia. Last, even if connectedness were to be reestablished and refugia provided, intervening habitats harbor introduced piscivores such as western mosquitofish that interdict and eat dispersing topminnows and their progeny. Elimination, exclusion, or management against such offending species is mandatory to prevent topminnow extinction and achieve recovery.

Key words: Gila topminnow, Poeciliopsis occidentalis, Colorado River, western North America, endangered species, management, recovery.

At the time of its discovery in the mid-1800s, the small, livebearing Gila topminnow, Poeciliopsis occidentalis (Baird and Girard), was widely distributed below ~1600 m elevation in the Gila River basin of Arizona and New Mexico in the United States, and in northwestern Sonora, México (Hubbs and Miller 1941). It now is extirpated from much of its range in the United States, persisting naturally in only a few isolated springs and stream segments (Fig. 1), and is listed as endangered by the U.S. Fish and Wildlife Service (USFWS 1994). Although more secure in México (Hendrickson et al. 1981), both this and the closely related P. sonoriensis (Girard) also are declining there (Campoy-R. et al. 1989, Varela-R. et al. 1992) and are listed (collectively as P. occidentalis) as threatened by the Mexican Secretaría de Desarrollo Social (SEDESOL 1994). I consider P. sonoriensis a full species (rather than a subspecies of P. occidentalis) based on data presented by Quatro et al. (1996).

Disappearance of the Gila topminnow is attributable to changes stemming from human activities. Before the 1800s, livestock grazing and timber harvest began to alter natural vegetation (Hastings 1963, Hastings and Turner 1965, Bahre 1991, 1995) that changed patterns in runoff, erosion, and sedimentation. Intensive water development for irrigation commenced in the 1800s, further altering flow patterns and discharge volumes of individual streams. Even with these negative impacts, the species continued to enjoy wide distribution. In the 1940s and 1950s, however, introduction and establishment of myriad nonnative species began to change the faunas of whole watersheds by restructuring aquatic communities (Minckley 1991). A downward spiral toward extinction for Gila topminnow coincided with the establishment and spread of another livebearer, the western mosquitofish, Gambusia affinis (Baird and Girard).

Rauchenberger (1989) elevated G. affinis and G. holbrooki Girard, long treated as subspecies of G. affinis, and the nominal G. speciosa Girard of Texas and northern México all to full species. Common names of these fishes were changed by Mayden et al. (1992) to reflect changed taxonomy to "central" (affinis, formerly "western"), "eastern" (holbrooki, formerly "eastern"), and "western" (speciosa). I retain "western mosquitofish" for affinis on the basis of comments by Clark Hubbs (personal communication), who

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pointed out that "the native range for G. affinis includes populations west of any G. speciosa. If a change is to be made, the common names should be C. holbrooki eastern, G. affinis western, and G. speciosa southern." "Mosquito-fish," used here for all nonnative Arizona populations, refers only to G. affinis, based on the morphology of 423 specimens (Arizona State University [ASU] Collection; 29 localities, statewide) confirmed as this species by Tao Hoc Thai (ASU; personal communication).

Western (and/or eastern) mosquitofish have been planted worldwide in attempts to control pestiferous insects, a practice continuing today (Courtenay and Meffe 1989). The aggressive Gambusia affinis (Myers 1965), comparable in body size, shape, and ecology to topminnows and native to south central United States and northeastern México, was first recorded in Arizona in 1926 (Miller and Lowe 1967) and since has spread to occupy much of the region (Fig. 2). Featuring strong jaw teeth and aggressive, carnivorous feeding behavior, it was soon indicted (Miller 1961) and then convicted as an effective topminnow predator (Minckley and Deacon 1968, Schoenherr 1974, 1977, Meffe 1983a, et seq.). The native livebearer sometimes disappeared only a few short months after mosquitofish were detected (Schoenherr 1974, Meffe 1983a).

As usual, there were exceptions. First, some topminnow populations coexisted for a long time with mosquitofish before disappearing (Minckley et al. 1977), and a few still do (USFWS 1984, Abarca et al. 1994, Woodman and Young 1997). In fact, other than in 2 springs
Fig. 2. Distribution of collection localities for non-native mosquitofish in the Gila River basin, United States and Mexico, based on ASU specimens and literature records.

and a creek where mosquitofish have not yet appeared, all 8 other natural sites where topminnows now remain are either cohabited by or directly accessible to mosquitofish.

Second, losses of only a small proportion of translocated-then-extirpated topminnow reintroductions were attributable to mosquitofish. Of 175 sites stocked (Weedman and Young 1997), 18 (10.3%) had topminnows that survived 3–20 yr, and 157 (89.7%) failed. This rate of success was disappointingly low to some (Simons et al. 1989, Hendrickson and Brooks 1991) but seemed reasonable to others (Minkelley 1995). It meant that the number of localities for wild populations had more than doubled since the effort began. At 96 sites a reason for topminnow disappearance was apparent (61 succumbed to unknown factors): 57 were desiccated, 27 were lost to flooding, 6 to winter cold, and only 1 or 2 each to mosquitofish, water quality, dredging, or livestock overuse.

The surviving, exceptional populations merit further consideration. Are there subtle factors just as dangerous as drought, flood, or mosquitofish responsible for topminnow extirpation? Should factors other than mosquitofish predation be considered in attempts to conserve and recover the species? I examined such possibilities by reviewing data for sites where topminnows occurred before and during early stages of mosquitofish establishment. I then compared these data with features at sites of long-term topminnow-mosquitofish coexistence as well as sites where translocated stocks seem to have established. Coincidence of topminnow localities with elevated winter water temperatures was far greater than expected. Thus, predation might not be the only factor involved in the Gila topminnow’s demise. The possibility is examined that distribution, abundance, and persistence are also influenced by temperatures in exceptionally cold winters.
REVIEW OF GILA TOPMINNOW ECOLOGY

Life-history Features and Habitats

The Gila topminnow is short lived with high reproductive potential. Average natural life span is <1 yr, and a female bears 5–20 young at 24- to 28-d intervals (Constantz 1974 et seq.). The reproductive season varies upward to 8–9 months from spring through autumn, and may be year-round (although depressed in winter) in warm, constant-temperature springs. Females sometimes superfetate, simultaneously carrying 2 or more cohorts of young, each at different stages of embryogeny, which reduces brood intervals (Schoenherr 1974, 1977, Constantz 1980). A female also can produce multiple broods from a single insemination, perhaps throughout life (Constantz 1981, 1989). Young achieve sexual maturity in warm water in 60 or fewer days (Constantz 1976, 1979).

The Gila topminnow occupies water a few centimeters deep in slow currents, tending to concentrate in protected inlets shoreward of sandbars or debris, or associated with aquatic or streamside vegetation (Minckley 1973, Meffe et al. 1983, Forest 1992). It lived originally in a variety of habitats, from shorelines and slackwaters of rivers to small streams, springs, and marshes. It endures both intermittency and moderate floods (Meffe et al. 1983, Meffe 1984b), although severe flooding eliminated some translocated populations (Collins et al. 1981, Weedman and Young 1997). The fish is omnivorous, eating mostly detritus and small items of aquatic or terrestrial invertebrates (Schoenherr 1974, 1977, 1981, Gerking and Plantz 1980).

Under natural conditions Gila topminnows were largely alone in their microhabitat, encountering only larvae or juveniles of 1 or 2 other native fishes, none markedly competitive or piscivorous. Among these, only desert pupfish, Cyprinodon macularius Baird and Girard, likely co-occurred throughout the year; ~75% of known locales for pupfish in Arizona (before it also declined to endangered status) also supported topminnows. Pupfish were far rarer than topminnows. Only 12 samples at 8 locales were known before 1930 (Fig. 1; including the undescribed Monkey Spring pupfish, Cyprinodon sp.) compared with about 50 collections at approximately 20 sites for topminnows. Although physical separation between the species is minimal in shallow water, interactions are rarer in deeper habitats since pupfish remain near the bottom while, as implied by its common name, the topminnow is near the surface.

Distribution and Abundance

Under natural conditions Gila topminnows must have expanded in geographic range and population size during wetter times of maximum habitat connectedness. As habitats diminished and fragmented with drought, most populations could only have been progressively reduced in size and then destroyed, until the species was ultimately isolated into a few remaining oases fed by reliable subterranean water sources. The strategy worked because dispersal barriers vanished; topminnows then could again repopulate as soon as dry channels resumed their flow. Predisposition to exploit such a transient system through life-history and habitat-selection traits included rapid population expansion. A biological “incentive,” a benefit to dispersing individuals despite danger of death from desiccation, was more food or some other factor reflected in greater reproductive output (e.g., higher fitness) as demonstrated by Constantz (1976, 1981). Not all individuals left the oases. Those that remained traded high risk with high profit in temporary waters for low-risk, low-profit survival in small, permanent habitats, thereby ensuring individual (and thus species) persistence.

Original topminnow environments were vastly different from those of today. Historically, precipitation ran more slowly off intact watersheds, and a larger proportion entered the water table. Violent floods were less frequent. Groundwater percolated downslope to fill floodplain alluvium and promote reliable baseflows in surface streams. Stream channels were geomorphically more complex, substrates more diverse and well sorted, and pools were common, scoured near tree roots, fallen logs, boulders, and banks, or behind beaver dams. Stream courses were scarcely or only locally incised. Riparian vegetation included gallery forests, dense shrublands, and riverine marshlands. Water temperature was ameliorated both in summer and winter by groundwater exchange and shading from riparian plants. In addition, no major predators other than fish-eating birds and invertebrates harassed or preyed on adult topminnows and ate their young.
Thermal Ecology

The Gila topminnow tolerates high water temperatures in summer (Heath 1962) and withstands most winter cold expected at low elevations in the Gila River basin. Nonetheless, its northern latitudinal and upper altitudinal distributional limits are apparent functions of winter water temperatures. This is no revelation since the Gila River basin is the northernmost penetration of this tropical genus (Rosen and Bailey 1963).

Low temperatures also influence the topminnow other than at the periphery of its geographic range. On 6–10 December 1978, nighttime air temperatures in much of the species’ range fell to or below −6.0°C (Anonymous 1979, Jones 1979), nearly 10° lower than in a “normal” year. Such a freeze, if lasting more than 12–20 consecutive hours, proves catastrophic to many warm-adapted Sonoran Desert plants, including, among others, some life stages of saguaro cactus (Cereus giganteus), shrubs (bursage, *Ambrosia* spp.), trees (palo verde, *Cercidium* spp.), and other organisms as well. Such events occur only sporadically (Bowers 1980).

On 11 December 1978, I found a few hundred dead topminnows in shallow, ice-covered backwaters of Ciénega Creek, Arizona. A thermometer was not available. A few (10s of individuals) were dead in flowing water, and fewer moribund, scarcely mobile fish could be forced from shoreline beds of plants. Upstream, near a discrete spring inflow and groundwater seepage, 10s of active individuals were concentrated where ice was absent and water was 3.0–5.0°C warmer to touch. In the same stream in winter 1990, which was not exceptionally cold, Simms and Simms (1992) recorded substantial declines in topminnow abundance at 8 sites (they reported no dead fish), but not at another site near a spring inflow. Additionally, seasonal fluctuations in population size in the constant-temperature Monkey Spring (~26°C; Constantz 1976) were small compared to those in more variable environments (Schoenherr 1974, Constantz 1976, Meffe 1983a).

It is not known whether populations at warmer sites were maintained by immigration toward springs (if physically possible) or recruitment through in situ reproduction, or if declines elsewhere reflected mortality from factors other than cold. Nonetheless, of 15 pre-1930 locales (before mosquito fish were prevalent) where Gila topminnows were collected, 10 (67%) were at or within a few kilometers of groundwater-fed marshlands or known spring inflows (in part, Hendrickson and Minckley 1985), and all but 1 of the 6 northernmost sites were associated with thermal springs. The exception was Ash Creek (Jennings 1987), where I know of no springs, although that stream flows into San Carlos River, which enjoys a number of thermal inputs. Only 1 of 10 sampling sites where topminnows were absent in collections during the same time period was near a known, major groundwater inflow.

Statistics on translocated stocks show similar trends, although these data clearly are biased since spring-fed habitats (due to permanency) lacking mosquito fish (or other introduced predators) were selected for stocking. Sixteen (89%) of 18 populations that persisted 3–20 yr were in springs or spring-fed habitats. Only 48 (30.6%) of 157 places where translocation failed were at or near springs or in spring- or marshland-associated creeks, while 109 (69.5%) were where thermal amelioration either was not noted or seems unlikely (personal observation and Weedman and Young 1997).

Human Impacts

The tenuous existence of Gila topminnows has been worsened by other human interventions. Dams, diversions, other water-control structures, and long, dry reaches of stream now comprise insurmountable barriers to fish dispersal among isolated islands of suitable habitat. Even where connectedness remains, stream channels are incised and shorelines are unsuitable for survival. Groundwater tables are lowered by channel incision and further yet by groundwater pumping. Removal of subsurface water for agriculture or other purposes results in dried springs as well. Moreover, springs and other artesian outflows are often "improved" by capping, impoundment, diversion, or other means (McNatt 1979).

Even where surface water persists, stream baseflows often are reduced to a mere trickle, flowing over barren sand and gravel, distantly bordered by vertical banks, and suffering rapid heating and cooling due to exposure, low volume, and reduced groundwater exchange. Riparian vegetation is physically disrupted by floods or dies as water tables are lowered too
deeply for roots to reach during drought. Flash floods are more common due to rapid runoff from denuded watersheds, and the power of flooding is concentrated downward as water rises vertically against cut banks. Both erosive and sediment-carrying capacity are greater with increased velocity in constrained channels, and transport of large sediment loads homogenizes bottoms so pools are fewer and more transient.

Furthermore, mosquitofish and other non-native species persist and flourish in altered or artificial habitats such as livestock watering ponds, from whence they invade natural habitats, including formerly dry reaches of streams. Finally, public health agencies stock both natural and artificial waters for mosquito control as soon as surface waters reappear. Whatever the circumstances, piscivorous nonnative species appear to intercept dispersing topminnows and reduce their odds of survival to recolonize. A few instances where topminnows disappeared and did not reappear although mosquitofish were not recorded may be attributable to such interception, but also may result from interdiction by physical barriers.

**TOPMINNOW-MOSQUITOFISH COEXISTENCE**

Both field and laboratory evidence confirms that mosquitofish predation decimates Gila topminnow populations. The exotic has achieved an almost cosmopolitan distribution throughout and beyond former topminnow range (Fig. 2). Of natural topminnow stocks that persist (Table 1, Figs. 1, 3), 5 remained isolated from mosquitofish as of 1995–96, 2 seem to be disappearing under stress from the exotic, 3 have shared habitat for a number of years, and another (discovered in 1994; Table 1), also contaminated by mosquitofish, has appeared only since wastewater disposal recreated permanent habitat in the Santa Cruz River. What allows coexistence in these last 4 areas?

**Physical Influences**

Long-term coexistence has long been attributed to habitat features. Meffe et al. (1983) implied disturbance as a factor in topminnow disappearance; e.g., they . . . persist in undisturbed habitats allopatric with mosquitofish, and decline or disappear where the exotic has invaded.” Courtenay and Meffe (1989) emphasized that mosquitofish most readily establish in disturbed habitats, but they did not quantify their contention. Yet, Gila topminnows seem to have survived throughout their natural range after the major disturbance (to the human eye) of regional arroyo cutting in the 1890s (Hastings 1959, 1963, Cooke and Reeves 1976) until mosquitofish appeared 30 yr later. Also, periodic flooding, often touted as a major negative disturbance, is tolerated by native topminnows but selects against mosquitofish (Meffe 1985, Minckley and Meffe 1987).

In Redrock Canyon (Table 1), an area of long-term coexistence (Binne et al. 1980, Stefferud and Stefferud 1995, Weedman and Young 1997), both species persist in rock pools and other depressions (often spring-fed) within and adjacent to erosive, high-gradient channels. Gila topminnows are consistently more abundant for a few months after floods, until mosquitofish reinvade from livestock ponds upstream and rebound to dominance. Postflood enhancement of Gila topminnow populations has been similarly documented in Sharp Spring (Meffe 1983a, 1985) and for related Yaqui topminnows in Black Draw, Arizona (Galat and Robertson 1992). If floods are frequent enough, they may thus provide a “hedge” against extinction of the native.

Coexistence also may be favored if habitat size and heterogeneity allow spatial segregation (Meffe 1985). This hypothesis is based mostly in theory and on long-term co-occurrences in the upper Santa Cruz River, Sonoita Creek, and Redrock Canyon. It also is possible, however, that the first 2 are occupied only sporadically, invaded after extirpation by fish from elsewhere (Minckley et al. 1977), and do not represent actual, long-term syntopy. Those in the mainstream Santa Cruz may be augmented or reestablished after extirpation from Sharp Spring and/or adjacent Heron Spring where Sharp Spring fish were introduced and established. Sonoita Creek also could receive migrants from Fresno Canyon and its tributary Coalmine Canyon. The “new” wastewater-inhabiting stock in the Santa Cruz River (in a reach mostly dry in the past and not then supporting any resident fishes; unpublished data) must have come from upstream in the Santa Cruz or Sonoita Creek, or both. It also is possible that unknown stocks are involved.
Table 1. General description and status of natural populations of Gila topminnow in the United States, based on Weedman and Young (1997) and original data; localities are indicated by numbers in Figures 1 and 3. The year in parentheses is when monitoring was last accomplished; statements of conservation status set in boldface type refer to that visit.

1. Sharp Spring (1995): low-volume flow through heavily vegetated channel, ~0.5 km long, isolated from Santa Cruz River except in flood; topminnow greatly outnumbered by mosquitofish, most common in extreme springhead.

2. Upper Santa Cruz River (1996, topminnow last taken 1983); heavily vegetated stream channel, commonly intermittent, with cut banks alternating with vegetated shorelines; subject to flood scour; topminnow occurs sporadically; consistently rare and often absent from collections (see also Minckley et al. 1977), perhaps extirpated.

3. Monkey Spring (1995): warm, constant-volume discharge charged little in past 30 yr (see, however, Minckley et al. 1991); topminnow the only fish present in headspring and outlet, the former with a livestock enclosure.

4. Cottonwood Spring (1996): warm, constant-volume discharge inside livestock enclosure; flows through short run into Sonoita Creek; topminnow the only fish present in springhead and run, sometimes occurring with native longfin dace (Agostia chrysogaster Girard) in creek, which is intermittent or sometimes dry.

5. Redrock Canyon, separated for sampling into Falls/Gate Spring (1996) and Cott Tank drainages (1996); typically intermittent channels subject to flooding, with small pools and streamside springs/seeps; topminnow rare along with longfin dace at former, abundant with mosquitofish at latter; population sizes of both livebearers and presence of piscivorous centrarchid fishes variable.

6. Sonoita Creek (1996): permanent reach in intermittent stream subject to flooding, bottoms sand/gravel, with some backwaters and pool-like habitats near obstructions; topminnow abundant, occurring with native longfin dace, desert sucker (Pentosteus clarki [Baird and Girard]), introduced mosquitofish, and 1 or more species of introduced cyprinid, centrarchid, and ikeatulid fishes.

7. Fresno Canyon (1996): stream smaller but similar to 6, above; topminnow present along with introduced centrarchids.

8. Cosmline Canyon (1996): stream smaller but similar to 6, above; topminnow abundant along with longfin dace and rare introduced centrarchid.

9. Lower Santa Cruz River (1996): relatively swift channel over sand bottom; topminnow present and common at 3 of 4 sites in a 5.0- to 6.0-km reach, occurring with longfin dace and desert sucker; mosquitofish taken in 1994.

10. Ciénega Creek (1995): permanent stream similar to locale 6, above; topminnow present along with longfin dace and Gila chub (Gila intermedia [Girard]).

11. Bylas Springs (1997): 3 small springs (S-1, S-2, S-3), originally flowing through narrow, heavily shaded, vegetated channels into marsh or directly into Gila River; S-3, from which all topminnows were extirpated, recently renovated, modified, and topminnow stock from S-1 (retained in an artificial refugium) reintroduced in 1999; S-2 renovated in 1996 (mosquitofish successfully removed), modified, and original topminnow successfully reestablished.

Biological Factors in Habitat Use

Also related to water quality are springhead occurrence and persistence of topminnows along with apparent exclusion (despite apparently ready access) of mosquitofish. Western mosquitofish and the related G. speciosa penetrate only into the lowermost spring runs within their native ranges (Hubbs 1995), parts of which surround a number of other endemic gambusias restricted to springheads in Texas, New Mexico, and northern México. Except under human-altered conditions (Hubbs 1957, 1971), mosquitofish do not move upstream to replace these spring-specialized gambusias. Hubbs and Springer (1957) even hypothesized a scenario of origin in which invading mosquitofish stopped short of springheads, resulting in isolation of progenitors of the endemics. Based on today’s examples (Marsh and Minckley 1990), topminnows share with these endemic gambusias an ability to live in springheads and the inability to cope with mosquitofish.

As fish habitat, springs have long presented a dilemma. Despite a significant number of western fishes depending for existence on springs or spring-fed environments (Meffe 1989), not many kinds consistently occupy the immediate areas in which subterranean waters rise to the surface. We rarely know why one succeeds in such places while another species fails (Courtenay and Meffe 1989, Hubbs 1995). A few springheads are simply too warm or present some other, insurmountable physiological challenge such as low dissolved oxygen (Sumner and Sargent 1940, Hubbs and Hettler 1964, Hubbs et al. 1967). Yet, most seem quite hospitable, at least to human senses. It seems
likely that springheads present one or more chronic extremes too severe over the long term for some species to succeed (e.g., constancy may exclude animals requiring thermal change for gonads to mature). Springheads most often are occupied by a single fish species, sometimes endemic, and often locked into the habitat by a specialization like stenothermy.

Some spring-inhabiting fishes may, in contrast, be equally capable of living elsewhere, often under apparently harsh conditions. Examples include pupfishes (genus Cyprinodon), some thriving equally as well in highly fluctuating habitats as in springs. Most of these taxa, despite their tolerances, avoid other fishes and tend to remain allotopic in particular
habitats marked by constancy (as in springs) or severity (high temperatures, hypersalinity, etc.), excluding all but themselves. Gila topminnows in the Gila River basin may be one of the last group, living for millennia as part of a depauperate aquatic biota essentially free of piscivores or even species in similar habitats, which may be reflected in their present susceptibility to predation (Meffe 1983a, 1985). In rivers of Mxico, Gila and Sonoran topminnows have dealt successfully over evolutionary time with larger fish faunas. Thus, their as-yet-unknown responses to mosquitofish (introduced in ~1978; Hendrickson et al. 1981) are important to document.

Mosquitofish seem more suited to habitats less constant than springs (see papers in Meffe and Snelson 1989) and survive under conditions of extreme variability, though not so severe as those tolerated by pupfishes. Unlike many springhead-inhabiting taxa, however, mosquitofish evolved and commonly occur where ubiquitous, predatory fishes are diverse and abundant. They also can spread quickly through artificial and natural habitats alike, so long as forces such as floods (Minckley and Meffe 1987) or environmental constancy do not interfere.

In light of all this, another plausible explanation for occasional topminnow-mosquitofish coexistence is that the native can recognize, occupy, and persist in springlike places within streams. Springs in stream bottoms are not exceptional, and extremely local conditions could give topminnows enhanced benefits (e.g., sufficiently deter mosquitofish success) for survival. Such refugia could exist where both fishes co-occur in the upper Santa Cruz River; flowing in a broad valley with a high water table and springs; Redrock Canyon, receiving groundwater in at least 6 places (Rinne et al. 1980, Stefferud and Stefferud 1995); and/or Sonoita Creek below Patagonia Lake (Fig. 3). In the last area the 2 fishes occupy borrow pits and channels downstream from an artificial reservoir. Permanency results from groundwater inflow (partially reservoir seepage) and enhanced stability below the dam. Floods are bypassed via a spillway (in part), and thermal variability is reduced by seepage, both simulating head-spring conditions. As noted before, springs and seeps from banks and marshlands also are common along Cienega Creek, which supports the largest existing topminnow population in the United States and where mosquitofish have not yet been detected.

An Unexplored Option

Another alternative perhaps pertinent to coexistence was examined by Hubbs (1991, 1992, 1996), who discovered that some western mosquitofish do not cannibalize their young, while others do. Non-cannibalistic individuals, if introduced and established in Arizona, might ignore young topminnows as well. Mosquitofish in Arizona almost certainly are of many different origins and times of stocking, and so benign stocks might be present, even though the single population tested (Hubbs 1992) was cannibalistic.

An Alternative Hypotheses

It seems more than coincidence that a large proportion of past and present topminnow localities are positioned at or near some form of groundwater inflow. I hypothesize that prolonged or extreme winter cold historically contributed and presently contributes to population extirpations, except in places where groundwater exchange or other factors ameliorate local water temperatures. Gila topminnow, like many other taxa with tropical and subtropical affinities, may be unable to survive prolonged winter cold. Coupled with other human-induced stresses, lack of cold resistance potentially leads to extirpation of northern, higher-altitude, and other unprotected stocks. As briefly reviewed above for Sonoran Desert plants, numerous examples of cold limitation are obvious in latitudinal and altitudinal distributional gradients, and fishes are no exception.

Discussion and Synthesis

Most terrestrial organisms recognize few barriers to dispersal and redistribute readily after population reductions. Fishes, absolutely restricted to water in linear systems with varying connectedness, and especially so in arid lands, may require more time or special conditions to recolonize. Thus, in other than the few places with permanent, relatively warm water throughout their geographic range in the Gila River watershed. Gila topminnows in the past lived “from feast to famine,” with highly variable population size and geographic range.
Historic conditions no longer exist and will likely not be reattained. The following interpretations of past conditions are integrated with today’s realities of reduced water supplies, barriers to dispersal, mosquito fish, and other factors acting against long-term topminnow survival in nature.

An Ecological Scenario

The original, widespread distribution of the Gila topminnow in the Gila River basin (Fig. 1) must have depended on dispersal from secure refugia in times of abundant surface water, maximal habitat connectedness, and moderate winter temperatures. The fish is small and does not require high-volume habitats, deals readily with variations in chemical and physical environment, and has generalized food habits; few piscine predators were originally present. Its high reproductive potential with stored sperm and superfetation allowed 1 or a few females, each potentially inseminated by more than 1 male, to reliably establish more stocks with more genetic variability than possible by most other fishes. Rapid maturation of young assisted local stocks, perhaps the progeny from a single female, to expand rapidly up- and downstream. Fish dispersing to exploit food, space, or other resources in temporary habitats enjoyed greater reproductive success and accelerated the dispersal process despite greater individual risk incurred by leaving safer refugia. More sedentary fish provided insurance for individual and species survival by remaining in or near the most permanent oases.

Expanded populations then were destroyed, progressively due to extended drought or abruptly by sudden winter cold, again leaving isolated remnants. Magnitude of extirpation depended on severity of conditions. But by then the period of connectedness had allowed stocks to mix among refugia, ensuring maintenance of genetic diversity and reducing effects of bottlenecks accrued from earlier events. New individuals or their distant progeny also reattained some original refugia, mixing with progeny of individuals that stayed home. And, alternatively and in addition, other fish finding new groundwater-fed habitats survived there. Under natural conditions, one way or another, assurances existed that future offspring were available to disperse when conditions again were right.

Possible Substantiation

Significant genetic divergences among today’s fragmented topminnow stocks (Monkey, Sharp, and Bylas springs, Cienega Creek; Fig. 3), attributed mostly to differentiation in isolation by Parker et al. (1998a, 1998b), alternatively may reflect genetic variation derived from elsewhere and accumulated in refugia through repeated cycles of immigration. Thus, maintenance of diversity may be relatively high due to random immigration of different genotypes into each subpopulation, resulting over repeated cycles in an accumulated genetic variability (Birky et al. 1989). If this is correct, topminnows spreading from various refugia under pristine conditions mixed their genomes in “good” times. Differentiation among stocks arose through alleles accumulating from elsewhere and bottlenecks (Chakraborty and Nei 1977). In new and old refugia alike, divergence could be relatively high or low depending on source(s) and number(s) of founders. A few individuals could increase the level of apparent differentiation (Maruyama and Kimura 1980), and many or a few founders each from a number of sources could cause it to decrease (Slatkin 1977). A combination of these 2 processes, driven repeatedly by weather, resulted in today’s apparent conditions. At a given moment in time, genetic or demographic equilibrium may seem minimal; averaged over a longer term, both likely exist.

In places like Monkey Spring, isolated by a substantial barrier (Minckley et al. 1991), unidirectional gene flow allowed differentiation in allotopy; Monkey Spring fish are genetically unique among 4 populations studied thus far (Parker et al. 1998a, 1998b). They average 0.62 private alleles per locus (sensu Slatkin 1985) for 5 polymorphic microsatellite loci compared with 0.14, 0.15, and 0.25 in 3 less isolated stocks (Bylas and Sharp springs, Cienega Creek). Genes from Monkey Spring nonetheless passed downstream to be assimilated and transferred among other stocks, as indicated in part by the reciprocals (shared alleles) in the above data (0.86, 0.85, and 0.75 shared loci, respectively). More variation is expected in the refugia least isolated from up- or downstream habitats into which dispersal occurs and from which fish potentially return.

This might be tested by examining existing populations throughout Sonora Creek and Santa Cruz River (Campoy-E 1996, Weedman
and Young 1997). I predict they are genetically similar to existing stocks in known refugia. And if not, I can always rationalize failure of the prediction by advocating extinction (or presence) of unknown stocks. Such a situation may be analogous to that of razorback sucker, *Xyrauchen texanus* (Abbott), in the Colorado River basin, where highest genetic variability is concentrated downstream, again concordant with greatest population stability, and has apparently not yet redistributed upstream following far colder conditions of the last period of glaciation (Dowling et al. 1996).

In conclusion, patterns of expansion and contraction of geographic range through linear stream habitats are common for aquatic organisms during wet and dry seasons and in wet versus dry years. These patterns may be extended to far longer time scales for species such as topminnows and desert pupfish (Dunham and Minckley 1998) under arid land conditions, or native trouts (Rinne and Minckley 1985), the last isolated as relicts in headwaters on cool regional highlands by the hot, dry surroundings of today. If a refuge is sufficiently reliable to protect it (from either a cold desert night or from glacial or interglacial epochs), a lineage may survive to provide individuals potentially available to disperse and breed with individuals from other refugia, repopulating whole drainages when conditions allow. It must have happened repeatedly through climatic cycles at both geologic and ecologic time scales. If not, the available alternatives were to evolve in isolation into a new form(s) or disappear.

APPLICATIONS TO MANAGEMENT

If this scenario of dispersal—extinction—redispersal—etc. approaches reality, human intervention has already been so disruptive that it may not be relevant to the modern day. In translocation-site decisions, however, considering thermal relations might result in greater success, and other interpretations from the anecdotal record may also be significant in furthering species maintenance.

I question a recommendation by Simons et al. (1989) to create what has come to be called management units, to preserve "at least one representative lineage from each of the 4 geographic areas in Arizona" (Monkey Spring, Sharp Spring, Bylas Springs, and Chínega Creek). Moritz (1994) defined management units genetically as "diverged in allele frequency and significant for conservation in that they represent populations connected by such low levels of gene flow that they are functionally independent." This may be true if today's human-created barriers to natural dispersal are considered significant, but it was certainly not the case under historical conditions when topminnows and many other western American stream fishes evolved and lived. Further, perhaps excluding the differentiated Monkey Spring population (Parker et al. 1998a, 1998b), the "evolutionary significant unit" (Waples 1995) for topminnows in the Gila River system is the whole population (or metapopulation), not its component parts, and it should be managed accordingly. For further discussion, alternative views, and citations relevant to conservation genetics of Gila topminnow, see Cardwell et al. (1998), Hedrick and Parker (1998), and Parker et al. (1998a, 1998b).

The following summarizes the 4 major disruptions that must be overcome to prevent extinction of the Gila topminnow, each followed by brief management recommendations that, when combined, could result in recovery of the species:

1. Present-day and potential future connectedness are greatly reduced or nonexistent, not only during drought but also in wetter times due to diversion and drying of whole rivers (e.g., lower parts of the Gila, Santa Cruz, and Salt rivers mainstems) and many lesser watercourses as well. Topminnow can no longer swim from "point A to point B." Individuals therefore must be translocated directly by managers.

2. Most refuge has been destroyed (through groundwater removal) or rendered inaccessible (through disrupted connections and see below) to recolonization by dispersing topminnows. Existing natural refugia (both natural and reestablished) must therefore be protected at all costs and remaining stocks kept at appropriate size and genetic quality. Artificial refugia and translocated populations also must be established and maintained, likely in perpetuity.

3. Ecological information indicates a pattern of dispersal from refuge in "good" times and retreat into refuge in "bad"
times. This pattern must be re-created periodically through direct transfers, which further involve acceptance of local extirpation countered by active and continued movement of individuals from less-than-permanent places back to reliable refugia by managers, to mimic the species' natural ecology. Monkey Spring fish should be maintained without influx of genes from other populations, but allowed to contribute to other stocks.

(4) Even if refugia remain present or are established and connectedness can in some way be reestablished, intervening habitats now harbor mosquitofish and other predators that interdict and devour dispersing topminnows and their progeny. This requires elimination, exclusion, or effective management against offending species. They must be eliminated from refugia and their nearby populations controlled to minimize the probability and frequency of invasion.

ACKNOWLEDGMENTS

Gila topminnow research has been pursued by numerous individuals. Principals at ASU were (alphabetically) George D. Constantz, Dean A. Hendrickson, Gary K. Meffe, and Allan Schoenherr; followed now by Philip W. Hedrick and his students. All are gratefully acknowledged for their contributions. James E. Johnson, formerly USFWS; Paul C. Marsh, ASU; John N. Kimme, U.S. Forest Service (USFS); and Kirk L. Young and his staff at Arizona Game and Fish Department (AGF) also contributed significantly. Taun Ho Thi, ASU undergraduate researcher, confirmed Arizona mosquitofish as representing Gambusia affinis.

Monetary support, permits, or access were granted by American Rivers, AGF, ASU, The Nature Conservancy, Sports Fishery Institute, U.S. Bureau of Reclamation, U.S. Bureau of Land Management, USFWS, and USFS. The many ranchers and ranch managers who granted access to private lands and other amenities also deserve special thanks. Debbie A. Brewer, Constantz, Thomas E. Dowling, Hedrick, Clark Hubbs, Johnson, Marsh, Schoenherr, and Peter J. Umack commented on and improved the manuscript; Dowling and Hedrick stimulated many ideas developed here, and Umack produced Figures 1–3.

LITERATURE CITED


Received 29 April 1998
Accepted 5 October 1998