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TRANSLOCATION AS A TOOL FOR CONSERVING IMPERILED FISHES: EXPERIENCES IN WESTERN UNITED STATES

W. L. Minckley

Department of Zoology and Center for Environmental Studies, Arizona State University, Tempe, AZ 85287-1501, USA

Abstract
Conservation efforts for imperiled fishes in western United States have included numerous translocations, either among natural localities or from nature to propagation facilities then back into nature. The goal has been to increase population size and dispersion while maintaining genetic diversity, thus increasing probability of survival. Environmental laws governing translocations of fishes for conservation purposes involve complexities often equally as difficult to cope with as the biological problems of species' endangerment. Translocations perceived not to impinge on resource use or proprietary rights may be readily approved, while those which interfere with actual or projected development may meet strong resistance. Major biological considerations include the suitability and security of transplant sites (assurances that each meets a taxon's life-history and other requirements) and appropriateness of transplanted individuals (genetic and population structure, sufficient numbers of individuals, freedom from disease, etc.) for establishing new populations. Success of translocation is difficult to define and major inadequacies exist in information exchange — the latter can be remedied by publication in the peer-reviewed literature. It is anticipated that fish translocations and the technology required to support them will expand along with future needs and desires to re-establish native biotic elements in depleted communities and ecosystems.

Keywords: conservation, translocation, United States, fish.

INTRODUCTION

The indigenous freshwater fish fauna of western North America is declining at an alarming rate (Minckley & Douglas, 1991; Mayden, 1992). Natural faunal reductions through fluctuating but ever-intensifying aridity over geologic time (Minckley *et al.,* 1986) have accelerated drastically due to human development of regional water resources. At least 20 fish species have become extinct in the region in the past century (Miller *et al.,* 1989) and –120 of the remaining 200 taxa are of special concern (Williams *et al.,* 1989). Most are in three groups, cyprinoids (minnows and suckers), salmonids (trouts and salmons), and cyprinodontoids (livebearers, killifishes and allies).

Destruction and alteration of aquatic habitats have been substantial. Fifty federal dams were already built in the region by 1930, and –1000 more, the largest capable of massive power generation, were constructed from 1930 to 1980 (Reisner & Bates, 1990). Where local surface water was inadequate, interbasin transfers of water were made or ground water was pumped, the latter often far in excess of recharge potential (Fradkin, 1984; Reisner, 1986). Water tables declined, resulting in the failure of springs and reductions in reliability of surface flow.

In addition to changes in physical habitat, which, other than total desiccation, might well have been withstood by this highly resilient stream-adapted fauna, native western fishes are increasingly subject to interactions with non-native species (Moyle *et al.,* 1986; Minckley, 1991). More surface water exists today than in the recent past, in the form of artificial ponds, reservoirs, canals and aqueducts. Alien fishes are enhanced in these mostly lentic artificial systems, from which they invade or are stocked into remnant natural streams and springs to prey upon, compete with and ultimately replace the indigenous biota.

Efforts in conservation of western fishes commenced in earnest after enactment and implementation of federal legislation, especially the Endangered Species Preservation Act of 1966 which evolved into the Endangered Species Act (ESA) of 1973. Legal protection of imperiled fishes thus began in the 1960s (Minckley *et al.,* 1991a). Conservation efforts since that time have included alterations in water use to enhance imperiled aquatic systems and native aquatic taxa and the setting aside of aquatic reserves (Williams, 1991). Another strategy has been to establish new populations through translocation from a jeopardized habitat to more secure places, with the goal of increasing population size and dispersion of imperiled species. The present contribution relates some experiences with translocation as a tool in the conservation of freshwater fishes in western United States, reports on some of the political and biological problems encountered, and deals with a few theoretical issues. Some tentative guidelines for translocation proposed by Williams *et al.* (1988) were used as an outline (Table 1).

Definitions

Unless otherwise noted, taxon, species and population are used interchangeably since conservation efforts may

Table 1. Some guidelines for transplantation of fishes for conservation purposes, modified and paraphrased from Williams *et aL* (1988)

(1) Select a transplantation site:
  (a) within the native range whenever possible;
  (b) in an authorized place, where
  (c) life-history requirements are fulfilled,
  (d) sufficient habitat can support a viable population,
  (e) potential for dispersal is restricted and/or acceptable,
  (1) possibilities of hybridizations are minimal or non-existent,
  (g) other rare or endemic taxa will not be adversely affected, and
  (h) the population is protected and secure.

(2) Conduct transplantation with an appropriate stock of:
  (a) sufficient numbers and character (genetics, size/age distribution, sex ratio, etc.);
  (b) known taxonomy and represented by sufficient voucher specimens; and
  (c) free of pathogens and disease.
  (d) Transport subjects carefully and quickly, and
  (e) introduce under favourable conditions.

(3) Follow with:
  (a) systematic monitoring;
  (b) restocking if necessary or warranted;
  (c) determination of causes of failure(s); and
  (d) thorough documentation of the entire program in peer-reviewed literature.

be directed at any definable entity. Translocation and transplantation are used as synonyms to describe any movement of a taxon from one place to another. Stocking is the physical act of putting an organism in a new place. Hendrickson and Brooks (1991) are followed in defining two types of stockings: (1) sites inside (= reintroductions) and (2) outside (= introductions) a species' native range. The term site refers to a point of stocking in the broadest sense, varying from a habitat to a drainage. Native range refers to the geographic area occupied by an entity before human intervention, including interconnecting waters where it reasonably occurred.

Preservation is the prevention of extinction, a first step in any conservation effort. Maintenance of evolutionary potential, 'the re-establishment of a population size, dispersion, and structure that will [over the long-term] define itself by allowing an organism to proceed along independent evolutionary pathways comparable with those it followed prior to disruption by human interference' (Minckley *et al.*, 1991a), is quite different. True conservation must therefore consider the entity as a single point in a continuum of evolutionary process. The goal is to conserve the evolutionary steps which led to a taxon as well as the potential steps it may take in the future. A formidable gap exists between saving an organism from extinction and ensuring it to be capable of programming its own future. A translocated population may be considered viable and conserved only after showing promise of sustaining itself over ecological time measured in tens to thousands of years.

SELECTING TRANSLOCATION SITES

Location and authorization

Most planned transplants of imperiled fishes are restricted to within their native ranges, largely due to the notion that a taxon interacting ecologically, genetically and physically within its natural environs is less likely to create problems than it would in a new habitat. Some cases of illicit or accidental transplants outside a species' range have resulted in explosive invasions to the detriment of natives. Spread of the non-native cyprinids *Cyprinella lutrensis, Hybognathus placitus,* and *Notropis girardi* in streams west of the continental divide was accompanied by dramatic declines in native minnows (Hatch *et al.*, 1985; Bestgen *et al.*, 1989; Douglas *et al.*, 1994). The sheepshead minnow *Cyprinodon variegatus* introduced in Texas and New Mexico has hybridized extensively with native Pecos pupfish C. *pecosensis* (Echelle & Conner, 1989), and mosquitofish *Gambusia affinis* widely stocked for pestiferous insect control (Courtenay & Meffe, 1989), feed voraciously on and replace native topminnows *Poeciliopsis* spp. (Meffe *et al.*, 1982; Meffe, 1985).

Once a taxon seems to qualify for translocation and an area has been selected, attaining consensus on (1) the necessity for translocation and (2) site selection has become the most complex step in transplanting a taxon. A diversity of governmental and non-governmental hurdles must be negotiated before any action. Even when a conservation objective is common to all, which is not often the case, different management units have conflicting mandates and goals. Also, governmental agencies embrace conservation legislation with varying degrees of enthusiasm and resolve (Johnson, 1980, 1985, 1987; Johnson & Rinne, 1982; Deacon & Minckley, 1991).

The ESA was amended in 1982 (US Fish & Wildlife Service [USFWS], 1984a) to recognize an 'experimental' category for translocated populations. The original intent was to relax controls to expedite research, but supplemental provisions of 'experimental, essential' and 'experimental, non-essential' were added due to political pressure. An 'essential' transplant enjoys protection of the ESA, and any action that either adversely or beneficially influences the taxon requires USFWS consultation and concurrence. Conversely, the 'non-essential' category waives most protection given by the Act. By concurring with the latter, agencies could cooperate with species recovery efforts and at the same time relieve themselves of much of the responsibility they would otherwise be required to embrace for protection of reintroduced or introduced populations of listed taxa. Translocations were therefore allowed to proceed where formerly blocked. On the negative side, 'non-essential' populations, and by default the entire habitats where they are stocked, remain unprotected (Deacon & Minckley, 1991; Hendrickson & Brooks, 1991).

Another negative result was increased bureaucracy, which greatly increased the time required for action. Authorization for either experimental category may take 2 or more years. Final arrangements to stock desert pupfish *Cyprinodon m. macularius* and Gila topminnow *Poeciliopsis o. occidentalis* on some federal lands were stalled for more than 5 years (Hendrickson & Brooks, 1991). Fortunately, although both were listed as endangered, both were also under propagation so neither was critically imperiled by the delay. The new categories also generated the nightmare of a geographic mosaic of relocated topminnows a few kilometres apart, some under full protection and others 'non-essential'

BIOLOGICAL REQUIREMENTS

Moyle and Sato (1991) reviewed ecological theory relevant to creation of reserves for native fishes, from which they formulated criteria for reserve design. Their priority order was rearranged and criteria paraphrased to emphasize transplant sites. Such places must (1) contain resources and habitat conditions necessary for a taxon to persist; (2) be able to support populations large enough to be self-sustaining in the face of genetic or demographic stochasticity, and large enough in area to maintain the range and variability in conditions needed to maintain natural diversity (at a site itself, and in its watershed or aquifer); (3) have sufficient within-boundary replication to avoid problems created by local extirpations; (4) be protected from edge and external effects in order to maintain internal quality (including protection of water sources and upstream areas, creation of terrestrial buffer zones, and erection of barriers precluding invasion by non-natives); and (5) each be replicated by one or more similarly protected areas distant enough that all will not be affected by the same disaster (see also Maitland, this issue).

Clearly, all these criteria are not met by most sites. In practice, (1), (2) and (3) are most consistently considered, and significant attention has also been afforded to (5). **All** of these can usually be accomplished locally, especially for small, short-lived species [which live <3.0 years, remain small in body size, and mature no later than their second summer of life (Hendrickson & Brooks, 1991; Minckley *et al.* 1991*a*)]. Maintenance of habitat size sufficient to promote natural diversity is exceedingly difficult where aquatic environments are already limited under arid-land conditions and any loss at all may detract substantially from a system. Large, long-lived species (those living >5.0 (to >50) years, achieving large body size, and maturing sexually their third (rarely second) summer or later) require large habitats, and setting aside of major watersheds for their conservation may seem improbable. Powerful economic forces such as mining, livestock grazing, and lumbering may, however, soon lose in competition with a more basic human requirement for drinking water. Thus, if native fishes can prevail a little longer, some may survive in rivers kept flowing to deliver domestic water supplies. Protection of refuge sites from edge and external effects **(4)** is being indirectly addressed through these same overdue trends toward watershed and riparian management to protect water supplies (Platts & Rinne, 1985; Rinne, 1988).

Both natural and artificial barriers have become commonly utilized as tools to protect upstream-dwelling species and communities from downstream invaders (Rinne & Turner, 1991). Yet barriers also increase the permanency of fragmentation of native fish populations, which is to be avoided if possible. Short-lived aquatic taxa in arid zones (and perhaps others over longer times) are, however, characterized by vast natural changes in population sizes accompanied by dramatic expansions and contractions in geographic range (Deacon & Minckley, 1974; Minckley, 1991). Thus, being a resilient generalist is important for survival.

Theoretically, permanence and reliability of an aquatic site may be of no greater (or lesser) biological importance than catastrophic variations (Sousa, 1984), so long as a taxon survives both extremes. The former promotes population stability and may select for specialization while the latter evokes population fluctuations which should select for adjustability, persistence and species' resiliency. Permanent springs provided small but reliable refugia during seasonal or episodic drought, or over geologic time. Survival was thus enhanced for those taxa which could attain such habitats and exist at small, highly fragmented population sizes for significant periods of time. Larger, less reliable marshes and streams persisted only in wetter years, decades or centuries. In doing so, however, these less-than-permanent habitats provided periodic connectedness. Gene exchange and maintenance of genetic diversity were thus facilitated by dispersal routes among refugia and periodic opportunity for larger populations to experience diverse selection pressures, all serving to counteract effects of small population sizes in drier times.

Human construction of dams and diversions, lowering of water tables through water mining and pollution changed the rules. Both permanent refugia and the more transitory habitat fragments that collectively comprise the natural ranges of many now-imperiled fishes are rendered inaccessible. The fishes are excluded from large parts of their former geographic ranges and neither natural nor unnatural extirpations can be countered by recolonization. Translocations are therefore required to take the place of natural dispersal. Impermanent habitats are thus important as transplant sites so long as individuals are provided access or physical transport among their original gene pools. Judicious use of impermanent sites also allows more latitude in achieving replication of populated habitats (5, above), which is a valuable asset in desertlands where aquatic habitats are scarce.

Potentials for dispersal, hybridization and impacts of translocated taxa on other endemic or rare taxa (Table 1) also are concerns in translocation programmes. Dispersal may be detrimental if a taxon carries unwanted traits or influences other species or violates agreements.

On the other hand, dispersal of translocated fish in well-connected systems may be anticipated and desirable to increase range and population size. Connectedness is obviously more limited in arid lands, but may occur through flooding with the same results.

Hybridization as an issue of concern hinges on the relatively high potential for interbreeding between distinct fish taxa (Schwartz, 1981). In fact, hybridization between taxa, one non-native, has proved a major problem in fish conservation in the western United States. Examples include diverse salmonids (Rinne & Minckley; 1985, Allendorf & Leary, 1988) cyprinids (Hubbs & Miller, 1943; Smith *et al.*, 1979), catostomids (Hubbs & Miller, 1953; Miller & Smith, 1981; Williams *et al.*, 1985), cyprinodontids (Echelle & Conner, 1989), poeciliids (Hubbs, 1971; Echelle, 1991), and centrarchids (Whitmore, 1983). Most western fishes evolved and naturally occur allopatric to any near relatives; lack of 'evolutionary experience' may make them more prone to hybridize than others. Imperiled populations may be sparse and translocated taxa are seldom stocked in large numbers, so the tendency for an uncommon form to mate with individuals of a more common taxon (Hubbs, 1955) comes to bear.

Other adverse effects of transplants, such as competition or predation on other endemic or rare organisms, have not yet been reported. The reciprocal, e.g. a negative impact of non-native predators on reintroduced native fishes in cases where predator removal was either not attempted (Marsh & Brooks, 1989) or failed (Marsh & Minckley, 1990; Minckley *et al.*, 1991b), may, however, be more common than realized.

Biological damage has also occurred with preparation of transplant sites by physical modification or chemical eradication of undesired organisms. Landye (1983) attributed loss of endemic hydrobiid snails in California springs to habitat modifications for Owens pupfish *Cyprinodon radiosus* reintroductions. Rinne & Turner (1991) and Propst *et al.* (1992) documented eradication of native fishes to prepare sites for introduction and reintroduction of imperiled trouts. DeMarais *et al.* (1993) quantified genetic changes in endangered chubs *Gila seminuda* after poisoning an unwanted exotic invader. Such events are especially important to avoid in limited habitats of arid lands, where local endemism may be predicted. Removal of native animals before modifications or chemical treatment, then reintroducing them (e.g. Hubbs *et al.*, 1978; Hubbs, 1980; Meffe, 1983), has proved effective in circumventing this problem.

Protection and security

Ideally, a translocation site should be secure and protected from imminent or future threats and dedicated to protect the subject taxon (e.g. Moyle & Sato, 1991). It might be assumed that a transplant site is far more secure than the locale of original occurrence and further that all translocations are intended directly to benefit a taxon, otherwise why would a transplant be performed?

Such is not always the case. Some translocations are on an emergency basis, such as a basic requirement for water, where in-field decisions are acted upon for expediency rather than long-term security. Others are for research purposes, where long term security and protection may not be too important. Some programmes have emphasized quantity rather than quality of sites, sometimes to demonstrate politically that something is being done when little is expected to be (or is) accomplished Also, the promise (or threat) of listing, underscored by an emergency translocation, is one way in which funds may be generated for conserving taxa not formally listed as threatened or endangered. Alternatively, some translocation has been intended in part to preempt formal listing of a taxon under the ESA (Johnson, 1985; Minckley *et al.* 1991*b*). The well-being of most translocated stocks may thus depend as much or more on binding agreements among parties concerned than on the quality and permanence of new habitat. Ecological security and protection of translocation sites and populations must also be accompanied by legal and political commitments.

Whatever the case, most translocations are sincere attempts to establish new populations as insurance against extinction. When ecological and political conditions are favourable, positive results can be realized. A number of taxa now exist in great numbers throughout wider distributions than would have been so without translocation (e.g., Simons *et al.*, 1989; Minckley *et al.*, 1991a,b; Prospt *et al.*, 1992). Further, in eight of ~50 instances of transplants summarized by Johnson and Hubbs (1989), Hendrickson and Brooks (1991), and Minckley *et al.* (1991*a*), a taxon would almost certainly have disappeared had action not been taken.

CONDUCTING A TRANSLOCATION

Sources for stocks

Few options may exist in selecting a source for translocation or captive breeding since taxa are often critically scarce by the time a decision is made for either. If choices are available, selecting which of a number of stocks to save may be extremely difficult. Each isolate may be unique and substantial life history, genetic and other information should be available (but often is not) for objective assessment. In the absence of data, alternatives are to translocate the rarest, one that seems most compatible with ecological conditions at a new transplant site, the one geographically nearest a new site (Williams *et al.*, 1988) or perhaps the most common stock, since it may be the only one judged large enough to withstand removal of fish for transfer.

Genetic concerns

Genetic management is being extended to both wild and captive native fishes (e.g. Buth *et al.*, 1987; Echelle *et al.*, 1989; Edds & Echelle, 1989; Minckley *et al.*, 1989). Thus, genetic data and methods for its acquisition and analysis are available to assist in selecting and evaluating sources for translocation (Ryman & Utter, 1987;

Schreck & Moyle, 1990; Hedrick & Miller, 1992). The goal is to maintain or maximize the genetic variation which remains, both within and among populations. Those populations demonstrating the greatest genetic variability are preferred as sources, since heterozygous individuals or lineages are thought by some to adjust more effectively to changing conditions than homozygous ones (Vrijenhoek *et al.*, 1985; Quattro & Vrijenhoek, 1989; Vrijenhoek, 1989; but see Hedrick & Miller, 1992). The rationale is to establish new stocks with sufficient individuals to reflect the genetic composition and survival capabilities of the source population.

Numbers of individuals to be translocated should be based on the numbers known (or suspected) actually to contribute genes to annual recruitment (the effective population size), rather than the gross number of animals in a population. Hundreds of individuals may be required, for example, where effective population size of a long-lived taxon like the razorback sucker *Xyrauchen texanus* may well comprise only a small proportion of the total (Minckley *et al.*, 1991b). Far fewer are required for short-lived taxa, e.g. a few pregnant mosquitofish with sperm storage, high frequency of multiple insemination, vast capabilities for dispersal and high reproductive rates (Smith *et al.*, 1989), would serve the same purpose. The number of recruits contributed by each adult also enters the equation. Equalization of contribution among individuals can, for example, increase the effective population size to twice that of a random-mating stock of comparable numbers (Denniston, 1978).

Conservation efforts may be directed at any level, species, subspecies, populations or even unique alleles (Meffe, 1987). Thus, perpetuation of less variable populations may also be desirable, especially when they represent unique phenotypes or even homozygous genotypes adapted to special conditions. Further, no single datum such as genetics takes precedence over another in efforts to preserve diversity. Extinctions of singular morphology, pigmentation, physiological attribute or other features of a local population are as irrevocable as losses of alleles. Changes in frequency of characters, whether alleles (Allendorf & Leary, 1988) or other features, are, however, not irrevocable. When variation is due to features with narrow geographic distributions, greater numbers of populations must be protected to maintain diversity. Fewer are appropriate when variations of a character or character sets are due to frequency differences in nearly all populations (Echelle, 1991).

With few exceptions (Meffe & Vrijenhoek, 1988), mixing stocks to increase genetic or other variability may be ill-advised. Co-adapted gene combinations of long-isolated stocks may be disrupted through interbreeding by forming gene associations less functional than the original (Dobzhansky, 1970). Among fishes, this phenomenon has been detected mostly in salmonids (Altukhov & Salmenkova, 1987; see also Meffe, 1986, 1987; Nelson & Soule, 1987; Keenan & Salini, 1990). Augmentation of stocks through introduction of distantly related individuals of the same species (or hatchery-produced fish from long-domesticated lines) are also of doubtful advisability.

When hybridization is a problem (Rinne & Minckley, 1985; Allendorf *et al.*, 1987; Allendorf & Leary, 1988), sources for translocation or other conservation action may be based on 'genetic purity'. Morphology (including coloration) may prove too variable for use in defining introgression (Rinne, 1985), so 'purity' cannot be verified without genetic analysis (Loudenslager *et al.*, 1986; Dowling & Childs, 1992). An acceptable frequency of foreign genes must then be decided upon, below which a stock is to be preserved and above which it is removed or restored (Campton, 1987). Allendorf and Leary (1988) suggested 1.0% foreign genes were both difficult to detect and unlikely to alter biological characteristics from a natural state. To maintain genetic diversity, however, even a highly introgressed stock must be considered irreplaceable if it comprises all that remains of a taxon (Echelle, 1991; Dowling & Childs, 1992; Dowling *et al.*, 1992a,b).

Captive propagation

Imperiled taxa are obviously more secure if multiple populations exist, and propagation facilities in addition to producing fish for translocation may provide that option. Freshwater fishes are amenable as a group to captivity. Most adults are readily captured, transported and maintained. They are more easily bred and reared than most vertebrates, produce large numbers of young ready to stock soon after hatching and grow to mature quickly, minimizing generation time (Johnson & Jensen, 1991). Production and holding costs are thus comparatively low. As noted before the ESA was even amended to facilitate translocations; 32 of 39 recovery plans for fishes listed under the ESA recommend some translocation, most with intervening propagation (Williams *et al.*, 1988). Further, propagation and stocking have long been popular in the United States and elsewhere and enjoy strong public acceptance and support (Stroud, 1986).

As evidence for this popularity, the USFWS Dexter National Fish Hatchery and Technology Center (Dexter NFH), New Mexico, was dedicated in the 1970s to conservation of imperiled fishes. Its goals are threefold: (1) to act as a refuge for imperiled fishes in case wild populations are lost; (2) to support research to determine and alleviate threats to survival; and (3) to propagate selected taxa of quality and in quantities sufficient to allow reintroduction (Rinne *et al.*, 1986; Johnson & Hubbs, 1989; Johnson & Jensen, 1991). Johnson and Jensen (1991) discussed the challenges of operating of such a facility, which are summarized in Table 2.

Twenty-four fish taxa were housed at Dexter NFH between 1974 and 1989, eight for propagation toward translocation as well as for protection and 17 primarily for insurance against extinction. Seven were maintained only for research, although data pertaining mostly to husbandry but also to ecology, genetics and taxonomy were collected for all species.

Table 2. Unique concerns and requirements for facilities dedicated to the preservation and propagation of imperiled freshwater fishes; abstracted from Johnson and Jensen (1991)

Subject(s)	Problem(s)	Remedy or remedial action(s)
Value of individuals and stocks	Irreplaceability, loss of genetic variability, possible damage to source population	Replicate all support systems; maximize personnel training and system surveillance to avoid mortality
Parasites and disease	Diverse taxa in proximity, high potential for exposure to new pathogens and for spread from stock to stock	Inspect individuals, quarantine, use chemical eradicants, and minimize handling
Water distribution and disposal	Spread of disease or other adverse factor, mixing of taxa, escapement	Use water only once through system, onsite disposal of all water, with no connections to local watershed
Onsite mixing of taxa	Hybridization, predation, competition, contamination of translocation sites	All equipment and personnel cleaned before moving between ponds, maximize personnel training in identification and security, control public access, and control possible non-human agents of potential transfers
Assignments of priority for residence and effort	Needs to conserve space, time, and funding	Emphasize subjects most threatened in the wild and with the greatest probability for recovery

Short-lived fishes tend to be self-sufficient in captivity, breeding rapidly and spontaneously in ponds to form large populations. They may thus be harvested periodically and stocked, or allowed to achieve self-perpetuating population sizes and persist in artificial pond environments. Desert pupfish have been maintained for decades in pools and other habitats constructed as refugia for the species in various desert reserves (USFWS, 1992).

This contrasts sharply with long-lived taxa, which are spawned artificially to maximize efficiency and provide control over production. It is inefficient to deal with the sporadic appearance of young over protracted reproductive seasons (as is characteristic of many long-lived taxa). Chemical induction of maturation synchronizes production. Females produce substantial numbers of ova (~100,000 for each 55-cm standard length razorback sucker; Minckley *et al.*, 1991b) and larvae may number millions from multiple pairings required, for example, to satisfy genetic concerns. Some species also disrupt the well-laid plans of fish culturists to curtail production and spawn unassisted to produce unanticipated and unpredictable numbers of 'volunteers'.

Other biological requirements

Numbers, sex ratio and age structure of fish to be translocated vary by species, source, size of habitat to be stocked and other factors. A sex ratio near 1:1 and a wide range of age/size classes intuitively should increase the probability of establishment (Williams *et al.*, 1988). In practice, a 1:1 sex ratio is assumed and age/size structure usually reflects that of the source population in other than hatchery fish. Sizes at stocking of year classes of hatchery fish are progressively larger through a season as growing individuals requiring more and more of the limited production space are transported and stocked.

Allendorf and Ryman (1987) considered 25 reproducing individuals of each sex an 'absolute minimum' for establishing salmonid populations under controlled hatchery conditions, which may be too few for any but the smallest translocation site in nature. Between 30 and 200 individuals are typically used to establish populations, mostly of short-lived taxa, in otherwise fishless and protected ponds at Dexter NFH (Johnson & Hubbs, 1989). Numbers stocked should further reflect data on effective population size of the taxon concerned, which may again be a partial function of habitat size. Greater numbers are also required when individual fish contribute unequally to recruitment or if a few fish are anticipated to become too widely scattered to find one another to breed in large diverse habitats.

Taxonomy

Taxonomy of source populations must be carefully assessed to avoid transplanting the wrong taxon or moving more than one species, which is at a minimum embarrassing. Further, lack of formal taxonomic recognition has hampered or precluded conservation efforts on behalf of populations (Minckley *et al.*, 1991*a*), and hesitation or inaction as a result of taxonomic confusion can endanger whole groups of fishes. Unresolved taxonomy has, for example, negatively influenced management toward recovery of endangered Colorado River chubs of the genus *Gila* for almost 30 years (Douglas *et al.*, 1989; Holden, 1991; Douglas, 1993).

Great care should be taken in locating both source and transplantation sites and documenting what specific stock is transplanted. Voucher specimens, or at a minimum photographic records, are necessary and original data on morphology, genetics, behavior and any other information on translocated stocks should be made part of the public record. Specimens sacrificed for identification, genetic analysis or assessments of disease and pathogens (Table 1) should be appropriately preserved and permanently housed for future reference.

Reasons for such care include the fact that new, unreported localities for a species can obscure and falsify original distributions (Hubbs & Miller, 1983). From the scientific view, original selection pressures may be relaxed and new ones imposed on an organism placed under new conditions and they may respond in phenotype and genotype. Devils Hole pupfish grew larger, more brightly colored and with different body shape in an artificial refuge than in the natural habitat (Williams, 1977). Changes in gene frequencies also may be associated with differences among sites, e.g. streams vs. ponds, and more specific factors like environmental contaminants or altered thermal regimes (Zimmerman & Richmond, 1981; Smith *et al.,* 1989). Rapid changes in life-history strategies occur in poeciliid fishes placed in new selective arenas (Trexler, 1989). Such potentially important changes are quantifiable only when specimens or data exist to set a baseline for comparison. From a practical view, the sudden appearance of a federally listed species in a near-completed development also can create problems, not only for developers but also for conservationists.

Parasites and diseases

Parasites are commonly transferred with their hosts, as they rightfully should so long as the parasite—host relationship is natural. Population sizes for diseases and parasites often, however, increase under close-spaced hatchery or other captive conditions (Williams *et al.*, 1988), which must be guarded against. Consideration should be given to the possible impacts of non-native parasites as well as the non-native, transplanted fish on the new area. Quarantine should be considered prior to stocking any taxon outside its native range. Transfer of wild stocks within their native ranges presents lower risks. Some stockings, both directly from the wild and of hatchery fish, have been precluded by infestations of non-native parasites (Hendrickson & Brooks, 1991; Johnson & Jensen, 1991).

WHAT HAPPENS LAST?

Determining success or failure

The intensity of monitoring translocated stocks has varied from incidental to thorough and from local for small habitats to basinwide in large and extensive watersheds. Prior to 1980 (Minckley & Brook, 1985), most monitoring was accomplished during general surveys at 2-4 year intervals. After formal programmes towards recovery of imperiled fishes were developed in the 1980s, assessments of short-lived species at first tended to be quarterly or biannually, with later efforts reduced to annual surveys (Simons *et al.*, 1989). Similarly, sites for long-lived taxa were sampled two or more times the year stocked, then annually or less frequently thereafter.

A razorback sucker programme (Minckley *et al.*, 1991*b)* with stocking and monitoring scattered throughout much of three major river basins was clearly too expensive to continue except at annual or less-frequent intervals in selected reaches; sampling large, difficult habitats such as reservoirs was later terminated. Another reintroduction effort for razorback suckers in California ended after less than 3 years, mostly due to difficulties in monitoring. Thus, most major programmes have passed with time from far too ambitious to substantially reduced and arguably insufficient efforts.

Monitoring goals should be to determine (1) survival and (2) establishment of translocated populations. Next, assuming initial success, (3) the quality and quantity of population growth may be evaluated. More individuals may be stocked if numbers of adults or some other population parameter seem inadequate. If genetic baseline data are available (e.g. DeMarais & Minckley, 1993), one may evaluate potential founder effects and alter gene frequencies by additional stocking, or at least know from genetic data if effective population sizes exist and random breeding is progressing. Another function of monitoring is (4) to provide opportunities for research, at a minimum the compilation of basic data on translocated populations themselves (i.e. population changes, responses to altered selection pressures, etc.) and toward a general store of knowledge on translocation as a conservation tool.

Reason(s) for failure can only be determined when monitoring is frequent enough to bracket the time of population disappearance narrowly. Aquatic habitats are at a premium in arid lands and determining reasons for failure and correcting or circumventing responsible factors (if possible), or at least understanding their probable frequencies, may allow for restocking. In one instance, topminnows disappeared after 10 years of 'success', over which time a large, viable population persisted in a permanent reach of a largely ephemeral stream through a number of alternating floods and droughts. They were not, however, able to survive a flood of the magnitude expected once a century (Collins *et al.*, 1981). It was concluded that this was one of the less-than-permanent' sites discussed above. Restocking was clearly appropriate and was performed, and a population has since persisted for 14 years with no human assistance.

Long-lived species in large habitats may be a different story. Consider that survival of only 0·1% of —15 million razorback suckers (not unusual for an iteroparous fish species; Dahlberg, 1979) stocked between 1981 and 1989 in the lower Colorado River basin (Minckley *et al.*, 1991*b*) would result in 15,000 fish distributed in an estimated 20,550 ha of available surface water. An average of less than a single fish per surface hectare is difficult to monitor! Further, 1-0% of such a population, only 150 wild 55-cm females (1-5 × 10 % of the total stocked; adding a male for each female and assuming each would pair = 2.0 × 10 %), could spawn at least 15 million eggs each year. Reproduction in this species may be in alternate years or less frequently, but longevity may be half a century (McCarthy & Minckley, 1987). The razorback sucker matures at 2-6 years old, depending on sex, habitat and other factors. Production of a year class might thus occur all at once the next year, or at any other time up to 10, 25 or 40+ years hence; it might involve isolated pairs yielding a few surviving young at scattered places, or large aggregations producing thousands of young; other scenarios could prevail; or it may never reestablish. Documenting 'success' or 'failure' for such a species presents a formidable challenge!

Documentation

Documentation lags dangerously far behind the expanding use of translocation for fish conservation in the western United States. Stocking can be legally authorized only by state and federal agencies, so records are required, to be filed as data or internal memoranda and often stored in regional and local offices. The next level of information is that of agency reports, the so-called 'gray' literature which blossomed in the 1970s and 1980s and has been recognized by some (Collette, 1990; Wilbur, 1990) as a major problem in fisheries research. Only limited numbers of reports are printed, distribution is often exclusively by request and few if any copies find their way into permanent repositories. Half of Hendrickson and Brooks' (1991) data on translocations of 40 fish taxa were based on personal communications, agency files and unpublished reports, all from the 1980s. Minckley *et al.* (1991b) had —350 citations (personal communications excluded) on razorback suckers, —50% classed as 'gray' and again mostly from the 1980s.

The author urges that formal documentation be planned from the onset, not provided, as has been largely the case, as a necessity for accountability. Administrators should mandate periodic publication of reports in local or regional journals, followed by summary papers in more widely distributed public outlets. Reports and summaries alike should deal quantitatively with at least the items listed in Table 1 and especially with careful analyses of both successes and failures. Hopefully, hypotheses on species and community ecology, genetics and other aspects of conservation biology may be formulated and tested along the way.

SOME CASE HISTORIES

As already noted, translocations of native fishes in the western United States began in earnest in the 1960s in response to imminent and actual extinctions, and some details on efforts that prevented some such catastrophes may further set the stage for discussion. Of eight critical cases, six survived through long periods of tenuous existence before relative security was attained. Two taxa, the Monkey Spring pupfish *Cyprinodon* sp. and Amistad gambusia *Gambusia amistadensis* went extinct despite efforts on their behalf (Johnson & Hubbs, 1989; Minckley *et al.,* 1991*a*). Neither of these taxa was treated differently from those which survived. Attention simply proved inadequate and the last few individuals were lost through human error (Minckley *et al.,* 1991a).

Survivors included the Leon Springs pupfish *Cyprinodon bovinus* (actions included removal of a hybridizing congener; Hubbs *et al.*, 1978; Hubbs, 1980), Devils Hole pupfish *Cyprinodon diabolis* (actions included extensive litigation; Deacon & Williams, 1991), Owens pupfish (Miller & Pister, 1971; Pister, 1991), Pahrump poolfish *Empetrichthys l. latos* (Minckley & Deacon, 1968) and two others, the Yaqui chub *Gila purpurea* and Big Bend gambusia *Gambusia gaigei,* which are selected here as case histories.

Yaqui chub

In one successful project, —200 Yaqui chubs (and a stock of Yaqui topminnows *Poeciliopsis o. sonoriensis)* were transferred in 1969 from a drying spring to a nearby, isolated creek in the same river basin. At that time chubs were abundant in the spring and present in lesser abundance at three other localities in the vicinity. The taxon was thought to be widely distributed in Mexico, which later proved incorrect. Its entire original distribution is now known to have comprised a few spring-fed habitats in a single drainage (DeMarais & Minckley, 1993) and in retrospect the entire range might well have been reduced in 1969 to no more than four localities.

Yaqui chubs were established in the isolated creek, and by 1976 that translocated stock was the only known population in the United States. The three other natural populations had succumbed to changes in water use and prolonged drought. In the next few years the creek was twice threatened with impoundment to create a fishing lake, proposals for which failed largely because of hydrologic factors but in part because of the presence of the federally listed topminnow (Yaqui chubs were not officially listed as endangered until much later, USFWS, 1984b). The stream then almost disappeared during natural regional drought in 1976; 225 chubs were moved from three remaining isolated pools to Dexter NFH.

A turning point came in 1977 when the creek resumed flow and its fishes survived. The stock at Dexter NFH had prospered. By 1979, a goal to set aside most of the natural range of the chub had been realized by land purchases and establishment of a National Wildlife Refuge. Beginning in 1980, Dexter NFH chubs were translocated back in lots of —50 to many thousands of individuals to and among renovated habitats. All translocations resulted in established populations and the chub is presumably as widely distributed today as a century ago. Further, its genetic features, which include substantial allozymic variability, did not change appreciably (DeMarais & Minckley, 1993).

Big Bend gambusia

Efforts for another imperiled form, the Big Bend gambusia, followed an even more tortuous path (Johnson & Hubbs, 1989). The taxon was described in the 1920s from a single spring that was totally dry when revisited in 1954. The taxon was rediscovered in 1955, occurring in small numbers in an artificial spring-fed pond also occupied by mosquitofish, which were apparently eliminating the endemic species. In 1956, 29 Big Bend gambusia were moved elsewhere, including two pairs to an aquarium, and the mosquitofish were poisoned. By 1957, all but two male and a single female aquarium fish had died and mosquitofish had reappeared in the pond. A new pool was dug and the three survivors were stocked, soon to produce a large population.

Mosquitofish invaded the second pool in 1960; 23 Big Bend gambusia were salvaged, nine died and 14 survivors plus 13 young born in captivity were stocked in another new pond. They were established and succeeded for 15 years, only to be decimated again in 1975 by unusual winter cold. Thermal water was diverted from another spring into the pool to ameliorate winter temperatures; the imperiled species flourished. Flooding in 1983 then flushed some individuals of the endemic form downstream to the original (1955) pool, which by then had developed stands of dense emergent plants, greater inflow—outflow of thermal water and persistent mosquitofish. By 1985 the mosquitofish had, in turn, been replaced by Big Bend gambusia, further extending the latter's range.

According to Hubbs *et al.* (1986), all Big Bend gambusia are 'homozygous for 60 allozymes, in full accord with inbreeding, bottlenecking, or a founder effect', as might be expected from its known history. It may well have existed naturally in the past as a small population subject to repeated bottlenecks (Echelle, 1991). Yet, the Big Bend gambusia show no signs of maladaptation, and replaced mosquitofish when spring-head ecological conditions were reinstated. The taxon now lives under full protection in a National Park, under guidelines which include this tiny fish having priority over human drinking water if drought or other event endangers the common supply, a notable precedent in an arid land!

DISCUSSION AND CONCLUSIONS

A major reason for hesitating to define 'success' of translocated stocks is the marked variability of data accumulated to date. Hendrickson and Brooks (1991) attempted to quantify trends from >400 transplants of 40 short-lived taxa into 'wild' habitats in the western United States (transfers into controlled facilities were excluded). They failed due to a general lack of comparability of intent, approach and follow-up by diverse programmes, organizations and individuals, and to variations in the extent and detail of reporting. For example, persistence times were rarely given, so a site could be scored as 'successful' only on the basis of being reported so by a cooperator or if the taxon persisted at the time of a 'last survey'. Information was insufficiently consistent for comparisons across taxa at levels other than the level of family, or of habitats, e.g. streams vs. lentic habitats, artificial vs. natural systems, etc. Even single vs. multiple stockings at a single site had to be treated as one, in part for the same reasons. Number of stockings per site that achieved total (1·4), intermediate (1.3) success (as defined above) and failure (1.2) showed little trend anyway.

An overall 'success' rate of 26.3% was computed for 407 sites. A single large programme involving reintroduction of Gila topminnow at 208 sites achieved a rate of 18-3%. When the latter was excluded, 199 sites (average 5·1 sites (2 to 33) stocked per taxon) succeeded 34·7% of the time. Three broad groups of taxa were identified based on degree of success: 14 established at all localities stocked, 17 realized some intermediate level of success and nine failed at all sites stocked. All totally successful and totally unsuccessful stockings occurred when numbers of sites were small (1 to 5, with an average of 1·9 sites stocked for each taxon at each extreme). Those intermediate in success rate averaged 21-4 sites (2 to 208) stocked per taxon (average 9-7 sites (2 to 33) stocked when topminnows were excluded).

Based on this it is clearly not yet possible to predict the success of translocations with any degree of accuracy, and it may never be. Probably, a —25-35% (multi-taxon) 'success' rate may be more than can be expected on a multigeneration basis. Almost 20% survival for a single, short-lived taxon like the Gila topminnow may also be acceptable over many generations. Timing is important. During wetter times survivorship will be high and during drought it will certainly be lower (Simons *et al.*, 1989; Hendrickson & Brooks, 1991). The same applied prior to the species' current, human-induced, imperiled state, but there were more populations scattered more widely and in more reliable habitats; barriers to dispersal, etc., were less prevalent. Further, the older a translocation programme the more time available for population extirpations. The topminnow effort included some translocations spanning —30 years; some other programmes were <5.0 years old.

Are the two case histories given above in fact successes in recovery based on reasonable interpretations of historical conditions? For taxa of naturally limited distributions they most likely are, since the animals persist in a diversity of habitats comparable with or perhaps greater that those in the historical record. As already outlined, native fishes under natural, arid-land conditions alternated between continuous or discontinuous distributions in connected or unconnected aquatic space. Their populations and almost certainly those of the species just discussed (excluding *C. diabolis* and *Cyprinodon* sp., which are/were single-spring endemic taxa) 'winked off and on' with seasonal or longer episodes of change, dispersal or lack of dispersal, etc. This was certainly the case with short-lived species and was almost certainly so for long-lived species in the light of the probable impacts on their well-being of known, longer-term climatic and geologic cycles.

Clearly, the success of transplanted stocks of fish (or other types of animal) of wider original distribution in an arid land like the western United States is difficult to define. Interim success might best be claimed when such a taxon survives in one or more of a number of sites over a few generations; only time will tell if these short-term 'successes' are true.

It must be kept in mind that premature reporting of a 'success' may have a major negative impact on a critical programme if, in fact, failure ensues. Too much success can also lull supporters into false security, resulting in down- or delisting of endangered taxa before the reasons for their original declines are fully understood. It seems doubtful that a delisted taxon might be relisted if it began to fail again. Failures tend to stimulate further efforts, to a point, or at least to increase the attention and thought being applied to imperiled taxa, communities or systems.

Errors and misjudgements resulting in taxon extinctions are serious, not only for the subject which disappears forever, but also for other taxa which may be undergoing similar management procedures. It must be remembered that minimum and maximum generation time for a pupfish may be a few weeks or months, while for razorback suckers it may be a few years or decades. The responses of these two extremes in life history strategies to management differ dramatically in scale, not only in time but also in space. The decision to report success or failure of a transplanted population or translocation programme should thus be made only after careful consideration of all the circumstances, and planning should always include the highest probability for error in favour of the resource.

After all this it may seem incongruous to assert that the author, in principle, opposes translocations. The technique should be used only as an emergency, stopgap measure for preservation of taxa. Managers in the western United States are in the unfortunate position of doing just that. Just as clearly, species conservation is less desirable than ensuring existence of habitat in which the species may perpetuate itself. For now, however, we must seek to conserve as many ecosystem elements as possible, with an eye toward broader, habitat-based management in the future. Translocations will thus almost certainly continue to be an invaluable way to avert population and species losses.

Early experiences have been valuable. They have indicated a lot of things to do and not to do, and alternative conservation strategies being applied through public and private actions will require further development of translocation technology. Rivers, lakes and spring—marshland complexes set aside as federal or state management areas or purchased as natural history reserves by non-governmental agencies (Williams, 1991) provide habitat for taxa now imperiled, if those taxa can be maintained until the habitat is suitable for their perpetuation. A shift of emphasis from single-species concerns to reconstruction, conservation and management of communities and ecosystems will result in mandates and desires to re-establish native faunal elements, and the circle will close with reintroductions of those elements which remain available (Price, 1989). Renovation of habitats contaminated by non-native trouts and restocking with native taxa by agencies otherwise dedicated to providing public sport fishing (usually for non-native species) has become common in the western United States. Addition of active management toward improvement of watershed and riparian conditions (Platts & Rinne, 1985), long recognized as major factors in deterioration of trout populations in the region (Rinne, 1988; Heede & Rinne, 1989), would make this an excellent contemporary example of such programmes. In some instances, such efforts are, in fact, underway.

An area of importance to know or estimate is the relative advisability of transplanting fish between and among natural sites vs. use of animals made available through *ex situ* propagation. One typically assumes wild fish to be genetically more fit, but fitness is attuned to the time and space in which an individual exists and translocation is into a new 'natural' place with new selection pressures. This may differ very little, or perhaps not at all, from placing the fish in a hatchery or from placing a hatchery propagated fish back into 'nature' in cases where intentional selection has not been applied in captivity. Without supporting data to the contrary, increased fitness should not be assumed from indirect, theoretical measures such as heterozygosity (Hedrick & Miller, 1992).

Costs of acquiring fish for direct translocation may be low compared with those for propagation, but hatcheries provide more individuals as well as control over size, sex and age distributions. Fewer fish are typically needed for broodstock than to translocate to one place from another, which helps ensure that sufficient numbers remain in nature to perpetuate the source population, and so on. The author is a strong proponent of mixed effort, simultaneous translocations of wild fish between natural habitats as well as into controlled conditions. If a taxon is rare enough to merit concern, it is rare enough to merit study in anticipation of a need for *ex situ* maintenance and an eye to future transplantation.

A justified criticism of translocation and especially of reintroduction is that the perpetrator may simply be providing more individuals to succumb to the same (often unknown) forces that originally extirpated the taxon. If the reason for extirpation is known, it should be removed prior to reintroduction. If not, reintroduction is one direct way the extirpating force can be again brought to bear on the taxon, and thereby identified. One of the most valuable components of the existing propagation programme at Dexter NFH for imperiled fishes has been the opportunities afforded for research (Johnson & Jensen, 1991).

Finally, a plea that what is done be summarized and made available through publication in the peer-reviewed literature. If such does not occur, more species and ecosystems and data critical for success in the battle for biodiversity will suffer from extinction. Each new generation of conservationists will be forced to start anew and our offspring may be forced to repeat history forever.

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