Genetic Aspects of Fisheries Rehabilitation Programs

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The stocking of indigenous or exotic fish species is often a desirable aspect of fisheries rehabilitation programs. Two strategies are proposed for the choice of fish for stocking. The first plan involves making separate collections of fish from each of several genetically different populations, performing all possible crosses between the different sources, and then stocking the progeny. In contrast to selective breeding programs, this strategy maximizes genetic variability and then relies on the environment for the selection of the most appropriate genotypes. The second plan is to sample populations from waters environmentally similar to those being rehabilitated that may contain preadapted genotypes. Application of this strategy should consider the use of gene banks or natural refugia as a source of preadapted genetic variability. When gene flow may occur between stocked fish and local populations, the second strategy should be used in favor of the first to minimize the impact on native gene pools. When choosing fish to implement either strategy, it is important to know the distribution of genetic variability within and between populations to sample adequately the variability present.

Key words: stocking, genetics, fisheries, rehabilitation, natural selection, exotic introductions, genetic introgression, gene banks, Great Lakes


Dans les programmes de réhabilitation des pêches, il est souvent désiré de stocker des espèces de poissons indigènes ou exotiques. Nous proposons deux stratégies de choix de l’espèce à ensemencer. La première comporte la collecte séparée de poissons de chacune de plusieurs populations génétiquement différentes, effectuant entre les différentes sources tous les croisements possibles, pour ensuite ensemencer la progéniture. Contrairement aux programmes de croisements sélectifs artificiels, ce plan porte au maximum la variabilité génétique et compte ensuite sur l’environnement pour la sélection des génotypes les plus appropriés. La seconde stratégie repose sur l’échantillonnage de populations provenant d’eaux ambiences semblables à celles qu’on veut réhabiliter et qui peuvent contenir des génotypes préadaptés. Si l’on adopte cette stratégie, il faudrait envisager l’utilisation de banques de gènes ou de refuges naturels comme sources de variabilité génétique préadaptée. S’il y avait probabilité d’échanges génétiques entre les poissons stockés et les populations locales, on devrait opter pour la deuxième stratégie afin de minimiser l’impact sur les pools de gènes indigènes. Pour

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ALTHOUGH many freshwater fishery environments have been disrupted by processes such as acid precipitation, point source pollution, hydroelectric power development, overfishing, and exotic introductions, some have occasionally become sufficiently restored to permit the rehabilitation of fisheries with indigenous or exotic species. Successful environmental restoration has, in turn, provided a unique opportunity for fisheries biologists to formulate and execute management plans to reestablish viable fisheries. Management initiatives that address ecologically extrinsic factors affecting fish populations are crucial to the success of rehabilitation programs and may take the form of habitat modification, prevention of habitat degradation, and fisheries regulations. These extrinsic factors, however, must be considered in combination with the intrinsic genetic factors of the fish populations to be manipulated. Recently, fishery scientists and managers have become increasingly aware of the importance of genetics in fish restoration and management (e.g. Calaprice 1969; Ihssen 1976; Utter et al. 1976; Smith et al. 1976; Moav et al. 1978; Allendorf and Utter 1979; Ryman and Ståhl 1980; Soulé 1980).

In this paper, we describe two rehabilitation strategies to use in choosing fish for stocking, discuss their rationale and implementation, and present some specific management applications. We have developed the strategies with special consideration for the fisheries of the Great Lakes, although the principles we consider may have general application for other freshwater fisheries.

**Strategies for the Choice of Fish for Stocking**

In waters that have been partially restored and are suitable for rehabilitation, formerly abundant fish species often have been lost or exist at low densities. As a result, the planting of either indigenous or exotic species is usually contemplated for most rehabilitation programs. The choice of fish for transplantation or for use as brood stock in hatcheries thus becomes an important consideration prior to the execution of stocking programs.

Fish cultural practices have historically involved some type of selective breeding, either planned or inadvertent. Intentional selection in hatcheries has often focused on single traits such as growth, color, shape, and disease resistance (e.g. Wolf 1953; Donaldson and Olson 1955; Toney and Bowen 1968). Because of the nature of such selective breeding, viability of hatchery fish may be reduced through a loss of genetic variation (Ryman 1970; Kincaid 1976; Allendorf and Utter 1979; Allendorf and Phelps 1980; Ryman and Ståhl 1980). We believe that the amount of genetic variability present within stocked fish may be a key factor in their potential fitness, i.e. their capacity to survive and reproduce in the existing environment. This fitness derives from a combination of many heritable traits that cannot presently be genetically partitioned and identified. As we cannot predict appropriate genetic combinations, it is best to resist the temptation to construct specialized genomes through artificial selection for stocking purposes.

Outlined below are two strategies for choosing fish to be used for rehabilitation stocking. The first strategy is to make collections from wild populations that represent the entire genetic diversity of the species, perform all possible crosses within and between the different sources, and then stock the progeny. This strategy maximizes genetic variability, and after stocking relies on the wild environment for selection of the most fit. This scheme is designed to increase the chances of stocking some fish with the proper genetic combination that will survive and reproduce in the newly restored waters. By holding wild fish only as long as required to make the crosses and raise the progeny to suitable (preferably very young) planting size, this plan should minimize inadvertent and potentially adverse hatchery selection. In some circumstances it may be best to continue to hold the parents in the hatchery to produce additional first-generation progeny in later years. This scheme should maximize the genetic diversity within the planted fish, provided that an adequate sample of the genetic variability within the species has been made. This strategy should not be used where the potential exists for interbreeding between stocked fish and indigenous populations. Such hybridization would break up previously existing and potentially adaptive gene combinations that occur in the wild populations.

The second strategy is similar to the first except that fish are chosen only from populations that occur in environments similar to those where stocking will occur. This plan should increase the possibility of success by using the end products of a history of selection similar to that which may occur in the waters to be stocked. The gene combinations successful within the donor populations hopefully will demonstrate similar fitness after transplantation. Sources of such preadapted fish may be from natural refugia within the restored waters or from outside the drainage basin. For example, the rehabilitation of lake trout in the Great Lakes might use trout from Lake Superior Shoal (a refugium) or from a large Canadian lake such as Great Bear Lake. These fish may be preadapted to the Great Lakes as a result of similar environmental pressures. The main difficulty with this alternative strategy is whether the perception of environmental similarity by the biologist will be the same as that of the fish. Although the first strategy is intended to ensure that some fit genotypes will be present among the stocked fish, the most adaptive genotypes may be only a small proportion of the planted fish. Use of the second strategy should increase this proportion.

In some waters suitable for rehabilitation efforts, irreversible habitat alterations have occurred and/or the community structure has markedly changed. In such cases, these waters may represent a unique environment found nowhere else in the geographic range of the species. The first strategy, which uses the entire genetic diversity of a species, is probably best for fisheries rehabilitation of such waters.
In other situations, the aquatic environments either have not been seriously altered or appear to have been restored to preexisting conditions. A species may be depleted or absent only in a local area, while populations occur in adjacent areas. The second strategy, which uses preadapted fish from the adjacent populations, should be chosen for the fisheries rehabilitation of such waters. If gene flow occurred historically among populations in these waters, then the donor populations may possess much of the genetic information that previously existed in the depleted population. Use of such preadapted genetic variability should enhance chances for successful rehabilitation and minimize the genetic impact on the adjacent populations from subsequent gene flow. Caution is advised in the use of the second strategy in areas of broad success, e.g., Pacific salmon returning to North American streams from the open ocean (Helle 1981). Transplanted stocks may not "home" accurately and problems with introduction may occur (Bams 1976).

Genetic Rationale and Implementation

Fundamental to the strategies discussed above is the premise that genetic variability within the stocked fish will be related to their overall fitness (survival and reproduction) in the new environment. During the early development of population genetics theory, Fisher (1930) recognized that the amount of genetic variation is positively correlated with the rate of evolutionary change by natural selection. This relationship is stated as the fundamental theorem of natural selection: the rate of increase in fitness of a population at any time is equal to its genetic variance in fitness at that time. Simply stated, genetic variability is the "stuff" on which evolutionary change depends (Lewontin 1974). Without genetic variability, stocked fish may be unable to adapt to new and changing environmental conditions.

Experimental evidence for the positive correlation between the amount of genetic variation and the rate of adaptation of populations has been provided by Ayala (1965) for the fruit fly, Drosophila serrata. Two populations were bred so that the one population initially had about twice as much genetic variation as the other. The populations were then allowed to "evolve" for 25 generations with intense competition for food and living space. During this period, both populations became gradually better adapted to this environment; however, the population that had the greater initial variation had a substantially faster rate of evolution as measured by its rate of population increase.

Implementation of the proposed strategies should take advantage of the existing genetic variation in the species of interest. Genetic variation in natural populations can exist in two fundamentally different levels of organization: within and between local populations. The total amount of genetic variation in a species can be estimated and subdivided into these two components by an examination of allelic frequencies using the technique of gel electrophoresis of proteins (Allendorf and Utter 1979) and the method of analysis presented by Nei (1975). This approach has been applied to rainbow trout (Salmo gairdneri). This species contains more electrophoretically detectable genetic variation than other closely related species of the genera Salmo and Oncorynchus (Allendorf and Utter 1979). The total genetic variation in rainbow trout of the Columbia River drainage, for example, has been 'partitioned' into a within-population component of 92.2% and a between-population component of 7.8% (Allendorf and Phelps 1981). Thus, the great majority of the genetic variation in these fish results from differences between individuals within populations. Other fish species show a similar distribution of genetic variation, i.e., a relatively low amount of genetic variation between populations, for example, bluegill (Lepomis macrochirus; Felley and Avise 1980) and striped bass (Morone saxatilis; Sidell et al. 1980).

In contrast, other species exhibit substantial genetic differentiation between populations, for example, brown trout (Salmo trutta; Ryman et al. 1979; Ryman and Ståhl 1981) and cutthroat trout (S. clarki; Loudenslager and Gall 1980).

Knowledge of the distribution of genetic variability within and among populations is necessary to collect fish that adequately represent the variability available for either strategy. If most of the genetic variability of a species is present within each population, then collecting fish from only a few populations will suffice. Conversely, as the amount of genetic differentiation increases between populations, fish from more populations must be included to obtain a satisfactory sample of the variation. In addition, the second strategy requires that care should be taken within the breeding program to preserve the parental genotypes as adaptation may be in the form of the original gene combinations and their interactions.

In addition to knowing the distribution of genetic variability, it is important to collect a large number of individuals from each population to obtain an accurate representation of the genetic variability within populations. Much of the discussion on effective population size given by Ryman and Ståhl (1980) is pertinent to this issue and will not be repeated here. In general, to minimize the sampling errors of founder effects, the number of parents used from each donor population should be greater than 50 for the first strategy and 100–200 for the second strategy (1:1 sex ratio).

Management Applications

Fish stocking as a management activity for rehabilitation can be divided into three general categories: introduction, reinforcement of remnant natural populations, and "put-and-take" fisheries. The discussion that follows addresses the choice of genotypes used and the genetic dangers inherent in each of these stocking practices.

The objectives of introduction stocking are to establish self-sustaining naturally reproducing populations of fish. This type of stocking includes intentional exotic introductions such as rainbow trout to Australia (MacCrimmon 1971) and reintroductions such as Atlantic salmon (Salmo salar) to Lake Ontario (Christie 1972).

Exotic introductions are by definition transplantations outside the normal range of the species; thus the use of preadapted genotypes as discussed previously is less likely to be possible since habitats and communities of donor and receiving waters will probably be different. In this case, the best approach is to introduce fish that represent as much of the genetic variability of the species as possible (the first strategy). Dangers in the introduction of exotics are well known, and considerable thought should be given to the possible ecological consequences of such stocking to the
structure and function of the community within the receiving waters (e.g. kokanee, \textit{Oncorhynchus nerka}, introduced to Lake Tahoe, Morgan et al. 1978). A potential genetic danger in exotic introductions is interspecific introgression, as isolating mechanisms may not exist between formerly allopatric species. This problem has been particularly evident between planted rainbow trout and indigenous cutthroat trout in North America (Behnke 1972).

Reintroductions of formerly indigenous species may succeed by either strategy for the choice of fish to stock. The decision of which strategy to use will be dependent on the biologist’s or manager’s perception of the ecological conditions of the restored waters. For example, in Lake Ontario in addition to substantial changes in the habitat, several major species have become extinct or greatly reduced, leaving the lake mainly populated with exotics, notably rainbow smelt (\textit{Osmerus mordax}) and alewife (\textit{Alosa pseudoharengus}) (Christie 1972). On the basis of the uniqueness of the habitat and community, the best chance for stocking success with Atlantic salmon may be to use fish that represent as much as possible of the total genetic variability of the species.

Other waters may be environmentally similar to conditions prior to perturbation, and the use of preadapted fish (second strategy) may speed the rehabilitation process. In some instances before extirpation, representatives of a species have been transplanted and preserved in hatcheries or other lakes, i.e. artificial or natural gene banks (Hynes et al. 1981). For example, before extinction lake trout from Lake Michigan were stocked in Green Lake, Wisconsin, where they now probably represent the only surviving remnant gene pool of Lake Michigan lake trout (Hacker 1956). Fish from gene banks may represent an unusual opportunity to use preadapted genotypes for reintroductions.

Reinforcement of remnant natural populations is the second category of fisheries management rehabilitation activities. The objective in this rehabilitation is to rebuild populations to acceptable abundance levels that will then be maintained by natural reproduction. In this case, a remnant of the original gene pool still exists within the system. Since it is difficult to assess the genetic importance of the remnant, we believe the best approach is to assume that it represents an important resource of preadapted genetic variability and therefore should receive high priority for preservation (see Soulé 1980).

If the remnant population is of sufficient size to serve as a gamete source, then the rehabilitation strategy of using preadapted genetic variability should be followed. An example would be the use of Superior Shoal lake trout for stocking purposes in Lake Superior, as previously discussed.

If the size of the remnant gene pool is insufficient to serve as the only gamete source and it must be supplemented, hybrids between the local native source and a donor source are a possible alternative. A few local males are capable of fertilizing many donor females, and the hybrids will possess a portion of the previously successful genotypes. Such hybrids sometimes have dramatically increased fitness as compared to the pure donor source (Bamz 1976). The donors should be taken from nearby sources, preferably from ones with which the stock being rehabilitated may in the past have exchanged genes.

The genetic variability extant in remnant populations, however, may not represent the amount that was formerly present. Insight into the degree of variability that previously existed may be provided by historical evidence of past population structure (e.g. Goodier 1981; Brown et al. 1981). When outside sources of fish are deemed desirable then natural or artificial gene banks and environmentally similar waters are the best sources of fish for stocking. The major danger in this circumstance is intraspecific genetic introgression between the introduced and native populations (Calaprice 1969; Krueger and Menzel 1979; Allendorf et al. 1980). Genetic swamping of native gene pools from external sources of fish would represent a loss of locally adapted genetic resources. Prevention of such hybridization may be possible by incorporating into stocking methodologies knowledge about the isolating mechanisms between populations (Horrall 1981).

The third category of rehabilitation stocking is “put-and-take” fisheries. Different from the other two management activities, this type of management depends on using hatcheries as artificial extensions of spawning and rearing habitat. “Put-and-take” stocking has been used for indigenous species that, as a result of limited or nonexistent spawning habitat, are unable to maintain population levels required to make exploitation feasible (e.g. Cayuga Lake lake trout management, Webster 1959). In this case, gametes for hatchery use would be best obtained from the local natural populations (second strategy) so as to benefit potentially from preadapted genetic variability. Managers who plan to use exotic species in “put-and-take” fisheries should consider the previous discussion on exotic introductions. A genetic danger in put and take stocking of either type of fish is introgression between hatchery fish and native populations. The planting of sterile fish would prevent genetic introgression and is feasible since reproductive fitness is unimportant.

**Summary and Conclusions**

Fundamental to the strategies proposed for the choice of fish for rehabilitation stocking is a recognition of the unpredictability of the fitness of the animals planted. Since the genetic factors of fitness are multiple and interactive, it is difficult to create fit genomes through artificial selection. Artificial selection for single traits also reduces genetic variability. Rather than reducing genetic variability, our first strategy is to choose fish that represent as much of the genetic variability of the species as possible, to perform crosses within and between populations, and to plant the progeny. By maximizing the possible genetic combinations, it is hoped that by chance some will be fit for the new environment and will, therefore, disproportionately contribute to the gene pool of subsequent generations. The second strategy is to sample from populations that exist in waters that are environmentally similar to those being rehabilitated and which may contain preadapted genotypes. A higher proportion of fit genotypes may occur among stocked fish by following this alternative. Where the danger exists of genetic introgression with local native populations, the second strategy should be used to preserve existing genetic resources.

To apply these strategies, the process of choosing populations to sample depends on a knowledge of the distribution of genetic variability in the species. Descriptions of genetic variability, within and between populations, are a prerequisite to implementation, but unfortunately are lacking.
for many species. Further research efforts should be directed toward this goal. Studies on population structures in un
perturbed areas may be particularly valuable in that they will allow comparison with the structure of new populations estab
lished. The electrophoretic studies on brown trout and other salmonids in Sweden (Ryman and StåhI 1981) represent
an Example of such research. In the tropics, before the genetic variability in populations can be described, basic taxonomic
studies will be required (Soulé 1980).

Rehabilitation management should include programs for monitoring the genetic effects of stocking activities. These
will be particularly important where remnant populations occur and the danger of genetic introgression with the stocked
fish exists. The use of genetic tags in planted fish (Allendorf and Utter 1979; Schweiger et al. 1977) provides a means for
the rapid detection of hybridization. Early detection of intro
gression would permit the development of alterations in stock
management procedures that could preserve the genetic integrity of remnant populations.

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