by secretion. Vasopressin stimulation might cause the atria to release the high molecular weight prohormone, which then undergoes proteolytic conversion in the plasma. However, Trippodo *et al.* (*13*) recently reported that the high molecular weight peptide extracted from rat atria is not converted to the low molecular weight peptide when incubated in rat plasma at 37°C. In addition, the fact that the perfusate from isolated hearts (*8, 10, 11*) and rat plasma contain only low molecular weight peptides (Fig. 2) (*6–8*) strongly suggests that proteolytic conversion occurs within the heart itself. Prohormone processing enzymes associated with membrane structure or secretory granules have been identified for a number of peptides including pro-opiocortin, somatostatin, glucagon, insulin, and adrenocorticotropic hormone (*14*).

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Conservation Genetics of Endangered Fish Populations in Arizona

Abstract. *Genetic diversity in remnant populations of the Sonoran topminnow* Poeciliopsis occidentalis *(Pisces: Poeciliidae) from Arizona, where the species is endangered, is compared with that in populations from Sonora, Mexico, where the fish is widespread and abundant. Geographically peripheral Arizona populations contain substantially lower levels of genetic variation than do Mexican populations near the center of the species' range. Allelic differences among three genetically and geographically distinct groups are responsible for 53 percent of the total genetic diversity in this species, 26 percent is due to differences among local populations within the groups, and 21 percent is due to heterozygosity within local populations. Recommendations for conservation and restocking efforts in Arizona are based on these genetic findings.*

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Alteration and destruction of natural habitats by human activities threatens many plant and animal species. Beyond the immediate possibility of extinction for geographically restricted and endemic forms, there is a more subtle threat: erosion of the genetic diversity upon which long-term persistence and adaptability depend. Habitat destruction can subdivide a species into a series of small, partially isolated demes (local populations) that may lose genetic variability through inbreeding and random genetic drift. Erosion of genetic variability may contribute to an immediate reduction in fitness and to constraints on future adaptive potential (*1*). Knowledge of the distribution of genetic variation within and between remnant populations of an endangered species is necessary if we are to design sound conservation programs (*2*).

The arid southwestern United States is a critical region for conservation of aquatic organisms because ground-water pumping, stream modifications, and widespread introduction of exotics have extensively disrupted the natural habitats of numerous endemic species (*3, 4*). For example, the Sonoran topminnow, *Poeciliopsis occidentalis*, was once the dominant fish in lowland streams, springs, and marshes of the Gila river system in Arizona (*5*). During the past 40 years, habitat destruction coupled with introduction of nonnative predaceous fishes, particularly the mosquito fish, *Gambusia affinis* (*4, 6*) have reduced formerly large and widespread populations of *P. occidentalis* to small, geographically isolated demes inhabiting tiny headwater springs and stream segments (*4*). In 1973 *P. occidentalis* was placed on the federal Endangered Species List (*7*). An effective conservation program for endangered Arizona populations requires not only familiarity with their regional ecology but also a broad knowledge of their genetic structure, including populations in Sonora, Mexico, where the species remains abundant. We report on the distribution of genetic variation in 5 Arizona and 16 Sonoran populations of *P. occidentalis*.

We surveyed the products of 25 protein-determining gene loci for electrophoretic variation, and 12 loci exhibited polymorphic phenotypes (*8*). Genetic variability is greatest near the center of the species' range, in populations inhabiting the Rió Matape and lower Río Sonora and Rió Yaqui (Table 1). Variability decreases at the northern periphery of its distribution and in upstream portions of most rivers. Numerical fluctuations in population size that lead to genetic drift and a loss of genetic variability are generally thought to be more severe in partially isolated peripheral populations (*9*). Although the immediate consequences of low heterozygosity in Arizona populations of *P. occidentalis* are not known, studies of a variety of organisms (including a related species of *Poeciliopsis*) indicate that growth rate, developmental stability, survivorship, and competitive abilities may be negatively affected (*1, 10*).

To assess relations among the 21 populations, pairwise genetic distances were computed from allelic frequencies and then clustered by the Distance-Wagner method (*11*). Three major groups were apparent in the resulting dendrogram (Fig. 1). Groups 1 and 2 correspond with morphologically defined subspecies that have previously been recognized in Arizona (*12*). Group 3, the most divergent group, inhabits partially isolated headwater tributaries of the Río Mayo above a man-made impoundment. However, differences among these groups cannot be attributed to recent disturbances. For example, the timespan necessary to explain genetic divergence between groups 2 and 3 is roughly equivalent to 2.8 million years; it is 1.7 million years for groups 1 and 2, and 4.3 million years for 1 and 3 (*13*). These estimates are consistent with the Pliocene–early Pleistocene separation of these drainage basins (*14*). Groups 1 and 2 intergrade in the Río Matape and the lower Río Sonora (locations M and N in Fig. 1), where populations are polymorphic for alleles that would elsewhere be diagnostic of the two groups. The multivariate coefficient of variation for morphological components also is highest at these sites (*15*), again suggesting intergradation. Opportunities for intergradation are provided by periodic flooding of rivers on the coastal plain of Sonora (*16*), but admixture is less likely in upstream montane areas. For example, the Gila river tributaries in Arizona are separated by impoundments and isolated dry reaches that contain some of the genetically least variable populations of *P. occidentalis* (Table 1). Similarly, low heterozygosity occurs in group 3 populations, which inhabit intermontane basins and are isolated by a manmade impoundment. The downstream Río Mayo population (location T) is more closely related to coastal plain populations of the adjacent Río Yaqui than to upstream populations (locations Q, S, and U) in its own river system.

For a geographically subdivided species such as *P. occidentalis*, genetic diversity must be evaluated within and among constituent populations. Total genetic diversity of a species can be partitioned hierarchically as follows (*17*)

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

where H_t is total diversity, H_c is genetic diversity within local colonies, D_{cr} is diversity found between colonies within rivers, D_{rs} is diversity observed between rivers within major subdivisions (groups 1, 2, and 3), and D_{st} is diversity between the groups. The importance of each hierarchical component can be expressed as a percentage of the total diversity (mean H_t for 25 loci = 0.107). Thus, divergence among the three geographical groups (D_{st}) contributes 52.8 percent of the total diversity in *P. occidentalis*. Remaining diversity is partitioned into 25.5 percent

Table 1. Genetic variability in *Poeciliopsis occidentalis*. The two measures of variability are P, the percentage of polymorphic loci per population, and $\overline{H}$, the mean percentage of heterozygous loci per individual.

Population		Sample size	Percentage of loci	
			P	$\overline{H}$
	Gila River			
A	Bylas Spring	24	0	0
B	Cienega Creek	22	0	0
C	Monkey Spring	23	0	0
D	Sharp Spring	62	8.0	3.7
	Río de la Concepción			
F	La Atascosa Cienega	30	4.0	2.0
G	Río Altar	68	8.0	0.3
H	Río Alisos	30	4.0	0.7
	Río Sonora			
I	Río Bocobachi	30	0	0
J	Río Arizpe	30	0	0
M	Ures, Sonora	60	20.0	8.7
	Río Matape			
N	San José de Pima, Sonora	60	32.0	11.6
	Río Yaqui			
E	San Benardino Ranch, Arizona	24	4.0	1.5
K	Cumpas, Sonora	30	12.0	3.2
L	Río Moctezuma	44	16.0	1.1
O	Río Nuri	30	12.0	4.2
P	Agua Caliente, Sonora	30	20.0	4.4
R	Est. Corral, Sonora	110	28.0	4.0
	Río Mayo			
Q	Río Cedros	30	0	0
S	San Bernardo, Sonora	30	0	0
T	Navojoa, Sonora	30	20.0	1.2
U	El Tabelo, Sonora	30	12.0	1.4

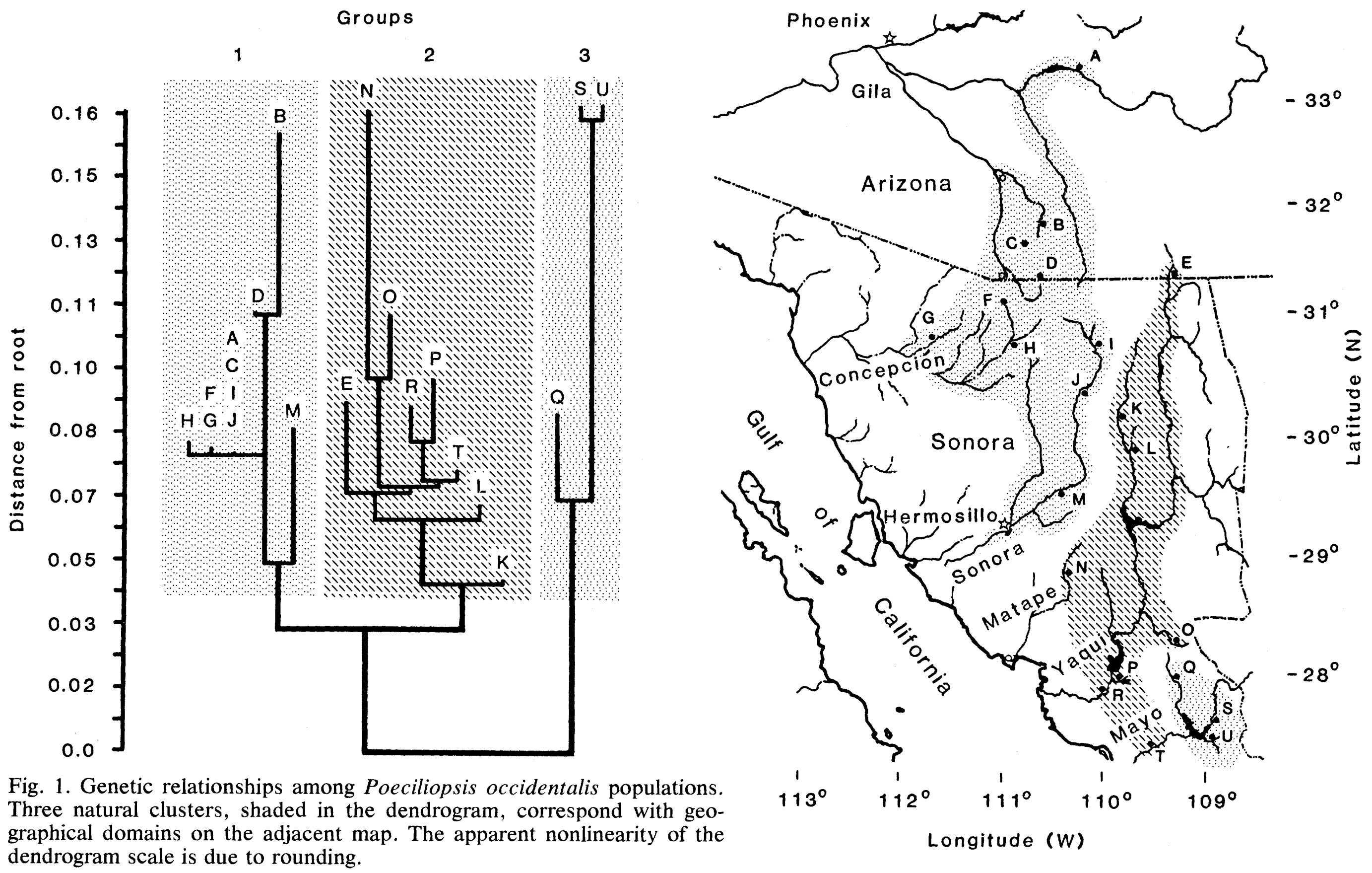

Fig. 1. Genetic relationships among *Poeciliopsis occidentalis* populations. Three natural clusters, shaded in the dendrogram, correspond with geographical domains on the adjacent map. The apparent nonlinearity of the dendrogram scale is due to rounding.

between colonies within rivers (D_{cr}), and 21.3 percent within colonies (H_c). Differences between river systems within the major groups (D_{rs}) are negligible (0.4 percent).

Management of the endangered Arizona populations is proceeding at several levels. Remaining natural habitats in Arizona are protected from future development, and efforts to control the predaceous and exotic *G. affinis* are under way (*18*). Several springs and marshes within the Gila drainage are being restocked with *P. o. occidentalis* derived from a hatchery population originating at Monkey Spring (location C) (*19*). Although restocking is a logical step toward maintaining this species in Arizona, the current plan has a flaw. Monkey Spring is a thermally stable, isolated springhead, and the resident fish are genetically invariant by our criteria (Table 1). In addition, topminnows from Monkey Spring display low fecundity (*20*). A better choice for restocking might be wild or first generation fish from a thermally fluctuating natural environment such as Sharp Spring (location D). These topminnows are genetically the most variable of the Arizona populations (Table 1), and females show high fecundity (*6*).

It is critical that the three major groups of *P. occidentalis* remain discrete in nature since 53 percent of the genetic diversity in this species results from intergroup differences. Hence, repopulation efforts in extreme southeastern Arizona should employ stocks from San Bernardino Ranch, Arizona (location E), or other localities within the upper Yaqui basin of Mexico (group 2). However, experimental mixing of stocks within each of the groups could increase local genetic diversity. Intragroup hybrids might prove to be more successful colonists than any stock deriving from a single population. Localized intragroup mixing could reverse effects of population subdivision caused by recent habitat destruction. Time for experimental studies of hybridization, fitness, and adaptive plasticity with most endangered species is limited. Yet such studies are feasible with this small, short-lived, viviparous fish, and conservation efforts based on genetic knowledge of remnant populations are possible.

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Reciprocal Inhibition and Postinhibitory Rebound Produce Reverberation in a Locomotor Pattern Generator

Abstract. *The central pattern generator for swimming in the pteropod mollusk* Clione limacina *consists of at least four pedal interneurons, two each controlling parapodial upstroke and downstroke. The two sets of antagonistic interneurons are linked by reciprocal monosynaptic inhibitory synapses, and all exhibit apparently strong postinhibitory rebound. This simple neuronal network produces reverberating alternate cyclic activity in the absence of tonic drive or apparent feedback modulation.*

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Patterned rhythmic activity can be generated in neuronal circuits in two ways, by including endogenously active neurons in the circuit (endogenous oscillators) or by making specific synaptic connections between neurons that are not spontaneously active (network oscillators) (*1*). In the latter case patterned activity is shaped not only by network synaptic interconnections, but also by intrinsic properties of central pattern generator neurons and, in many cases, by tonic or phasic drive from outside the pattern generator. In perhaps the simplest circuit capable of generating an alternating two-phase activity cycle [two antagonistic neurons connected by reciprocal inhibitory connections (*2*)], both intrinsic burst-terminating properties of component cells and an overall tonic drive to the network are necessary for the production of continuous alternating activity (*1*). The addition of another intrinsic membrane property (postinhibitory rebound) to a similar two-phase circuit generates stable cyclic activity without tonic drive in a computer-modeled network (*3*). Postinhibitory rebound contributes to the generation of rhythmic activity in a number of central pattern generator circuits (*4*). Here I report on a central pattern generator network that includes reciprocal inhibitory connections between antagonistic pattern generator interneurons, each of which exhibits strong postinhibitory rebound. This network produces continuous, stable oscillations in the apparent absence of (i) tonic drive to the network and (ii) intrinsic oscillating properties of member neurons. The network directly controls swimming in the pteropod mollusk *Clione limacina*.

Forward or hovering swimming in *Clione* is accomplished by alternate dorsal and ventral flexions of a pair of laterally projecting winglike parapodia. Swimming is a continuous, spontaneous activity. High-speed film analyses indicate that the two wings move in synchrony with virtually symmetrical upstroke and downstroke movements (*5*). The pattern generator for flapping wing move-