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CONSERVATION GENETICS IN THE MANAGEMENT OF DESERT FISHES

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Abstract: The status and security of fishes in North American deserts has steadily declined in this century due to man's activities in this naturally fragile region. We address genetic aspects of the population structure of desert fishes as applicable to conservation and recovery programs by developing two zoogeographic models of isolation and gene flow. In the Death Valley model, populations are isolated, with no chance of natural gene flow among them. Genetic diversity within populations tends to be low, but genetic divergence among populations within a species is high. In the Stream Hierarchy model, a complicated hierarchical genetic structure exists and is a function of geographic proximity and connectivity of habitats. Within-habitat genetic diversity tends to be higher, and among-habitat differentiation lower, than in the Death Valley model. These two systems must be recognized as distinct, and managed differently. We also suggest three areas of experimentation needed to better understand and manage genetic stocks of desert fishes: relationships between heterozygosity and fitness, experimental mixing of similar stocks to examine effects of increased heterozygosity, and analysis of the relative roles of genetic adaptation and phenotypic plasticity in local differentiation.

## INTRODUCTION

Fishes in the Sonoran, Mohave, Great Basin, and Chihuahuan deserts of North America are declining at an alarming rate. At least 20 taxa have gone extinct in the last several decades (Meffe, in press) and many more are in immediate danger of similar fates (Williams et al., 1985). This major conservation problem has prompted governmental agencies and academic scientists to conduct research on basic ecologies and life histories, develop propagation programs for species perpetuation and reintroduction, and restore degraded habitats. We address here a different aspect of conservation of this highly endangered fauna, the application of population genetics to management and long-term perpetuation of desert fishes.

## DESERT AQUATIC SYSTEMS

North American deserts are extremely arid, with high geographic relief, heavily dissected drainages, and widely dispersed surface waters. Natural aquatic systems in these regions are fragmented on both broad geographic and local scales. In addition to being isolated, desert aquatic systems can experience enormous physico-chemical fluctuations, such as in streams and rivers (Minckley and Meffe, 1987), or constant but harsh conditions, as in some springs (Deacon and Minckley, 1974). The extreme **isolation** and severe abiotic conditions have led to a high degree of phenotypic divergence of fishes, often with small populations living in small habitats (Miller, 1958). Many taxa are relicts from better-watered times that have been trapped in isolated springs and streams during the last 10 - 12,000 year

post-pluvial period. This has resulted in a high degree of endemism (Williams et al., 1985).

Several genetic and demographic consequences of such an isolated, fragmented distribution are likely, including: 1) local divergence via natural selection or genetic drift; 2) little or no gene flow among isolated demes that might otherwise moderate losses of genetic variability after population crashes; and 3) little or no recolonization of isolated habitats after local extinction. Southwestern desert fishes are thus a vulnerable, "extinction prone" group due to the limited geographic range and isolation of many species.

Added to this natural fragility are major anthropogenic disturbances of two types: habitat destruction (impoundment and diversion of rivers, groundwater pumping, and drying of surface springs) and the introduction of a huge diversity of exotic fishes, many of whom prey on, compete with, or hybridize with native species (Naiman and Soltz, 1981). Management of such a fauna over the long-term must therefore consider the genetic consequences of both natural fragmentation with small population sizes, and artificial disruption by man. General and philosophical aspects of genetic management of fishes have been outlined elsewhere (Meffe, 1986, 1987; Ryman and Utter, 1987). Herein, we consider more specific approaches of genetic studies and experimental manipulations of rare and endangered southwestern fishes.

## DIVERGENCE, MIGRATION, AND GENE FLOW

Two demographic factors, genetically effective population size and migration rate, will affect the degree of divergence among local colonies of fishes. Colonies diverge from one another as a consequence of local selection pressures, mutation, and random genetic drift; drift alone can cause considerable divergence among small colonies. The rate of divergence due to drift in turn depends on the genetically effective size of the local populations ( $N$ ).  $N$  represents the number of breeding adults in each generation, and is affected by sex ratio, pattern of mating, and variance in reproductive output among individuals (Crow and Kimura 1970).

Gene flow via migration ( $m$ , or the proportion of individuals exchanged between colonies per generation) maintains genetic variation within colonies and retards divergence among colonies. Divergence occurs as a product of  $N$  and  $m$ . If  $N$  is small, colonies tend to diverge rapidly, as a result of random processes. High rates of gene flow ( $m$ ) are needed to maintain genetic homogeneity among them. As long as  $N m > 1$ , local colonies will tend not to diverge significantly with regard to the types of alleles present (Allendorf 1983). Thus, a pair of large populations with mean  $N > 10,000$  that exchange individuals at a rate of  $m = 0.001$  will not diverge significantly by chance alone, since  $N m > 10$ . However, a pair of small populations with  $N < 1000$  and with a similar rate of gene exchange would diverge, since  $N m < 1$ .

This scenario is based on the assumption that colonies are

dispersed geographically as if they were islands and gene flow can occur equally among all the islands. As we discuss below, this scenario may be an appropriate description for some aquatic systems (the Death Valley Model), but for most fresh-water fishes, riverine habitats impose a more complex population structure (the Stream Hierarchy Model).

#### ZOOGEOGRAPHIC MODELS OF GENE FLOW

We envision two models of genetical population structure in desert fishes. The existence of these different zoogeographic models must be recognized in management programs aimed at habitat restoration and restocking of fish populations.

The Death Valley Model - Death Valley and similar intermontane basins of the southwest contain a series of extremely isolated springheads and small streams that were connected in pluvial times when the basins were filled by inland lakes and seas (Miller 1948; Miller and Hubbs 1948). As a consequence of natural post-Pleistocene drying trends, these habitats now contain remnant fish populations that were formerly part of a larger interbreeding population. Presently, geographical isolation among colonies is complete ( $m = 0$ ; Fig. 1), and divergence is accelerated by small colony sizes and possibly strong, local selection pressures.

Total genetic diversity of a species in this model ( $H$ ) consists of diversity within colonies ( $H_c$ ) plus differences among colonies within the total range ( $D$ ) (Nei 1975). If a species is endemic to a single locality, then the latter term drops out

and total genetic diversity consists of heterozygosity within the single site. As colonies lose variation and become more homozygous via genetic drift, random differences among colonies also accumulate through time. Since we envision no migration ( $m = 0$ ) to counteract these processes, both the decline of  $H$  and the growth of  $D_{ct}$  are simple functions of  $N$  within colonies.

Depending on its mode of action, natural selection will alter the effects of genetic drift. Directional selection may accelerate divergence for locally adaptive traits, but divergence will be slowed for characters that are under **some** form of stabilizing or balancing selection throughout the range of the species. This model is exemplified by pupfishes (genus Cyprinodon) and killifishes (genus Empetrichthys) which are naturally isolated in many remnant springs and streams in Death Valley and adjacent basins in California and Nevada (Miller, 1948).

Considerable evidence exists for morphological, physiological, behavioral, and life historical differences among populations of desert pupfishes (Naiman and Soltz 1981), supporting this model. Turner (1974) was the first investigator to study genetic population structure in these fishes. His electrophoretic studies of pupfishes in and near Death Valley revealed little overall allelic variation. However, most variation occurred among, rather than within, these remnant populations. For example, Cyprinodon nevadensis contains three recognized subspecies that occur in isolated habitats of the Amargosa basin. Most of the thirty gene loci he examined were homozygous within

populations, but four were polymorphic in one population. Cyprinodon diabolis and C. salinas, which apparently derived from C. nevadensis since the drying of Death Valley, presently occur in single isolated habitats, and each species appears to be homozygous at most loci for alleles that occur in C. nevadensis. However, each species also contains some unique alleles that may have arisen via mutation since isolation from the presumed ancestor. Unfortunately, one cannot compute genetic diversity statistics from the data presented in Turner's pioneering study, but in general the data are consistent with our model: very little polymorphism occurs within, and considerable divergence occurs among, populations.

In managing a genetic population structure represented by the Death Valley Model, we need not be concerned with human interruption of gene flow. Such gene flow has historically not existed, at least not since ancestral lakes have desiccated. To the contrary, we should take precautions to avoid creating gene flow among populations that are naturally isolated and may therefore be in the process of adaptive radiation. Artificial gene flow would tend to reduce or eliminate genetic divergence among localities (D), which may represent a substantial proportion of the genetic diversity in the species.

The major concern for fishes in the Death Valley model is maintenance of high N within localities. Crashes due to man's intervention have occurred, jeopardizing several species' existence. In August 1969, the Owens pupfish (Cyprinodon radious) nearly went extinct when its' only known habitat



completely dried (Miller and Pister, 1971). Fortunately, some 800 fish were rescued, literally at the last minute, and held in captivity until spring flow resumed. Likewise, existence of the Devil's Hole pupfish (Cyprinodon diabolis) was jeopardized when the water level in its' single habitat was being lowered by groundwater pumping. Only a Supreme Court decision to halt development in the region restored flow, and maintained this habitat (Pister, 1979, 1985). Thus, the goal for conservation efforts of fishes in this model is simply to maintain strong, isolated populations.

A more complicated version of the Death Valley model occurs with Cyprinodon macularius in the vicinity of the Salton Sea sink in southern California. Using Turner's (1983) electrophoretic data, Echelle et al. (1987) were able to partition total genetic diversity into H and D<sub>ct</sub> components. Polymorphism within lakeshore colonies accounted for about 70% of the total genetic variance, and differences among colonies accounted for about 30%, contrary to expectations of the Death Valley model. However, this is easily explained in context of the hydrologic history in this region. These populations have been repeatedly subjected to isolation and possible reconnection during several rounds of drying and flooding in the lake basin. According to Turner (1983), Holocene Lake Cahuilla occupied this basin, followed by drying, followed by Wisconsinian Lake LeConte, followed by drying once again. From 1905 to 1907, the basin was flooded with water that broke out of the Colorado River irrigation system. Apparently, these cycles of reconnection have permitted the

maintenance of significant variation within local populations. The recent flooding of the Salton Sea sink due to human intervention may also have prevented the pattern of local differentiation observed in Death Valley.

It is instructive that the most isolated population of *C. macularius*, in Quitobaquito Spring in the upper Sonoyta basin of Arizona, does exhibit a level of genetic differentiation that is roughly comparable to that observed among Death Valley **pupfish** populations (Turner, 1983). This isolated population was recently described as a distinct subspecies, *C. macularius eremus* (Miller and Fuiman, 1987).

The Stream Hierarchy Model - The second pattern of population structure occurs in desert fish that inhabit one or more **dendritic** river systems, with varying degrees of connectedness and gene flow (Fig. 2a). In this case, local demes are only partially isolated from other gene pools, with some probability of gene flow among them. Periodic or permanent connections allow some migration and gene flow among habitats, and local population divergence is less extreme than in the Death Valley Model. A hierarchical genetic structure results, wherein higher frequencies of gene flow correspond to greater similarity among demes. This hierarchy of genetic divergence is a function of geographic connectedness of habitats: localities that are frequently connected and exchange population members will have greater genetic (and presumably phenotypic) similarities than localities that infrequently or never experience gene exchange.

In such a hierarchical system, total genetic diversity of a

species ( $H_t$ ) consists of within-colony diversity ( $H$ ) plus differences among colonies within a river ( $D_{cr}$ ) plus differences among rivers within major drainage systems ( $D_{rs}$ ) plus divergence among drainages occupied by the species as a whole ( $D_{st}$ ). More complex hierarchies may develop depending upon levels of connectivity and extent of the species' range. During wet years, patches connect and allow migration by fishes; dry years isolate habitats and stop gene exchange. Natural climatic variation thus connects and separates local demes in a hierarchical structure that is a function of geographic distance and river discharge. This model is typified by numerous species in the Gila River drainage of southern Arizona and likely represents fishes in many lotic systems in the southwest.

Interruption of the stream hierarchy by habitat alteration can change patterns of gene flow among localities and disrupt natural genetic structure in two ways. Movement of fishes among naturally isolated populations introduces gene flow that historically might not have occurred, thus decreasing  $D_{cr}$ ,  $D_{rs}$ , or  $D_{st}$ . Conversely, impoundment of rivers, pumping of springheads, or other alteration of drainage patterns can fragment and isolate populations that would normally experience gene exchange (Figure 2b). Such actions should cause a general decline in local genetic diversity ( $H$ ) and a corresponding **increase** in divergence among colonies within a drainage system ( $D_{cr}$  and  $D_{rs}$ ).

Habitat destruction and population segregation is presently the greatest threat to the preservation of genetic diversity in

river dwelling fishes of the American Southwest. Because of limited water availability, many southwestern streams have been dammed or diverted, completely changing flow characteristics and connectivity patterns (Minckley and Meffe, 1987), while extensive groundwater pumping has depleted ancient aquifers and caused many isolated springs to cease flowing (Williams et al., 1985; Pister and Unkel, in press).

An example of hierarchical population structure in an endangered fish species occurs in the Sonoran **topminnow**, Poeciliopsis occidentalis. This livebearing fish is native to the lower Colorado River drainage of Arizona and New Mexico, and several major drainages in Sonora, Mexico. It was extremely abundant through the Gila River basin of southern Arizona, including numerous springs along watercourses, as recently as the 1940's (Hubbs and Miller 1941; Minckley and Deacon, 1968; Fig. 3). A rapid decline ensued over the last four decades to the point of inclusion on the Federal Endangered Species List in 1973.

Decline of the topminnow is attributed to widespread habitat destruction, and replacement by the introduced mosquitofish (Gambusia affinis) (Meffe et al., 1983; Meffe, 1985). In 1983 the topminnow occurred in 15 natural habitats in the United States. Presently, the fish occurs in 12 natural localities in Arizona (Fig. 3), all of which are isolated headwater springs or streams, but remains abundant in Mexico where mosquitofish have not been systematically introduced.

Vrijenhoek et al. (1985) studied genetic diversity in five

remnant Arizona populations of Sonoran topminnows and 16 populations throughout its range in Mexico. In general, local diversity ( $H$ ) declined at the northern periphery of the **species'** range, and in upstream sections within rivers (Figure 4, Appendix 1). Fluctuations in population size that lead to losses of genetic variance are more likely to occur in these peripherally isolated montane localities.

This broadly distributed riverine species exhibits the expected hierarchical population structure. Pairwise genetic distances among the 21 populations (Appendix 1) were clustered by the Distance-wagner method, resulting in three genetically-defined groups (Figure 4). Group I consists of fishes in the Gila River of Arizona and rios de la Concepcion and Sonora, of Mexico. Fishes from the Rio Matape, Rio Yaqui and the lower Rio Mayo constituted group II, and fishes from the upper Rio Mayo are in group III. The first two groups correspond to morphologically-defined subspecies previously recognized (Minckley, 1973); the third group, in the partially isolated headwaters of the Rio Mayo, **was** the most genetically divergent.

We performed a hierarchical partitioning of genetic diversity using the differences among the three groups as the highest level of the hierarchy ( $D_{st}$ ). The bulk of genetic diversity in this species is represented by divergence between the three geographical groups (52.8%; Figure 4); 21.3 % of the variance is contained within colonies ( $H$ ), 25.5 % is due to differences between colonies within rivers ( $D_{cr}$ ) and only 0.4 % is attributable to differences between rivers within the major

subdivisions (D<sub>rs</sub>). This hierarchical approach, which recognizes the degree of connectedness between habitat patches, indicates that conservation of genetic diversity in this species should distinguish geographic groupings and include plans for their continued separation. Combination of fishes from different groups could erode the largest proportion of genetic variance in the species; management and manipulation should thus be conducted only within each grouping.

Sonoran topminnows have been propagated at the Dexter National Fish Hatchery near Dexter, New Mexico since 1976 for reintroduction throughout the natural range of the species in Arizona (Minckley and Jensen, 1985). At least 100 field sites had been stocked through 1985 with fishes from Dexter (Brooks, 1986; Simons, 1987).

The initial stock for hatchery breeding originated in Monkey Spring, Santa Cruz County, Arizona (site C, Fig.4). This is an isolated, thermally stable springhead in the Santa Cruz drainage that has likely not fluctuated in temperature more than 1 C for thousands of years (Constantz, 1975). Topminnows in Monkey Spring have no detectable allelic diversity at the 25 loci examined in our study (Appendix 1). This genetically invariant group also has low fecundity (Schoenherr, 1977; Constantz, 1979) and is likely to be physiologically intolerant due to its constant environment. We recommended that the hatchery stock be replaced with fish from Sharp Spring (site D), a population from the same genetic subdivision (Vrijenhoek et al. 1985). The Sharp Spring population has higher fecundity (Meffe, 1985) and growth

rate (Vrijenhoek and Sadowski, **unpubl.** data) than the Monkey Spring stock. This population is also a better candidate for broad-scale reintroduction because it naturally experiences wide environmental fluctuations (Meffe et al., 1983; Meffe, 1984), and has detectable allelic variation ( $H = 3.7\%$ ; Appendix 1). Our recommendation has been followed, and as of 1986 Sharp Spring fish constitute the hatchery stock for all introductions and experimental work within the group I region.

A special case of the Stream Hierarchy model is the situation in which a species occurs in only one river system. As in the Death Valley model, total genetic diversity can be partitioned into two components:

$$H = H + D$$

ct

Because connections can occur between neighboring stream sites during annual rainy seasons, or between more distant sites during periods of extreme flooding, we expect much less diversification among populations than was observed in Death Valley pupfishes.

Echelle and coworkers (1987) recently described such population structure for four pupfish species inhabiting streams in the Chihuahuan desert of New Mexico and Texas. Cyprinodon pecosensis is the most broadly distributed of these four species, and only 7.7% of its total genetic diversity is attributable to differences among populations spread along a 200 km portion of the Pecos River in Texas. Cyprinodon elegans and C. bovinus are each restricted to single creeks within the Pecos River drainage. The differences among local colonies ( $D$ ) that are only a few kilometers apart accounted for 10.8% (C. elegans) and 1.4% (C.

bovinus) of the total genetic diversity in each species.

Cyprinodon tularosa is restricted to several partially isolated habitats that are spread over several hundred kilometers in the Salt Creek drainage of New Mexico, and  $D_{ct}$  accounts for 19.0% of its total genetic diversity.

Assuming that the values of  $D_{ct}$  obtained for these four species reflect an equilibrium between the divergent effects of genetic drift and the convergent effects of gene flow, we can roughly estimate the effective migration rate ( $N_m$ ) among colonies from the equation  $D_{ct}/H = 1/(4N_m + 1)$  (modified from Crow and Kimura 1970). For C. tularosa,  $N_m$  is approximately 1, which can be interpreted as the equivalent of one migrant between populations per generation. The effective migration rate is much higher along the 10 km portion of Salt Creek inhabited by C. bovinus, being roughly equivalent to an exchange of 17 to 18 individuals between colonies per generation. Values for C. pecosensis and C. elegans, respectively, are 3 and 2 individuals per generation.

These estimates, however, are sensitive to the underlying model of population structure (Slatkin 1985). Although accurate in a true island situation, they likely underestimate gene flow in a hierarchical situation, and more realistic models of population structure are needed. Even if such models were available, though, it is likely that each dendritic system would have idiosyncratic properties that would require simulation to more accurately estimate gene flow. Thus, no single analytical approach would pertain in every case. Nevertheless, a useful



rule of thumb is that an exchange of one individual between populations per generation within a river system would maintain most of the allelic diversity, but would not swamp the opportunity for local adaptation (Allendorf, 1983).

Management of species such as these Cyprinodon should be aimed at preserving the integrity of each species while maintaining its genetic variability. Movement of fish of the same species among colonies within a river (except, perhaps, for C. tularosa, which has the highest  $D_{ct}$ ) would likely pose no specific problems since this appears to occur naturally. However, precautions should be taken to avoid mixing between species. If mixed, it is likely that all four of these curinodon species could hybridize (see Turner and Liu 1977; Cokendolpher 1980); introduced Cyprinodon variegatus have already hybridized with native C. pecosensis (Echelle et al. 1987).

INTO THE FUTURE - HOW DO WE PROCEED WITH MANAGEMENT OF  
SOUTHWESTERN FISHES?

The coming decades will present tremendous challenges to the manager of dwindling aquatic resources in the southwest. Continued population growth in the region will further drain limited natural resources, the spread of exotics will further impact local biota, and the status of native species will certainly continue to decline. However, careful management, based on sound genetic and ecological studies, can slow or reverse these negative trends. One of the more powerful tools in the effort to maintain healthy, diverse populations is the

application of genetic principles to management.

We particularly emphasize the need to incorporate experimental studies of population genetics and fitness into management of endangered fishes to better predict survival and long-term success of remnant populations. Such research would directly benefit the target species, and the principles could be applied to management of other taxa as well. Desert fishes provide opportunities that do not exist with most endangered species. Populations of whooping cranes, cheetahs or condors cannot be manipulated to determine optimal genetic structure. However, such studies are feasible with many endangered fishes. We thus recommend pursuit of at least three areas of experimentation that would benefit management of threatened and endangered fishes in the southwest:

- 1) Test the relationship between heterozygosity and individual fitness - Studies with a variety of organisms have resulted in a "heterozygosity concensus", the belief that overall fitness is enhanced by genetic diversity (Frankel and Soule, 1981; Mitton and Grant, 1984). However, we know little of actual mechanisms of heterozygote superiority, nor whether all species or populations are affected similarly by heterozygosity. Experimental studies of relationships between genetic diversity and growth rates, survivorship, fecundity, developmental stability and competitive ability are needed to determine the importance of maintaining populations with high heterozygosity. Such studies are currently underway in our laboratories with

**poeciliid** fishes, and early results indicate superior fitness of more heterozygous individuals in some cases; we encourage exploration of such questions in other groups.

2) Experimentally mix genetic stocks - Although we strongly discourage mixing stocks among major genetic subdivisions, we encourage stocking experiments that combine populations from within the same subdivision. Such experiments would permit evaluation of the effects of mild outcrossing, and may prove to be valuable in restocking efforts. For example, in ***P. occidentalis*** from Group I in Arizona, Cienega Creek and Monkey Spring fish are both homozygous for all loci examined (Appendix 1). Preliminary laboratory results **indicate** that Monkey Spring fish may grow slower than individuals from the more polymorphic Sharp Spring population (Vrijenhoek and Sadowski, unpubl. data). Because they are fixed for alternative alleles at two loci, crosses of Cienega Creek (CC) and Monkey Spring (MS) stocks should increase heterozygosity for these and many other loci. Tests of relative fitness of the CC/MS "hybrids", the parental stocks, and the Sharp Spring stock would indicate how outcrossing and concomitant increase in heterozygosity affects fitness. If such experimental crosses prove to be more robust than single-locality fish, their use in stocking new field sites should be considered. Existing natural localities should always remain genetically pure, however.

We have experienced some negative reactions to the suggestion of mixing stocks within a drainage system, and on one occasion were labeled "rabid interventionists". We are far too

late to be interventionists, however. Intervention has taken place over the last 50 years by numerous state and federal agencies altering watercourses to the point that they are no longer recognizable as desert aquatic systems. Intervention is the result of a rampant and uncontrolled **influx** of millions of people into the desert southwest, thus placing an extraordinary burden on surface and ground waters. Intervention has occurred through lack of an **intelligent** national land use ethic that would prohibit wholesale transformation of a biome from arid desert to mesic farmland and sprawling metropolises.

We are not interventionists, but rather "restorationists", attempting a policy that would restore a system to an approximation of its former self. In a stream hierarchical system that has undergone radical changes to the point that some natural populations are extinct and others are artificially **isolated**, we favor restoration of gene flow and diversity to mimic the natural situation, rather than maintaining an unnatural and zoogeographically perverse "status quo". Estimates of effective migration rates from genetic structure statistics can give us a rough guideline for the extent of gene flow that should be considered.

3) Test the relative roles of genetic adaptation and developmental plasticity in local phenotypic differentiation - Desert fishes are notorious for **phenotypic** differentiation among localities (Miller 1948; Minckley, 1973). This differentiation may be the result of genetic differences or plastic developmental processes influenced by the local environment. Identification of

the causes of phenotypic differentiation is important to management of individual populations. If differentiation is genetic, it is critical to maintain the diversity represented by differences among colonies (D<sub>cr</sub>). If differentiation is simply a plastic response to local conditions, then a particular phenotype may be induced from a broad range of genotypes by creating the proper environment. The latter may occur in a goodeid fish in Mexico (Turner et al., 1983), a cichlid in Cuatro Ciénegas, Mexico (Kornfield et al., 1982; Liem and Kaufman 1984), several African cichlids (Greenwood, 1965), and Arctic charr (Vrijenhoek et al. 1987). Thus, we need critical experiments that separate true genetic differentiation (local evolutionary change) from simple environmental induction of unique morphs.

#### A FINAL QUESTION

We conclude by raising a final question, one which we cannot definitively answer, but which is critical to all conservation programs. What are our objectives in conservation biology? Specifically, what should we conserve? Species? Subspecies? Individual populations? Unique alleles? This is a difficult question, and perhaps the most important philosophical issue facing us, for we cannot design effective conservation programs until we identify specific goals.

The answer may depend upon the organism of concern, and economic constraints. For a tiger or rhinoceros, we may have to settle for a representative type of the species, for it may be difficult to do otherwise, since natural and financial resources

are limiting. It is also unrealistic to expect to conduct experimental work on the genetic structure of such taxa.

However, we can do much more with desert fishes. It is far less costly to maintain regional, local or even allelic diversity in these fishes - they can be easily manipulated, local habitats are available or can be made available, and fish can be kept in small refugia such as hatcheries, or even aquaria.

In particular, the Sonoran topminnow is a model organism with which to develop a conservation program with a sound genetic basis. The topminnow is more abundant than many endangered species, and much is known about its ecology, physiology, and genetics (Constantz, 1975; Minckley et al., 1977; Schoenherr 1977; Bulger and Schultz 1982; Meffe 1984,1985; Vrijenhoek et al., 1985). It is easy to raise in captivity and hardy under field and experimental conditions. Concerted efforts in recovery of this species, currently underway by several groups, could benefit endangered species programs at large by developing sound management schemes, including application of genetic principles and field and laboratory experimentation of fitness responses to management programs. With this species at the forefront, we have an excellent opportunity to restore an entire endangered fauna to some semblance of its historical condition; as conservation biologists, this should be our goal.

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FIGURE LEGENDS

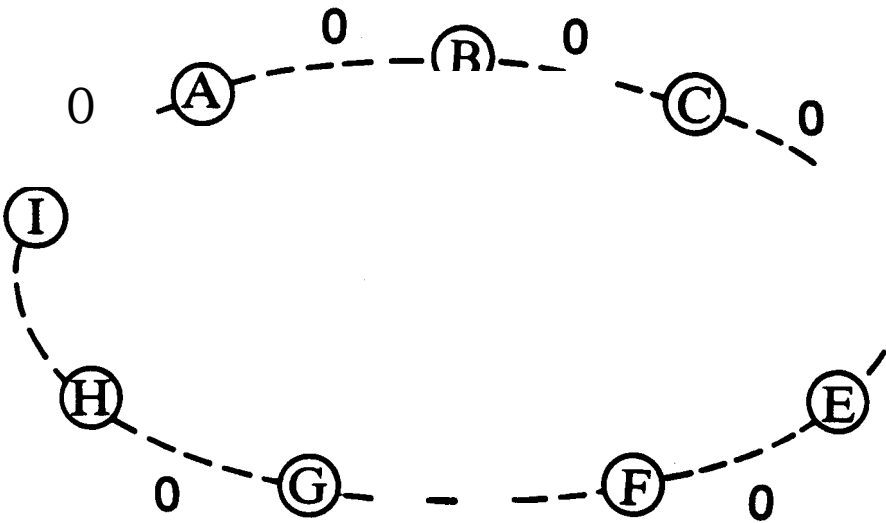
Figure 1. Graphic representation of the Death Valley model of population structure. Isolated springs and streams (represented by A - I) have no chance of natural gene flow among them ( $m = 0$ ).

Figure 2. Graphic representation of the Stream Hierarchy model of population structure. a) Hypothetical natural situation. Sites A - J represent 10 natural populations separated by various probabilities of connectivity. Sites A, B, C, E, F and H are springheads, I is a marsh, and the remainder are stream segments. Numbers refer to hypothetical probabilities of connection between that habitat and habitats further upstream over the long term. Numbers should not be interpreted as estimates of gene flow ( $m$ ). b) Hypothetical disruption of situation **illustrated** in 2a. In this case, dams and pumping of springheads have severely altered habitats and probabilities of gene flow. Two populations (D and I) are extinct, and most others have reduced connectivities.

Figure 3. Distribution of Poeciliopsis occidentalis in Arizona. The historical distribution, as of about 1940, is shaded; circles are distribution as of late 1987. Solid circles are the Gila subspecies (P. o. occidentalis, genetic group I) and open circles are the **Yaqui** subspecies (P. o. sonoriensis, genetic group II).

Figure 4. Genetic relationships among Poeciliopsis occidentalis populations. The dendrogram produced three clusters that correspond with geographical distributions on the map. (reprinted with permission from Vrijenhoek et al., 1985).

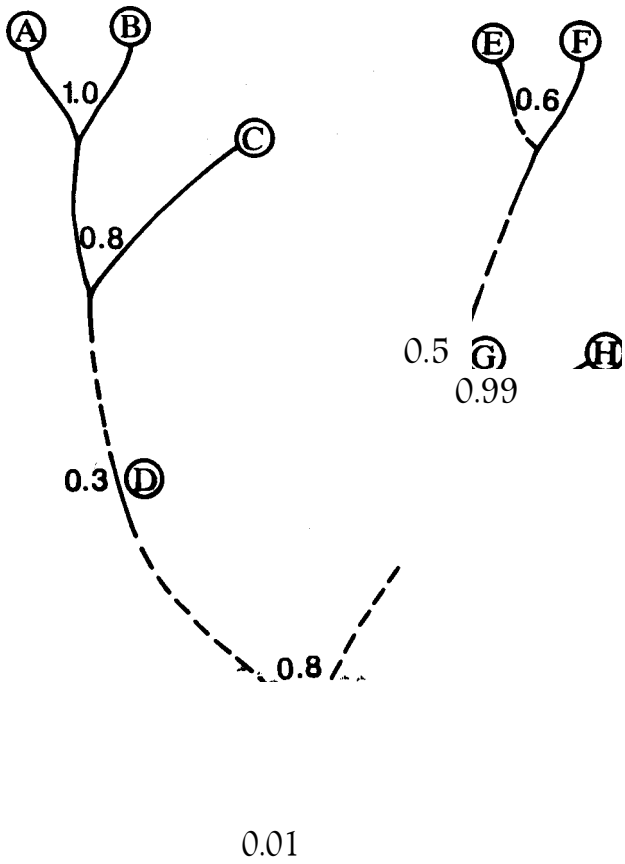
# DEATH VALLEY MODEL



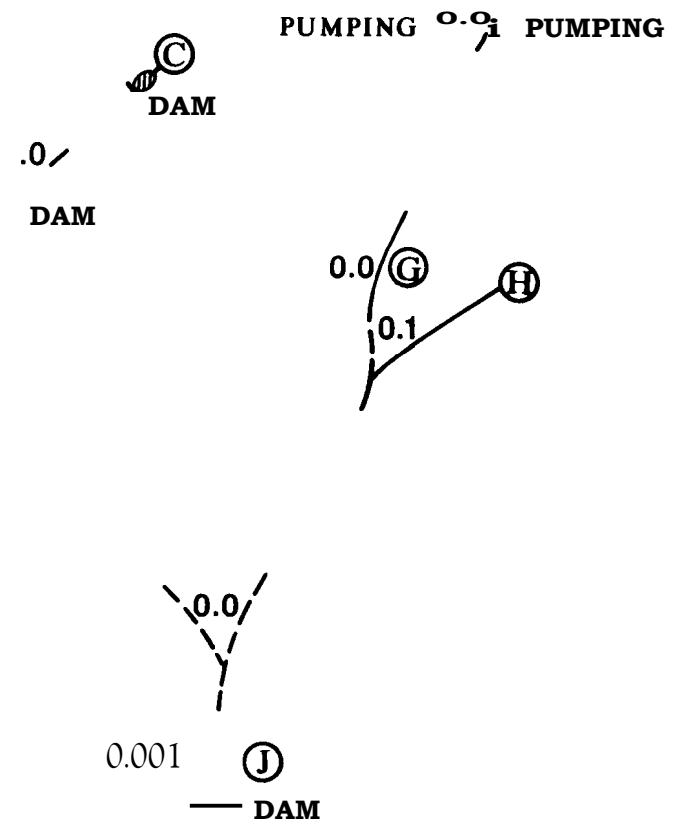
$$H_t = H_c + D_{ct}$$

# STREAM HIERARCHY MODEL

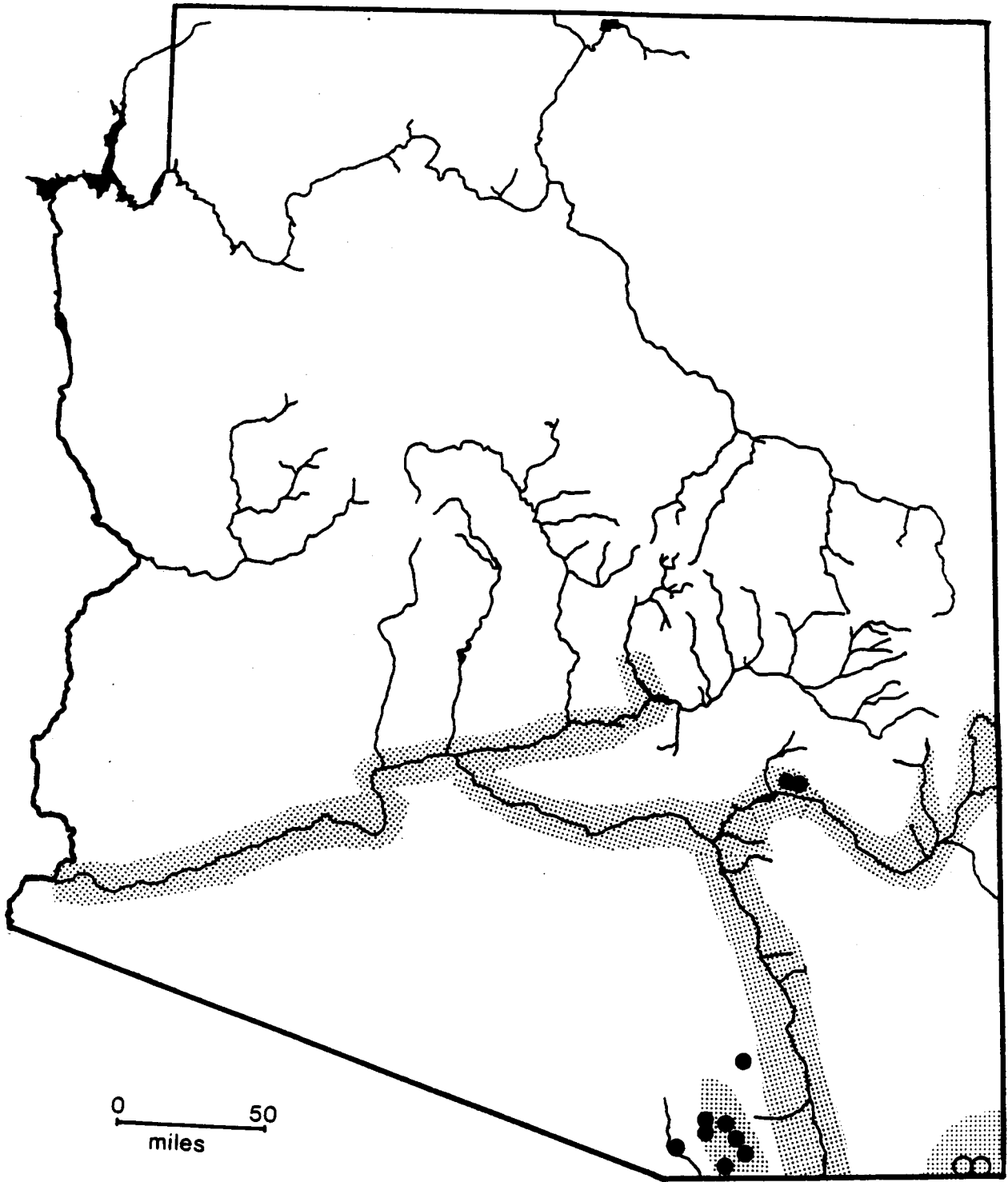
**Natural Flow**



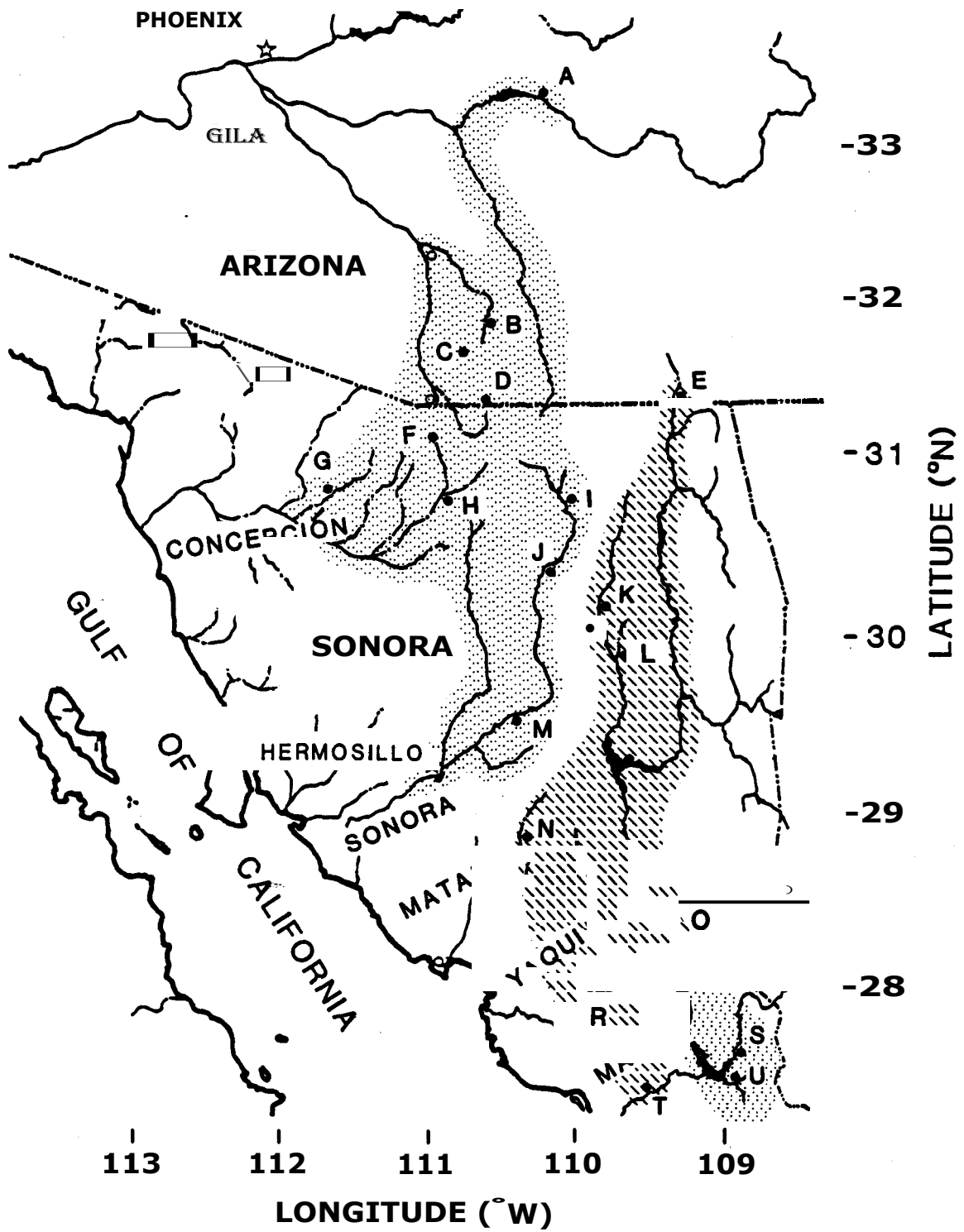
**Disrupted Flow**



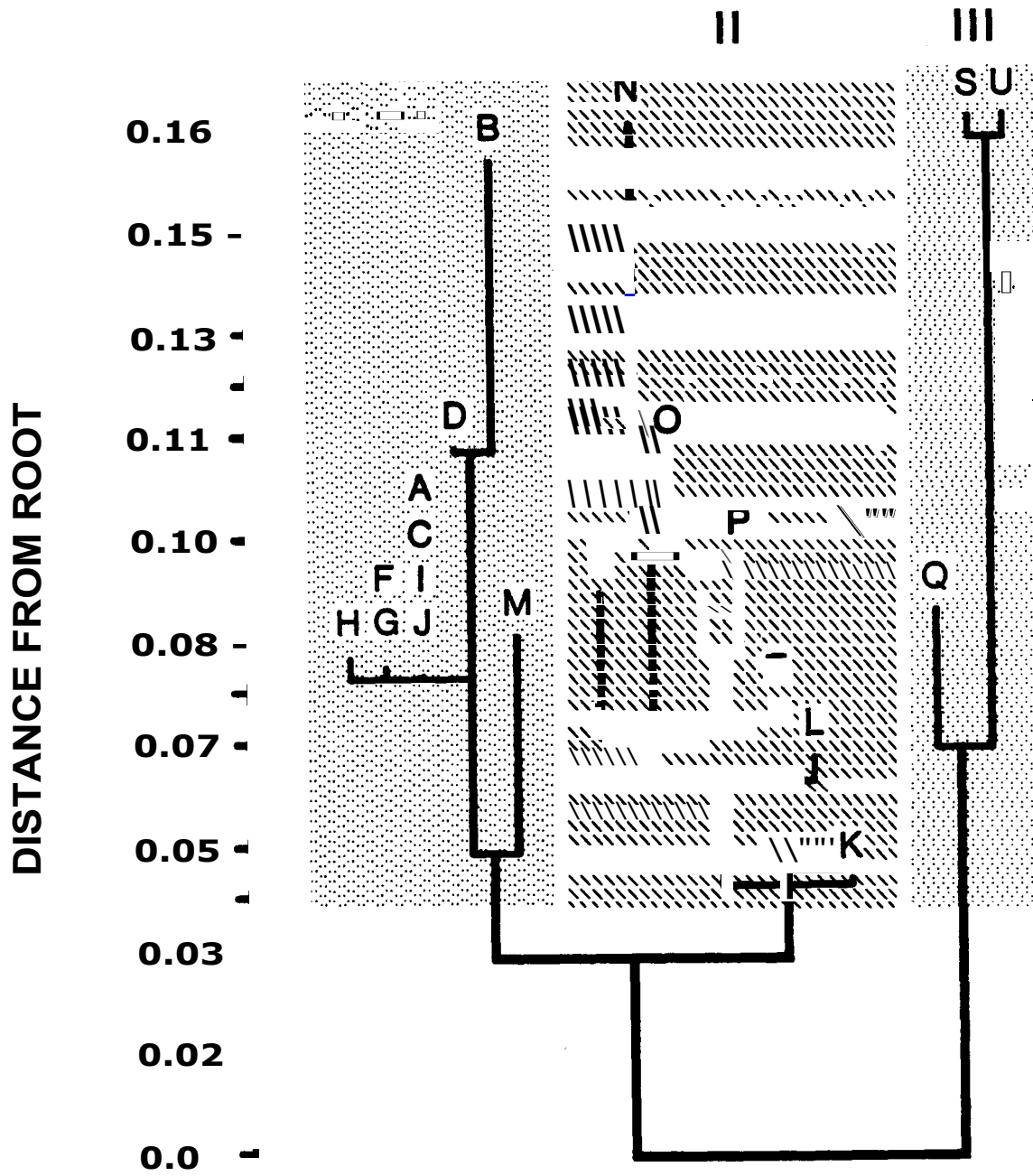
$$H_t = H_c + D_{cr} + D_{rs} + D_{st}$$







# GROUPS



Appendix 1

Allelic frequencies in *Poeciliois occidentalis* (in total, 25 loci were examined; see Vrijenhoek et al 1977). Sample size (N), percentage of loci that are polymorphic (P), and mean percentage of heterozygous loci per individual (H) are given for each site.

RIVER:	El Estero				Concepcion				Sonora			Matape		Yaqui					Mayo			
SITE#:	A	B	C	D	F	G	H	I	J	M	N	E	K	L	O	P	R	Q	S	T	U	
N:	24	22	23	62	30	68	30	30	30	60	60	24	30	44	30	30	110	30	30	30	30	
Ldh-1 a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.70	1.00	1.00	1.00	.98	.83	.76	1.00	1.00	.94	1.00	
c															.02	.17	.24			.60		
Ldh-2 b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.63	.96	1.00	1.00	1.00	1.00	
Pgd f	---	1.00	---	.55	.02										.53							
a	1.00	---	1.00	.45	.98	1.00	1.00	1.00	1.00	1.00	.79	1.00	1.00	1.00	.47	1.00	1.00	1.00	1.00	1.00	1.00	
											.21	---										
Pga a	---	---	---	---	---	.02																
b	1.00	1.00	1.00	1.00	1.00	.98	1.00	1.00	1.00	.70	---	---	.31	.21							---	
c									---	.30	1.00	1.00	.69	.79	.95	1.00	1.00	1.00	1.00	1.00	1.00	
															.05							
b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.71	.73	1.00	1.00	1.00	1.00	.90	.90	1.00	1.00	1.00	.94	
Gpi-2 a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.93	1.00	1.00	1.00	1.00	.88	.96	1.00	1.00	1.00	1.00	
Aat-3 f					---	.01	---															
b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	
Idh-1 a	---																					
b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.61	.66	1.00	1.00	1.00	1.00	1.00	.79	1.00	1.00	.99	1.00	
Mdh-1 f					---	---																
a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.96	.97	1.00	1.00	1.00	1.00	
Mdh-2 a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	---	---	.97	.01	
																				.03	.99	
Es-4 a	1.00	---	1.00	.70	1.00	1.00	1.00	1.00	1.00	1.00	.38	.42	1.00	1.00	1.00	1.00	1.00	1.00	---	.99	1.00	
																				.01	1.00	
a	1.00	1.00	1.00	1.00	1.00	1.00	.92	1.00	1.00	.73	.40	1.00	1.00	.97	.32	1.00	.96	1.00	---	1.00	---	
Sod a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.64	---											
(TO) b									---	.36	1.00	1.00	.71	1.00	1.00	1.00	1.00	---	1.00	.98	.90	
P:	0.0	0.0	0.0	8.0	4.0	8.0	4.0	0.0	0.0	20.0	32.0	4.0	12.0	16.0	12.0	20.0	28.0	0.0	0.0	20.0	12.0	
H:	0.0	0.0	0.0	3.7	2.0	.3	.7	0.0	0.0	8.7	11.6	1.5	3.2	1.1	4.2	4.4	4.0	0.0	0.0	1.2	1.4	

\* Sites: (A) Bylas Spring; (B) Cienega Creek; (C) Monkey Spring; (D) Sharp Spring; (E) San Bernadino Nildlife Refuge; (F) La Atascosa Cienga; (G) Rio Altar; (H) Rio Alisos; (I) Rio Bocobachi; (J) Rio Arizpe; (K) Cuapas; (L) Rio Moctezuma; (M) Ures; (N) San Jose de Pima; (O) Rio Nuri; (P) Agua Caliente; (Q) Rio Cedros; (R) Est. Corrat; (S) San Bernardo; (T) Navojoa; (U) El Tabeo.