Conservation Genetics and the Management of Endangered Fishes

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"... wild species must have available a pool of genetic diversity if they are to survive environmental pressures exceeding the limits of developmental plasticity. If this is not the case, extinction would appear inevitable." (Frankel 1983, p. 3).

ABSTRACT

The emerging field of endangered fishes management has yet to fully incorporate conservation genetics into recovery programs. Genetic aspects of small populations must be considered at the outset of management programs in order to maximize probability of their long-term survival and continued adaptability. Total genetic variance of a species consists of within population genetic diversity, and the differences found among populations; both types of variance should be maintained to maximize adaptive flexibility of endangered fishes. Forces that erode genetic variation include small population size, population bottlenecks, genetic drift, inbreeding depression, artificial selection in captivity, and mixing of distinct genetic stocks. These can lead to increased homozygosity, loss of quantitative variation, and exposure of deleterious recessive alleles, all of which may reduce fitness. Suggestions for genetically sound management of endangered fishes include genetic monitoring of natural and captive populations, use of large numbers for captive breeding where feasible, selective mating to avoid inbreeding where necessary, minimization of time in captivity, and separate maintenance of distinct stocks.

Since passage of the Endangered Species Act in 1973, fisheries scientists have dealt with the problem of maintaining declining populations of rare fishes. These organisms have been intensively studied under natural conditions (Minckley 1973, 1983; Naiman and Soltz 1981; Meffe et al. 1983), have been reared extensively in captivity for restocking in native habitats (Toney 1974; Hamman 1981, 1982a, 1982b; Johnson and Rinne 1982), and are the objects of large investments of money and manpower. However, the field of endangered fishes management is new and still largely experimental. For example, there is only one hatchery facility for endangered fishes, located at the Dexter National Fish Hatchery (DNFH), New Mexico, established in 1974. Extensive experience in recovery work is generally lacking, and many conservation efforts are by necessity trial-and-error attempts at saving a species from immediate extinction, without full regard for long-term prospects of survival.

As experience in conservation of rare fishes accrues and recovery plans are devised and implemented, it is appropriate to address genetics in the welfare of endangered fishes. Until now little attention has been paid to long-term genetic health of rare fishes. This is understandable since some recovery efforts have been eleventh hour, unplanned attempts at avoiding extinction (e.g., Hubbs and Brodrick 1963; Miller and Pister 1971). As the science of endangered fish conservation matures it is imperative that a genetic foundation underpins recovery efforts, since long-term conservation of any endangered species will likely fail if genetic aspects are ignored at the outset (Frankel and Soul6 1981).

My purposes here are two-fold. First, in a primarily theoretical treatise, I call to the attention of endangered fishes managers the nature of potential genetic problems in management programs. Second, I suggest courses of action as first approximations toward minimization of genetic deterioration of an endangered stock. Detailed plans should eventually be based upon experience gained with early recovery programs, with collaborative input from population geneticists, aquaculturists, and others with pertinent expertise.

Several caveats must be made at the outset. First, the literature on genetics of endangered fishes is very small. Consequently, basic principles were derived from other taxa and from a variety of fields including aquaculture, sport fisheries, animal husbandry, zoo care, and population genetics. Second, there is a decided bias in this work toward southwestern fishes, due to both my own familiarity with that region, and the fact that 61% of U.S. fishes originally listed as endangered are endemic to the southwest (Johnson and Rinne 1982). Third, this paper is concerned only with genetic aspects of conservation, with no comment on other factors that will have strong bearing on management decisions such as economic, political, or social constraints. I fully recognize that budgetary and facility limitations may severely restrict the extent to which theoretical genetic con-
The central problem in conservation genetics is loss of genetic variation resulting in erosion of evolutionary flexibility. This potentially leads to a poorer match of organism to environment, increasing the probability of extinction (Simpson 1953). Managers of endangered species are presented with remnants of a formerly larger, more diverse gene pool, and are charged with maintaining that pool in the face of continued environmental deterioration. Our major concern should be maintenance of existing genetic variance since evolutionary flexibility is a function of genetic diversity (Fisher 1930; Simpson 1953). Total genetic variation within a species can be separated into at least two components (Chambers and Bayless 1983; Hamrick 1983). First, is variation within individual populations (demes) upon which natural selection acts. If this variation is reduced, there is less of a basis for future selective change (adaptation) within populations. Second, is variation among different populations. Loss of variation at this level results in convergence of populations toward one "type" and a narrower range of "options" for the species. Both types of variation should be maximized to maintain full potential for evolutionary change within a species.

**Goals of Endangered Fishes Management**

Management of endangered fishes should be compatible with three conservation goals: maintenance of viable populations in the short term (= avoidance of extinction), maintenance of the capacity of fishes to adapt to changing environments, and maintenance of the capacity for continued speciation (Soule 1980). Extinction avoidance is the first and obvious goal of any conservation program, and is the most obvious aspect of conservation efforts. However, managers should not be satisfied simply with attainment of this goal. Since all environments ultimately change and will probably change at an ever-increasing rate through man's influence, conservation programs must also maintain the capacity of fishes to genetically adapt (i.e., evolve). This is a long-term goal that is critical to species maintenance *in perpetuity* (Frankel and Soule 1981), and is the primary focus of conservation genetics. Finally, the ultimate aim of conservation programs should be the capacity for continued speciation. When confronted with only a few remaining individuals of an endangered species, it may seem ludicrous to be concerned with anything but the immediate salvage of that genome. However, ignoring long-term goals will only postpone the inevitable: extinction of a unique genetic line that is the result of millions of years of continuous evolution. Serious conservation efforts must consider the ultimate, long-term goal of continued evolution. "The sights [of a conservation program] often are set for the short term, although perpetuity is its ultimate objective. Genetic wildlife conservation makes sense only in terms of an evolutionary time scale. Its sights must reach into the distant future" (Frankel 1974, p. 54).

### The Central Problem

The central problem in conservation genetics is the loss of genetic variation resulting in erosion of evolutionary flexibility. This potentially leads to a poorer match of organism to environment, increasing the probability of extinction (Simpson 1953). Managers of endangered species are presented with remnants of a formerly larger, more diverse gene pool, and are charged with maintaining that pool in the face of continued environmental deterioration. Our major concern should be maintenance of existing genetic variance since evolutionary flexibility is a function of genetic diversity (Fisher 1930; Simpson 1953). Total genetic variation within a species can be separated into at least two components (Chambers and Bayless 1983; Hamrick 1983). First, is variation within individual populations (demes) upon which natural selection acts. If this variation is reduced, there is less of a basis for future selective change (adaptation) within populations. Second, is variation among different populations. Loss of variation at this level results in convergence of populations toward one "type" and a narrower range of "options" for the species. Both types of variation should be maximized to maintain full potential for evolutionary change within a species.

**Within-Population Variance**

Population size is the single most important factor in sustaining a high level of genetic variation within a deme (Soule and Wilcox 1980; Frankel and Soule 1981). However, a simple population census (N) alone is not indicative of the genetically effective population size (Ne), for many individuals may be pre- or post-reproductive and others may contribute nonproportionally to the next generation. Thus, Ne, defined as "the size of an idealized population that would have the same amount of inbreeding or of random gene frequency drift as the population under consideration" (Kimura and Crow 1963), is utilized in population genetic analyses. Ne is nearly always less than N because of three factors:

1. Sex ratio—If the sex ratio of breeding adults departs from 1:1, Ne and genetic variation are reduced. The effective population size with respect to sex ratio is determined as
   \[ \text{Ne} = \frac{4 \cdot Nm \cdot Nf}{Nm + Nf} \]
   where Nm and Nf are the number of breeding males and breeding females, respectively (Frankel and Soule 1981). For example, with a population census of 100 fish, we can compare Ne under the condition of 50 males and 50 females, versus 10 males and 90 females. For the former, \( Ne = 4(50)(50)/100 = 100 \) fish. In the latter, \( Ne = 4(10)(90)/100 = 36 \). A population of 50 males and 50 females is nearly 2.8 times larger, in a genetic sense, than is one of 10 males and 90 females.

2. Progeny distribution—In an idealized population, the number of offspring per family is distributed in a Poisson fashion (Senner 1980; Frankel and Soule 1981). Deviations from this distribution, with some matings producing disproportionately more offspring, will bias the representation of contributed gametes in the next generation and thereby lower Ne. A biased progeny distribution will affect Ne as \( Ne = \frac{4N}{(2 + \sigma^2)} \) (Franklin 1980), where \( \sigma^2 \) is variance in progeny distribution. For example, if 1000 breeding females reproduced in a Poisson fashion with a mean of two offspring and a variance of two (in a Poisson distribution, variance = mean), \( Ne = \frac{4(2000)}{2 + 2} = 2000 \). However, if one female produced 1001 offspring, and the remaining 999 fish produced one each, the mean remains at two, but variance is now 31.6 and \( Ne = \frac{4(2000)}{2 + 31.6} = 238 \). The effective population size of the next generation is thus drastically reduced by disproportionate offspring production.

3. Population fluctuation—Whenever a population declines, the genetic variance for all future generations is contained in the few survivors. Since those individuals represent only a sample of genetic variance contained in the original population, Ne is reduced by fluctuations to low levels. Ne
is affected as the harmonic mean of population sizes in each generation, or $1/Ne = 1/t (1/N_1 + 1/N_2 + \ldots + 1/N_t)$, where $t = \text{time in generations}$ (Franklin 1980). Comparison of the following two populations illustrates the importance of fluctuations to $Ne$. In the first, there are 100 fish for each of 5 consecutive generations, for an arithmetic mean of 100; $1/Ne = 1/5 (1/100 + 1/100 + 1/100 + 1/100 + 1/100) = .01$, and $Ne = 100$. In the second case, the arithmetic mean is also 100, but the population fluctuates each generation as follows: 100, 10, 300, 10, 80; $1/Ne = 1/5 (1/100 + 1/10 + 1/300 + 1/10 + 1/80) = .045$, and $Ne = 22$. In this case, $Ne$ for five generations is reduced by 78% through population crashes.

The importance of $Ne$ to population genetic structure is immediately realized in consideration of three closely related problems of small populations: bottlenecks, drift, and inbreeding.

**Genetic Bottlenecks.** A bottleneck is a sudden and dramatic decline in numbers (Nei et al. 1975). Bottlenecks effectively sample (although not necessarily randomly) a few individuals from a larger gene pool, resulting in a remnant population with less overall variation. The degree to which the new population is genetically depauperate will depend at least on genetic diversity of the source population, size of the bottleneck, and the degree of randomness of selection of individuals.

Loss of variation during a bottleneck has two components (Nei et al. 1975). First, is reduction in variance of quantitative traits. The proportion of quantitative variation remaining after a single bottleneck is approximately $1 - \left(\frac{1}{2N}\right)^t$, where $N$ is the number of individuals surviving (Frankel and Soulé 1981). A small number of individuals contains most of the genetic variation of a source population (Fig. 1): two individuals contain 75% and 10 contain 95%. Therefore, unless a bottleneck is very severe or is prolonged over several generations, it will not drastically reduce the amount of quantitative variation.

Second, and more critical, is loss of specific, and usually rare alleles in a bottleneck (Denniston 1978). Alleles at frequencies of, say, 5% or less, contribute little to overall genetic variance, but may periodically be important to the population as a whole (Frankel and Soulé 1981). Figure 2 illustrates the effect of bottlenecks of various sizes on rare alleles, assuming a locus with initially six alleles at frequencies of .90, .02, .02, .02, .02 and .02. With a bottleneck population size of 10, there would be an average loss of more than three alleles at this locus. Considering the repetition of this loss over hundreds or even thousands of similarly variable loci, such losses can be considerable.

**Genetic Drift.** Genetic drift is random change in gene frequency due to sampling error in small populations (Li 1976). It is, in effect, a prolonged bottleneck leading to repeated loss of variance until, in its ultimate form, all loci are fixed, with complete absence of genetic variance. Even in the presence of moderate selection pressures, drift can be a potent force in small populations (Wright 1931, 1948).

The depletion of genetic variation through drift is estimated by $\left[1 - \left(\frac{1}{2N}\right)^t\right]$, where $t$ is the number of genera-

![Figure 1. Proportion of original genetic variance remaining in populations of various sizes after a single bottleneck.](https://example.com/figure1.png)

![Figure 2. Expected number of alleles present after a single bottleneck in populations of various sizes, derived from a source population with six alleles at frequencies of .90, .02, .02, .02, .02 and .02. Expected number of alleles remaining at a locus is calculated as $E(n) = m - \sum (i - p_i)p_i$, where $m = \text{original number of alleles}$ and $p_i$ is the frequency of the $i$th allele (from Denniston 1978).](https://example.com/figure2.png)
tions at population size N (Frankel and Soulé 1981). This formula, and the concept of genetic drift, simply represents a chronic bottleneck. However, whereas a bottleneck may do little harm in one generation, a prolonged bottleneck can seriously reduce variance (Fig. 3). The longer the period of drift, and the smaller the population, the greater will be the loss of variance. For example, only 60% of original variance will remain in a population of 10 after 10 generations. A population of 100 will retain 95% in that time, but if followed for 100 generations (only 100 years in an “annual” fish), variance is reduced to 60.6%. For 1000 years this value drops to 0.67%. Clearly, drift can be quite detrimental to long-term genetic health in small populations. Even in the short term, drift can significantly reduce proportion of polymorphic loci (P), average number of alleles per locus (Ma), and average heterozygosity per individual (H). For example, a hatchery stock of Montana west-slope cutthroat trout (Salmo clarki lewisi), derived 14 years earlier from approximately 60 wild individuals, exhibited reductions of 57% (P), 29% (Ma), and 21% (H) compared with the original stock (Allendorf and Phelps 1980). Other studies of natural (Avise and Selander 1972; Vrijenhoek 1979; Vrijenhoek and Lerman 1982) and captive (Ryman and Stahl 1980; Cross and King 1983; Taniguchi et al. 1983) populations of fishes also illustrate the importance of drift.

**Inbreeding Depression.** Inbreeding depression is possibly the most serious and yet most nebulous problem facing managers of endangered fishes. Inbreeding, or consanguinity, is defined as the mating of individuals related by common ancestry (Jacquard 1975; Falconer 1981), that is, those that share more genes in common due to descent than individuals randomly selected from the population. It is a relative concept because the degree of consanguinity is considered relative to that of a base population, and thus there is no absolute measure of inbreeding. The most useful measurement is the increase in inbreeding per generation, expressed as \[ \Delta F = \frac{1}{2Ne} \]. This formula illustrates that a smaller effective population size is more susceptible to inbreeding effects (Fig. 4).

Contrary to random drift and bottlenecks, inbreeding does not affect overall genetic variance in the population per se. Rather, inbreeding results in a predictable increase in homozygous genotypes (Frankel and Soulé 1981) differentially affecting different traits. Fitness characters (those related to reproduction, Robertson 1955) and others with low heritabilities (Falconer 1981) are most affected by consanguinous matings. Consequently, such traits as fecundity, fertility, age at maturity, clutch size, growth, or survivorship will be greatly depressed by inbreeding (Bowman and Falconer 1960; Wright 1977; Senner 1980). Data from domesticated animals demonstrate that a \( \Delta F \) of 10% will result in a 5–10% decline in individual reproductive traits; if total reproductive performance is considered in aggregate, this may amount to an overall 25% decrease (Frankel and Soulé 1981). This is an unacceptable level of depression, particularly if it occurs over an extended number of generations. Franklin (1980) and Soulé (1980) suggest that a 1% level of inbreeding is tolerable in the short term, amounting to an effective population size of 50. Population sizes in excess of 500 are suggested for the long term.

![Figure 3. Proportion of original genetic variance remaining in populations of various sizes after 1 to 10 generations.](image)

![Figure 4. Inbreeding depression as a function of Ne. A selfing hermaphrodite would have 50% of its heterozygous loci become homozygous each generation as a result of inbreeding. A population of 10 would experience a 5% increase in homozygosity each generation.](image)
Data on inbreeding effects in fishes are impressive, and include severe body deformities, growth reduction, behavioral changes, and reproductive failures in such forms as convict cichlids, *Cichlosoma nigrofasciatum* (Winemiller and Taylor 1982), carp, *Cyprinus carpio* (Moav and Wolfarth 1963, ref. in Mrakovic and Haley 1979), zebra fish, *Brachydanio rerio* (Mrakovic and Haley 1979), brook trout, *Salvelinus fontinalis* (Cooper 1961), and rainbow trout, *Salmo gairdneri* (Aulstad and Kittelson 1971; Gjerde et al. 1983; Kincaid 1983). Although species and populations differ markedly in their resistance to inbreeding depression (Ralls et al. 1979; Frankl 1980), and magnitude of inbreeding effects cannot be predicted beforehand, "... the unavoidable conclusion is that relatively small amounts of inbreeding can do tremendous damage to the reproductive potential and productivity of a fish stock." (FAO/UNEP 1981, p. 10).

A different conservation genetics problem is the imposition, knowingly or otherwise, of *artificial selection* upon a wild stock, leading to a state of domestication (Brisbin 1974). That fish respond by genetic change to selection in captivity is well established in salmonids (Vincent 1960; Donaldson 1970; Kincaid et al. 1977) and other groups (Moav et al. 1978; Hynes et al. 1981). By relaxing natural selection, or replacing it with random or directional artificial selective forces, the fate of propagated populations may be jeopardized. Assuming that natural selection has already optimized most character states of populations in their particular habitats, any deviation from those states, even those advantageous in captivity, would not be beneficial in nature. "... genetically based performance under one set of conditions (i.e., hatchery) may not be correlated with performance under a different set of conditions (stream, lake, natural area). If the goal is to release stock in a different environment from that where they are bred, then the brood stock selection practices must be designed to avoid unconscious selection and inbreeding." (FAO/UNEP 1981, p. 25).

Frankel and Soule (1981) discuss four types of selection in captivity that can affect genetics: selection for increased productivity, selection for a (perfect) type, selection for tractability, and non-selection. Selection for increased productivity in fishes can occur when the most fecund females are continually used to develop a breeding stock. Although this is most efficient in a propagation program, it can be deleterious in nature, where optimal clutch size is a function of predation risks, growth rates, adult and juvenile mortality schedules, food availability, etc. (Stearns 1976, 1977). Since increased fecundity may be maladaptive in nature, this type of artificial selection should be avoided.

It may also be tempting to select for a particular type, such as larger or smaller, more or less aggressive, more colorful, etc. This is analogous to directional or stabilizing selection and can reduce quantitative or qualitative gene pool variation. The third type of artificial selection, for tractability, is really a subset of selection for a type. It occurs when less aggressive animals are used for breeding because they are easier to handle. The practice of non-selection occurs when the survival probability of sick or abnormal individuals is increased by the captive breeding program; this may increase the incidence of deleterious genes in the population.

Effects of Variance Reduction Within Populations

Thus far, I have presented sources of genetic variance reduction within populations, under the implicit assumption that loss of variance is undesirable. What specific genetic and phenotypic changes, however, will arise from reduced variance, and what is the evidence that these changes have adverse effects? Loss of genetic variance has three major effects: increased homozygosity (leading to reduced fitness), loss of additive variance, and increase in deleterious recessive alleles.

There is little doubt that increased homozygosity can lower an individual's fitness (Beardmore 1983) although actual mechanisms for this reduction are not known. With respect to relative fitnesses of hetero- and homozygotes, there exists a "heterozygosity consensus," which is "... the belief based on laboratory and farm experience that heterozygosity is most efficient in a propagation program, it can be deleterious in nature. "... genetically based performance under one set of conditions (stream, lake, natural area). If the goal is to release stock in a different environment from that where they are bred, then the brood stock selection practices must be designed to avoid unconscious selection and inbreeding." (FAO/UNEP 1981, p. 25).

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With respect to the second problem, additive genetic variance is generally lost at the same rate as heterozygosity

\[
\left( \frac{1}{2N_e} \right) \text{ per generation} [\text{Franklin 1980}] 
\]

The major cause is genetic drift, which of course may be powerful in small populations. The reader is referred to Fisher (1930), Franklin (1980) and Falconer (1981) for more detailed discussions of additive genetic variance. The third point, increase in deleterious recessive alleles, has been discussed in the section on inbreeding.

Among-Population Variance

Now we approach a very different problem, that of genetic variation among populations. Spatially isolated populations of organisms, with little to no gene flow among them, will tend to genetically diverge either through different selective forces or random drift (Endler 1977); in its extreme form, this leads to speciation. Any isolated population of fishes is a potentially unique gene pool with characteristics that may differ from all other demes. This is particularly evident in salmonids, which demonstrate the potential for extensive genetic divergence of fish stocks (Donaldson 1971; Busack et al. 1979; Stahl 1981, 1983). Consequently, in cases where endangered fishes exist in more than one natural population, we have at our disposal a powerful management tool: the potential existence of genetically distinct groups with which to recover the species. This is not a trivial observation, for it allows the manager flexibility in building breeding stocks, re-introduction to field sites, and other management
actions. For example, if an endangered fish retains viable populations in both constant springs and fluctuating streams (e.g., Vrijenhoek et al. 1985), the manager has a choice of which gene pool to use for propagation, whether to combine fish from both, or which gene pool to use for stocking a new field site. Natural populations can be kept genetically isolated, mixed and isolated captive stocks can be developed, and gene pools used for introduction can be better matched to the environment. It is therefore critical that variance among naturally isolated populations, however subtle, be preserved and exploited through continued isolation wherever possible.

Another problem in mixing naturally isolated demes is potential loss of coadapted gene complexes (Dobzhansky 1970). This occurs when genes from one deme, which are closely linked and “coadapted” to work well with one another, are broken up by hybridization into gene complexes that do not function together as well. It is quite common, for example, for first generation hybrids to be robust, but then to lose fitness over subsequent generations, presumably as coadapted gene complexes are broken up (Roughgarden 1979). Evidence for such “outbreeding depression” is provided by Dobzhansky and Pavlovsky (1958) in fruitflies, Alstad and Edmunds (1983) in pineleaf scale insects, and Stahl (1981) in Atlantic salmon (salmo salar). Rasmuson (1981) pointed out the need for further understanding of the importance of outcrossing to locally adapted gene complexes in fishes. At present, it appears that the potential exists for fitness reductions in fishes due to loss of coadapted gene complexes.

In addition to mixing naturally isolated groups, between-population variation can be lost through “convergent selection,” that is, common artificial selective forces in hatcheries or modified natural habitats. If fishes from physically, chemically, or biologically different field sites are raised in common hatchery environments, the same artificial selective regimes will be applied to all. If this continues for several generations, or if the forces are strong, the practice has the potential of selecting for a common hatchery stock and thus eliminating between-stock variation. Such convergence in Atlantic salmon was documented by Stahl (1983). Similar results may be obtained if differing natural habitats are altered in the same ways, introducing new and common selective forces.

Alternatively, formerly widespread, contiguous populations that have been separated by man into isolated demes suddenly face the genetic problems of small populations outlined above. In this case, supplemental gene flow by man among these artificially isolated groups may be necessary to maintain a larger Ne in each deme and thus “genetically mimic” the natural situation. In this case, continued isolation is not desirable, since the demes were large gene pools until man’s intervention.

### Options For Managing Endangered Fishes

Synthesis of the above information allows development of management plans that minimize genetic damage and maximize chances of long-term genetic health of small populations (Table 1). Perhaps the most important step toward sound genetic management is collection of data on population structure and genetic and morphological variation (Allendorf and Phelps 1981; Ryman 1981; Hamrick 1983). Without these data, we can only make blind decisions regarding preservation of genetic variation. This was recognized in the FAO/UNEP report of 1981 (p. 11), which stated “A good knowledge of the population structure in the management of fisheries cannot be exaggerated . . . Only when stocks are properly defined can the fishery be managed optimally.” They also emphasized (p. 11) that “When re-introduction of a locally extinct population is contemplated, earlier baseline information might allow a closer matching of the introduced fish to the original population. Proper genetic matching would increase the likelihood of successful re-introduction . . . Other things being equal, populations of maximum electrophoretic variation should be selected for introduction because this probably increases the likelihood of evolutionary adaptation to a novel environment.” Useful information for such attempts would derive from electrophoretic and chromosomal analyses, and morphometric and meristic studies designed to obtain estimates of available intra- and inter-population variation. Present examples include work on western trouts (Behnke 1970, 1979), pupfishes (Turner 1973a, 1973b, 1974, 1984), and the Sonoran topminnow (Vrijenhoek et al., 1985).

Detailed genetic analyses should be conducted on any endangered fish to determine how variation is distributed within the species and how best to preserve that variation (as per Chambers and Bayless 1983; Loveless and Hamrick 1984). In the case of aquatic organisms, it is convenient to partition genetic variance into that contained within localities, between localities within drainage systems, and between drainage systems (Chambers 1980). Vrijenhoek et al. (1985) conducted such an analysis on the endangered Sonoran topminnow (Peciohipis occidentalis) and found total genetic variation in the species to be composed of diversity within localities (21%), between localities within drainages (26%) and between three major genetic groups, equivalent to subspecies (53%). This analysis indicates it is vital to preserve representatives of all three groups, and of somewhat lesser importance (although not unimportant) to maintain

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### Table 1: Recommended actions to maximize long-term genetic health of endangered fishes

| 1. Monitor genetics of field and captive genetic populations. |
| --- |
| Effects: |
| Reduces erosion of quantitative variation. |
| Reduces loss of rare alleles. |
| Reduces inbreeding potential. |

| 2. Maintain largest feasible genetically effective population size of captive stocks. |
| --- |
| Effects: |
| Reduces the several types of artificial selection. |
| Reduces “domestication.” |
| Minimizes chances of bottlenecks, drift, inbreeding, and catastrophic loss of the stock. |

| 3. In small captive populations, avoid inbreeding through selective mating. |
| --- |

| 4. Keep stocks in hatchery environments for as short a time as possible. |
| --- |
| Effects: |

| 5. Maintain separate stocks of distinct populations to preserve among-population variance. |
| --- |
multiple populations within groups. Only when armed with such knowledge can the manager make informed decisions with respect to preservation of genetic resources.

Electrophoretic analysis of all brood stocks should be conducted to determine levels of genetic variation, from which all subsequent variation will be derived. Such analysis can be completed without sacrificing individuals: muscle, fin, blood, or even skin mucous (M. H. Smith, personal communication) for example, may be obtained for testing with little damage to the fish. Subsequent captive generations should also be sampled periodically (every few generations, if they are retained in captivity for that long) to determine changes in allele frequencies or detect loss of alleles. Such programs have revealed significant genetic deterioration of hatchery salmonid stocks (Ryman and Stahl 1980; Cross and King 1983; Stahl 1983), and could provide the basis for management decisions with respect to genetic welfare of captive endangered fishes. It is only through informed genetic monitoring that we can reasonably expect to maintain rare fishes for extended periods of time.

In all cases of intervention for management, the largest feasible Ne should be initiated and maintained in a captive breeding program (Table 1). "It is inevitable that some of the natural variability of a species is inadvertently lost when individuals are established as founders of a hatchery stock, and that more and more variability is inadvertently lost in each generation of intensive hatchery production" (Wilkins 1981, p. 217). As a result, the "basic rule of conservation genetics" (Soule 1980) is that a genetically effective population size of 50 is the minimum requirement for short-term survival (on the order of several generations). This number will result in a 1% ΔF per generation, which is tolerable for several generations. For long-term genetic health, Franklin (1980) suggests a minimum Ne of at least 500, with an associated inbreeding coefficient of 0.1% and a low rate of genetic drift. Of course, larger populations than this are desirable. Ne in any case may be maximized by maintaining equal sex ratios of breeding adults, insuring even progeny distribution by individual breeding and culling of excess offspring (Franklin and Soule 1981), and avoiding population crashes. Such action will minimize further erosion of quantitative genetic variation through bottlenecks or drift, and will reduce loss of rare alleles and inbreeding effects. These problems can also be countered by periodic introduction of wild individuals (from the same locality as the original brood stock) into the captive population.

If a large population cannot be acquired or maintained in captivity, inbreeding can still be avoided by a controlled selective breeding program that minimizes relatedness of mated individuals (Tave 1984). One example of such a breeding scheme is outlined in Fig. 5; many other schemes are possible (e.g., Flesness 1977; Senner 1980). An innovative program that actually utilizes inbreeding to an advantage in cases where few founders are available and others cannot be obtained was successfully applied to the rare Speke's Gazelle (Gazella spekei) by Templeton and Reed (1983).

Stocks should be kept in hatchery environments only long enough to accomplish outlined breeding goals such as scientific investigation or building a reintroduction stock. Minimizing time spent under artificial conditions reduces the probability of bottlenecks, drift, inbreeding, artificial selection, domestication, catastrophic losses or disease. By "circulating" populations through a hatchery and quickly back into the wild, one can avoid most of the pitfalls associated with genetic changes in captivity, and thereby maintain healthier populations of endangered fishes. Smith and Chesser (1981, p. 18) emphasized this point: "To prevent the loss of genetic variability caused by drift and inbreeding, it is important that hatchery and restocking programmes do not maintain spawning stocks as independent units for long periods (Ryman and Stahl 1980). Periodic replacement of hatchery fish with those from natural populations is also advised to prevent possible adaptations of fish to hatchery conditions; these adaptations may not be advantageous in natural environments."

Separate stocks of isolated populations (Table 1) will maximize inter-population variance, maintaining potentially distinct forms and thereby allowing greatest flexibility in management. For example, if a particular field locality is to be stocked with an endangered fish, we have the option of selecting from among several stock populations, and can choose the one whose habitat of origin most closely matches the new site. By not mixing wild populations, we retain the option of experimentally combining portions of these demes in the future, should adverse effects of small populations appear; if initially combined, however, the populations cannot later be separated.

A Final Caution

I have herein outlined theoretical aspects of genetic perils faced by small populations, supported by appropriate data wherever possible, and have suggested actions that may be taken to minimize these problems. For many species, stated goals simply cannot be met or even closely approximated because facilities or budgets are not adequate, or the number of extant individuals is minimal (e.g., Gambusia gagei, Poe-
ciliidae; the entire world population at one time consisted of two males and one female; Hubbs and Brodric 1963). This does not imply that recovery efforts will fail and should be abandoned, but rather that the best approximation to genetic guidelines possible under individual circumstances should be made. This paper is intended solely as a guide to sound genetic management; principles and suggestions should not be considered "absolute," and endangered species programs should not be abandoned if the guidelines herein cannot be rigorously met.

The models outlined in this paper are based on current, and certainly incomplete understandings of genetics of small populations and may not be entirely applicable to some species. For example, the Devil's Hole pupfish (Cyprinodon diabolis, Cyprinodontidae) has apparently existed for thousands of generations with populations hovering near several hundred individuals (Miller 1948). Classical genetic models predict that continual inbreeding should probably have already led to extinction of this species, yet it still thrives in its single locality. The point here is that, although our current knowledge of conservation genetics is incomplete and perhaps inaccurate in some cases, it is the best information presently available. Even if strict adherence to these basic principles proves unnecessary in particular cases, it is a conservative approach to species maintenance since it inevitably maximizes remaining genetic variation. The task of endangered species maintenance in perpetuity is admittedly difficult but there are few alternatives if we wish to conserve fishes for more than a few generations. The genetic dangers faced by any small population appear to be great; the costs of ignoring this fact may be even greater.

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