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THE BIOLOGICAL BASIS FOR THE DEFINITION OF SPECIES OF ANADROMOUS SALMONIDS UNDER THE ENDANGERED SPECIES ACT

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The rationale for the Endangered Species Act (ESA) of 1973 as amended in 1978 can be paraphrased as follows: Every animal species - as well as isolated populations within some species - represent unique and irreplaceable groups of organisms containing actual or potential ecological, scientific, historical, recreational, esthetic and educational value; all such groups warrant responsible management and-where necessary-protection. The assessment of the current status of such groups, leading to possible protective or remedial actions, requires a sound biological basis for the identification of both species and populations.

This report is an initial response from the Northwest and Alaska Fisheries Center to a mandate from the National Marine Fisheries Service to assess the status of certain stocks of anadromous salmonids relative to the ESA. It is intended to serve as part of a basis for subsequent documents that will identify specific problems and recommend courses of remedial action. The complexities and uncertainties of defining and identifying species and populations are examined primarily in the context of salmonid literature. Syntheses are made from these data to outline the general requirements for defining species and distinct population segments for the implementation of such definitions in accordance with the ESA. Numerous reviewers of the initial draft of this report provided supplemental information, identified unclear or erroneous statements, and suggested various modifications to clarify the presentation. I thank each reviewer for this necessary assistance which resulted in a more complete and a clearer statement.

DEFINITION AND CHARACTERIZATION OF SPECIES

The reality of the taxonomic level called "species" is accepted among most biologists within the framework of the definition: "Species are groups of inter-breeding natural populations that are reproductively isolated from other such groups" (Mayr, 1970). The recognized species of salmonids are generally consistent with this definition. Each of the five species of Pacific salmon (*Oncorhynchus*) that are indigenous to North America frequently exist sympatrically with one or more congeneric species (Aro and Shepard, 1976; Atkinson et al., 1967). Yet these species remain readily identifiable throughout their ranges. The coastal forms of steelhead (*Salmo gairdneri*) and cutthroat (*S. clarki*) trout likewise occur sympatrically; although they are fertile in laboratory crosses (J. Mighell, NMFS, personal communication), they do not significantly interbreed in nature.

It would appear at first glance, then, that there are no problems among anadromous salmonids at the species level with regard to the identification of such groups. This picture is deceptive, however, and such a conclusion is premature. The five species of Pacific salmon and the two trout species mentioned above have each evolved and diverged from common ancestors for periods probably exceeding 10^5 years (Neave, 1958). One may safely assume that their ancestral forms very likely resembled one another much more than do the forms existing today.

Sympatric Populations

Assuming that the processes leading to speciation (e.g., see Stebbins, 1971) are more or less continual, it is reasonable to suggest that populations in the process of incipient speciation currently exist in salmonids. Evidence for non-interbreeding of conspecific salmonid populations that coexist in the same area would support the contention that these populations are genetically

isolated from one another and are in the early stages of processes leading to complete reproductive isolation (i.e. speciation). Such evidence exists from investigations of salmonid populations and some of it will be briefly reviewed below.

Innate tactic responses leading newly emerged salmonid fry either upstream or downstream to lakes serving as nursery areas have been demonstrated in Sockeye salmon (O. nerka) from diverse geographic regions (Raleigh, 1971; Brannon, 1972). These responses were altered through individual crosses involving both inlet and outlet parents indicating the inadaptive nature of natural crosses between inlet and outlet populations of a given drainage. This inadaptiveness infers the genetic isolation of such populations sharing an otherwise common environment.

Two morphologically distinct groups of Bonneville Whitefish (Prosopium spilonotus) were found to coexist in Bear Lake on the Utah-Idaho border (White, 1974). Each form was distinct with regard to growth, and to age and size at maturity. It was recommended that each group be given tentative recognition as different species.

Direct evidence for non-interbreeding of two Brown trout (Salmo trutta) populations co-existing in a small Swedish lake has been recently reported by Ryman et al., (1979). These groups (identified on the basis of distinct biochemical genetic profiles) had different growth rates and spawning areas. The authors postulated that one group was a relict population that had been isolated within a glacial refuge about 125,000 years ago while the second represented a more widespread group of brown trout that recently reinvaded the area. Although it may be argued whether or not these two groups are sufficiently reproductively isolated to warrant their classification as distinct species, they are clearly diverging towards such a distinction. Similar sympatric populations of Swedish char (Salvelinus alpinus) have also been reported (Nyman, 1972).

Direct evidence for sympatric populations of sockeye salmon has been found in sockeye salmon populations of the Lake Washington drainage near Seattle. Genetic differences of proteins have identified a population of non-anadromous sockeye salmon in Issaquah Creek of the Lake Washington drainage near Seattle that is distinctly different not only from other non-anadromous and anadromous sockeye salmon populations of this drainage but also from all sockeye salmon populations outside of this drainage that have been studied (Utter et al., in press).

The above examples describe diverged and sympatric conspecific populations of salmonids that are in presumably early or intermediate phases of speciation. It is very likely that other - possibly numerous - similar instances exist among such species of salmonids in view of the recent and isolated efforts that have been made towards their detection.

Allopatric Populations

Another segment of the species question concerns nominally conspecific populations that are temporally or geographically isolated from other populations. These populations may be in various stages of incipient speciation, but their capabilities for maintaining genetic isolation under sympatric conditions cannot be assessed. The inland cutthroat trout complex represent a series of geographically isolated groups of populations where recent estimates of genetic distances demonstrate substantial genetic divergence among some of the groups suggesting incipient speciation (Loudenslager & Gall, in press). A detailed examination of the population structure of the coastal group (*S. clarki clarki*) over a limited geographic range (Campton, 1980) indicated a strong tendency to maintain the integrity of local populations further suggesting the possibility of isolates within this group that may be diverging towards speciation.

Pink salmon (O. gorbuscha) is the best known example of temporal isolation in salmonids. Their rigid two-year life cycle has led to two distinct gene pools throughout their species range. Extensive geographic surveys of genetic variation have identified a greater similarity within a year class - regardless of geographic origin - than between year classes - even in the same streams (Aspinwall, 1974; Johnson, 1979; Donnelly et al., 1979). Even and odd year pink salmon have also evolved different intrinsic growth rates (Ricker et al., 1978), distinct geographic distributions (Aro and Shepard, 1967; Atkinson et al., 1967), and differential temporal and distributional spawning patterns having a heritable basis within individual drainages used alternately by both year classes (Helle, 1970; Taylor, 1980). It is evident that the two year classes are diverging towards ultimate speciation if their genetic isolation persists.

Nominal Species

The phenotypic plasticity and diverse life history capabilities of many salmonids have historically confused the species picture in some instances. Thus, two phenotypically different groups having non-overlapping geographic distributions and distinct life history patterns may be categorized as separate species and yet be sufficiently closely related to not warrant such a distinction.

The current taxonomic status of rainbow trout (Salmo gairdneri) and related population groups is a possible example of this situation. This group of populations comprises two recognized species (S. gairdneri and S. aquabonita) plus a third population complex - the redband trout - that has not been formally named but has been elevated to species rank in much of the current literature (see Gold, 1977). Although it is beyond the scope of this report to make a detailed review of these groups (see Behnke, 1965; Gall et al., 1976; Gold, 1977;

Wilmot, 1974) it is pertinent to examine the genetic similarity (i.e. values between 0 and 1 averaging the level of detectable genetic similarity between two populations over all loci examined - usually greater than 20, see Rogers, 1972; Nei, 1972) among these recognized species groups in contrast with those among the subspecies of cutthroat trout. Loudenslager and Gall (in press) have reported an average genetic similarity (based on electrophoretic data from approximately 40 loci) of about .85 among three major interior subspecies of cutthroat; Campton (1980) has identified a similar divergence of the coastal subspecies from other cutthroat groups. The genetic similarity among the rainbow-golden-redband trout complex (based on data analogous to the cutthroat trout comparisons) is above .925 in all comparisons between populations (Allendorf and Utter, 1974; R. Smith, personal communication - data for Ph D thesis, Univ. of Cal., Davis). The purpose of making this contrast is not to debate the validity of the species rank in one group or the subspecies rank in the other (although such a debate based on a detailed presentation and synthesis of the known facts of the matter is clearly in order), but to point out the pitfalls inherent in the necessarily arbitrary nature of species classification, particularly at the early stages of divergence.

It is evident, then, that uncertainties do exist concerning species classification and identification among salmonids. Some of these uncertainties are directly important to consider with regard to the implementation of the ESA because of the converse possibilities of either considering two or more non-interbreeding groups to be a single panmictic unit or granting unwarranted separation to minimally diverged populations. These problems will next be considered at the within-species level.

DEFINITION AND IDENTIFICATION OF DISTINCT POPULATION SEGMENTS

The processes resulting in the formation of distinct intraspecies populations are the early phases of those ultimately leading to speciation, with the primary distinction being (by definition) the absence of reproductive isolation. The strong homing tendencies of anadromous salmonids make this group particularly susceptible to the formation of such populations. Given this common characteristic, it is tempting to formulate a generalized model for migratory salmonids in which a hierarchy of areas, major streams and tributaries is used to define the basic population unit.

The model does provide a useful first approximation of reality. The regularity of the return of various species with regard to location and time has been well documented in the salmonid literature (reviewed in Ricker, 1972). Examinations of comparative genetic attributes of these runs in different species (as methods have become available) have demonstrated that genetic similarity tends to increase directly with geographic proximity (Utter et al., 1974; Kristiansson and McIntyre, 1976; May, 1975; Grant, 1977; Thorgaard, 1978; and Allendorf and Utter, 1979).

The model has significant deficiencies, however, that precludes its use as the sole criterion for defining distinct population segments of anadromous salmonid species. It assumes a single continual radiation of population segments from an initial starting point and fails to consider geological or biological events that may result in discontinuities of such a predicted radiation. Thus, the model would predict that the greatest similarity would be within major drainages when considering proximal populations of the Columbia and Fraser Rivers just upstream and downstream from the Cascade Crest. However, morphological and biochemical evidence have independently shown just the opposite to be true (Behnke, in press ; Allendorf, 1975; and Utter et al., 1979).

The conclusion that the populations either east or west of the Cascade Crest have respectively the greatest similarity regardless of drainage is supported by knowledge of recent geological events that explains the adjacent location of diverged populations. Geographic discontinuities of population units of coho and chinook salmon that deviate from the model have also been reported (Allendorf and Utter, 1979).

A second deficiency of the model is the tacit assumption of a relatively uniform capability for radiation among the different anadromous species. Much evidence has accumulated to indicate that capabilities for radiation differ significantly among anadromous salmonids as a reflection of the evolution of distinct life history patterns (reviewed in Utter et al., in press). In addition, transplantations[1/] interfere with heritable patterns of homing precision (Ricker, 1972) and further complicate innate differences among species in the formation of discrete populations groupings.

The above discussion does not negate the application of the model, but places strict limits on its use. Generalizations cannot be made between species because of differing geographic ranges of interbreeding populations. Generalizations within species must consider the possibility of natural or man-made discontinuities.

1/ Intentional transplantations and introductions of stocks by man significantly compound the problem of population identification and discontinuity; the population units described here - unless specifically designated otherwise- are presumed to be a reflection of natural distributions, and the topic of introduced populations will be considered in a later section.

Data Required for Identifying Population Segments

It is pertinent at this point to ask about the kinds of data that are required to best identify a distinct population segment since the model based on homing requires supplemental data in order to provide generally reliable information. An ideal set of data should have a purely genetic basis because data reflecting environmental variables could indicate homogeneity among genetically discrete populations occupying similar habitats and thus give misleading information. These ideal data should reflect the particulate nature of genetic variation at individual loci (i.e. Mendelian variation) in order to quantify genetic differences. The magnitude of measurable differences between any two populations should be a direct reflection of the total genetic variation that separates these groups. A sufficient sampling of variant loci would be needed to increase both the probability of finding genetic differences between populations and the accuracy of measurements estimating relationships among populations. Finally, these data should be attainable with reasonable efforts so that statistically meaningful sample sizes can be obtained.

The ability to define distinct population segments in salmonid species has been limited in the past through the absence of data fulfilling the above criteria. A review of morphological, physiological and behavioral approaches, used to examine the distribution of genetic variation within species of Pacific salmon (Ricker, 1972) indicated (1) that much genetic variation existed among populations of Pacific salmon and (2) that homing had a strong genetic basis and was the most definitive indicator of population structure. Nevertheless, the discreteness of the underlying genetic variation remained unknown and this precluded any quantification of purely genetic differences among populations.

Homing has also been excluded as a primary criterion for population definition because of the limitations outlined above. The inability of these methods to generally provide reliable genetic definitions of population structures does not negate the overall value of these data which cumulatively add great wealth to understanding the biology of Pacific salmon and which occasionally (usually through a combination of distinct homing and timing) actually identify discrete population segments.

Studies of allelic variations of proteins (i.e. electrophoretically detected biochemical genetic data) have recently received increasing attention as a tool in fisheries research and management (Reviewed in Utter et al., 1974; Allendorf and Utter, 1979), and fulfill more of the idealized criteria outlined above for data required to identify discrete population segments than any other known method. The use of protein data has added a new dimension to the study and understanding of inter- and intra-specific relationships of salmonids. Indeed, most of the recent advances in the understanding of such relationships are the direct result of interpretations of protein data.

Although protein data are a valuable addition to the tools used to study the genetic structure of populations, they should not be regarded as a panacea. For instance, it may be properly concluded from consistently different frequencies of allelic variants in collections of fish from two different areas that a real genetic difference exists between the populations of these areas. However, the absence of variation among different collections taken within each area does not - in itself - justify concluding that the collections of that area were drawn from a single genetically homogenious population.

The validity of this principle can be illustrated in two examples. Allendorf (1975) initially identified two major population groups of steelhead trout in the Colombia River where the upstream populations were not strongly separated within the upper Columbia River or Snake River branches. Subsequent

data based on additional protein systems (Milner, 1977) strongly separated steelhead trout of the Dworshak Hatchery (Snake River) from populations of the upper Columbia River. The second example concerns the Yellowstone cutthroat trout (S. clarki bouvieri) for which biochemical genetic data from geographically distinct populations have revealed minimal allelic frequency differences (Loudenslager and Kitchin, 1979). Nevertheless, populations within the subspecies have demonstrated a large diversity of physiological adaptations to widely different environments (Varley, 1979) and innate differences of tactic responses have been observed in emergent fry from inlet and outlet streams in Yellowstone Lake (Raleigh and Chapman, 1971). Thus, the absence of protein variation among populations did not preclude the existence of considerable genetic diversity.

The possibility that the geographical distribution of protein variation more heavily reflects environmental rather than life history variation is another point that requires examination. It has been implied to this point that the latter situation is correct. Perhaps the point is not an important one for this document where the primary objective is the identification of discrete populations rather than the quantification of relationships among them. However, if the geographical distribution of protein variants strongly reflect environmental variation, then a single interbreeding population may have different frequencies of protein variants in different environmental settings and other variables having a less discrete genetic basis (e.g. meristic counts) may be more appropriate markers for the actual genetic structure of the population. The consistency of allelic frequencies of protein variants in populations of anadromous salmonids has been recently examined throughout life cycles in single generations, between generations, and among overlapping year classes. All comparisons demonstrated the temporal stability of allelic

frequencies and justifies their use primarily as markers of variation among populations rather than among environments (Utter et al., in press). An analogous situation exists in man - where relationships deduced by the distribution of protein variants approximates anthropological estimates of true relationships while a different set of relationships based on external morphological features is more a reflection of ancestral environments (Cavalli-Sforza, 1974 and Patterson, 1978).

What, then, are appropriate data requirements for identifying discrete population segments within an anadromous salmonid species having established (1) that a model based only on homing is inadequate by itself, and (2) that sets of protein data are necessary but generally incomplete for adequate identification? The complexities of different situations preclude a simple generalized solution. Rather, each situation must be regarded as unique which - in fact - it is. However, a logical sequence of processes can be outlined which should lead to satisfactory results:

I. Accumulate background data on the region in question. What is the history of the species in this area? (transplantation records or reliable anecdotal information; population sizes, spawning times and spawning locations - past and present; man induced changes in the environment; compilation of all available allelic frequency data; any studies pertaining to this species in or from this region could contain valuable information). What is the geological record of the region? (data suggesting former isolation in presently continuous drainages that may have resulted in a multiplicity of populations).

II. Collect data from a systematic sequence of samples from this area. Initially sample at extreme ranges of the area using data from Phase I for guidelines. Collect protein data and measure other biological variables (e.g. meristic, timing and growth data) that may provide clues suggesting reproductive isolation. Measure physical and biological aspects of habitat differences. Synthesize data from initial sampling to determine the next approximation towards identification of population structure of the region.

III. Determine the structure and biological status of the populations of the area. Successive approximations based on preceding samplings, data collections and syntheses lead ultimately to an answer based on a thoughtful and thorough analysis of the best available data.

The process is necessarily vague. Beyond the early stages of Phase II there is no way to realistically estimate the amount of work (and hence the cost) involved in obtaining the ultimate answers because of the numerous uncertainties that vary with every situation; such is the nature of scientific inquiry. Nor is there any certainty as to what methods will provide the ultimate answers, particularily in instances where differences detected by protein data are minimal. Cytogenetic studies have complemented protein data in examining the genetic structure of steelhead populations (Thorgaard 1977a; 1977b) although the amount of intraspecific variation is not nearly as extensive as protein variation and therefore, may not be generally applicable. A promising process which examines enzymatically fragmented mitochondrial DNA (Avise et al., 1979) may also be acceptable when this process becomes further developed. Other procedures that detect some degree of genetic variation remain useful but lack the capability of precise genetic identification of distinct population units.

On the other hand, the three-phased format outlined above is flexible and applicable both to inter- and intra-specific problems. Proper implementation in conjunction with the ESA promises a wealth of new insights into the structure of salmonid populations and the dynamics of speciation.

Finally, it is important to recognize that many situations may require remedial actions prior to a time frame that would permit the full implementation of this process. Provisional decisions based on incomplete data (i.e. Phase I) may be necessary in such instances. Final decisions could then be based on subsequent revisions as additional data became available through the fulfillment of Phases II and III.

BIOLOGICAL IMPLICATIONS OF TRANSPLANTED AND HATCHERY POPULATIONS

The management of anadromous salmonids in the western United States during the last century has involved the development of hatcheries and the mass transplantation of fish stocks. These developments considerably complicate the applications of the ESA to managing these populations. Some of these complexities are principally non-biological and will not be examined here. For instance, the question of whether or not an artificial run that is self perpetuating (e.g. the sockeye salmon run in the Cedar River near Seattle) should be protected under the ESA is pertinent, but beyond the scope of this report. Questions pertaining to some of the biological complexities are examined below.

What is the biological impact of transplanted or hatchery adapted populations on indigenous populations? This question is a major concern in current salmonid management and its answers have a direct bearing on implementation of the ESA. There has been much conjecture concerning the possibility of negative effects on native populations of supplemental plantings of non-native and hatchery fish. A major potential threat - over and above competition, predation and disease communication - is interbreeding of introduced fish with

native populations. Until recently, it has been difficult to directly measure these effects although Behnke (in press) has reported morphological evidence of interbreeding of introduced salmonids with native interior cutthroat trout populations, and the ultimate replacement of much of the native interior cutthroat trouts with introduced or hybrid forms. A negative result of this introgression has been the apparent loss of the capability for large growth that formerly existed in some interior cutthroat populations. Loudenslager and Gall (in press) have confirmed and quantified some of this introgression with allelic frequency data based on differing characteristic protein patterns of native and introduced species.

Some data are accumulating on the genetic impact of hatchery plants on native populations. A long term study by the Washington State Department of Game is in progress on the Kalama River to study the immediate and long term interactions of hatchery planted and indigenous steelhead trout populations. Hatchery fish are identifiable by a specially bred protein variant (i.e. genetically marked) so that the variant will be passed on to descendents and the actual genetic impact of these plants can be measured indefinitely beyond the first generation (Crawford et al., 1978; 1979). Reisenbichler and McIntyre (1977) - also using genetically marked fish - identified genetic differences affecting growth and survival between hatchery and wild steelhead trout of the Deschutes River where performance of wild fish was best in stream environments and that of hatchery fish was best in pond environments. The Washington State Department of Fisheries has been engaged in a long-term commitment to study the genetic impact on naturally spawning fish of selected chum salmon enhancement projects since 1976 and has currently extended these efforts to other salmon species (Seeb and Wishard, 1977). A study is in progress which will compare the genetic structures of steelhead trout populations of the

Skagit River in Washington (Campton, 1979) where heavy hatchery plantings have been made for many years, with those determined from recently completed studies of tributaries of the Fraser River of British Columbia (Parkinson, 1980) where management is based on native fish; these comparisons should provide valuable insights into the effects of hatchery management on population structures.

The above investigations are model studies for measuring the genetic impact of hatchery fish on native populations. More studies of this nature are clearly needed, particularly in situations where management involving large scale transplantations and artificial propagation is just beginning (e.g. ocean ranching). It is now both technically feasible and economically realistic to quantify the genetic impact of transplanted and artificially propagated fish on native fish over time and space; it is irresponsible to ignore this capability.

Can endangered populations be perpetuated by artificial propagation? Behind this question lies a more penetrating question with regard to the ESA: does artificial propagation of endangered populations irrevocably alter those qualities that make a particular population worthy of protection under the ESA? The evidence is compelling that the process of "domestication" genetically alters the adaptive qualities of a population (e.g. see Reisenbichler and McIntyre, 1977, cited above). However, a systematic examination has not been made to determine whether or not domesticated populations retain the capabilities to revert to the original wild state. If generally affirmative data are obtained, the primary focus can be on perpetuation of the population, regardless of changes in the habitat.

There is a great deal of evidence demonstrating the capability of domesticated rainbow trout to become established in diverse habitats (MacCrimmon, 1971; Behnke, 1965; VanVelson, 1978). This evidence is consistent with the recent finding of high average heterozogosity within most domesticated strains of rainbow trout (Allendorf and Utter, 1979; Busack et al., 1979), and suggests that many hatchery strains have retained a sufficient pool of genetic variation to adapt to a variety of natural habitats despite a century of domestication.

However, this possibility has not been adequately tested by controlled experimentation or systematic observation, and even if true, it would be dangerous to extrapolate to even closely related species (or subspecific taxa) where a data base is minimal or non-existent. Recent observations have demonstrated that genetic variation is often lost in the process of establishing hatchery strains from wild populations of salmonids (Ryman et al., in press; Allendorf and Phelps, in press); thus a representative sampling of the gene pool in question must be obtained in establishing a cultured population. It is also important to recognize that species or populations requiring protection under the ESA have most likely lost much genetic variation through severe reductions in population sizes and therefore probably have gene pools with significantly reduced levels of genetic variation relative to those of outbred rainbow trout populations. Such populations may therefore lack the genetic plasticity to adapt to conditions of culture or to subsequently re-adapt to natural environments. Conversely, the flexibility of artificial culture has not been considered to this point, and it is feasible to simulate natural conditions to a much greater extent than is commonly done in salmonid hatcheries. The possibilty of perpetuating wild populations of salmonids by artificial propagation in conjunction with the ESA therefore cannot be generally resolved

at this point; each situation will probably have to be separately considered following a thorough examination of its pertinent biological attributes.

SUMMARY

The validity of most recognized species of salmonids under the biological species concept is supported by evidence from diverse sources. However, the specific status of a number of recently diverged populations remains uncertain. It is particularly important to consider the possibility of unrecognized reproductively isolated populations for protection under the ESA.

Innate life history differences among species as well as numerous uncertainties within species preclude the use of a generalized model based on homing as the sole or primary means of defining discrete population segments of anadromous salmonid species. A process involving successive samplings, analyses and syntheses of data from populations of a particular area is suggested. A major requirement of this process is reliable genetic data. The capability for the detection of allelic proteins by electrophoretic methods has provided a major tool for identifying and measuring genetic differences among populations and species. These data are necessary, but insufficient for identifying most population segments and must be complemented by other biological and life history data as well as by historical and geological information. Provisional classifications of threatened or endangered populations on the basis of incomplete data may be necessary in many instances, but final classifications should depend on complete sets of data.

Transplanted and hatchery populations complicate the identification and management of anadromous salmonid populations under the ESA. Some evidence is cited that indicates a potential or actual adverse genetic effect of hatchery or transplanted fish on some native populations, and current studies designed to

measure such effects are mentioned. The technical and economical feasibility for measuring these effects suggest that such measurements should be a requisite for new or extended transplantation and hatchery operations.

Further data are needed to determine whether or not threatened or endangered species and populations can be artificially perpetuated and still retain the capability to adapt to wild environments upon reintroduction to native hatitats. This capability apparently exists in some domesticated strains of rainbow trout. However, large differences exist in the intrinsic levels of genetic variation between most domesticated populations of rainbow trout and many threatened or endangered natural populations of salmonids.

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