POPULATION GENETICS OF ENDANGERED CATOSTOMID FISHES OF NORTHERN CALIFORNIA

Contract: FG-8143

Draft Final Report: April 1, 1991

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INTRODUCTION

Three catostomid species native to northern California and southern Oregon are federally and state listed endangered species: Modoc sucker, (Catostomus_microps Rutter), shortnose sucker (Chasmistes brevirostris Cope), and Lost River sucker (Deltistes luxatus (Cope)). Each of these species have been reported to be experiencing census declines to critical levels due primarily to habitat alterationand loss and hybridization with other sucker species (Williams et al. 1989).

The Modoc sucker is known from only two disjunct areas: the Turner-Hulbert-Washington Creeks drainage and the Rush-Johnson Creeks system (Moyle 1974). Threats to this species include continued habitat loss to grazing induced erosion and drought conditions and presumed hybridization with Sacramento suckers (Catostomus occidentalis Ayres). Erosion of stream barriers has allowed Sacramento suckers access to Modoc sucker spawning sites. If Sacramento suckers hybridize with Modoc suckers and genetic introgression occurs, pure Modoc suckers may vanish. The most current census estimate of only 1,300 individuals (Mills 1980) suggests quick action must be taken to prevent the Modoc sucker from slipping towards extinction. Such action must focus on saving the "purest" Modoc sucker populations.

As with the Modoc sucker, both the Lost River sucker and the shortnose sucker have experienced substantial population reductions. Extensive habitat alteration has occurred and interspecific hybridization has been postulated. Morphological evidence indicating hybridization of shortnose suckers with Klamath smallscale suckers (Catostomus rimiculus Gilbert and Snyder) in Copco

Reservoir (Miler and Smith 1961) and Klamath largescale suckers (Catostomus snvderi Gilbert) in Clear Lake Reservoir (Williams et al. 1985) has been reported.

Cope (1879) described the Lost River sucker as be a member of Chasmistes Jordan but it is now recognized either as a member of Catostomus Le Sueur (Robins et al. 1980) or as the sole extant representative of the genus Deltistes Seale (Miller and Smith 1967, 1981). Native to most of the Lost River system, the range of the Lost River sucker has been severely restricted; Coots (1965) reports that draining of Sheepy Lake, Lower Klamath.Lake, and Tule Lake in the early 1920's reduced the suckers' census to critical levels. The Lost River sucker is now known primarily from Copco Reservoir, Clear Lake Reservoir, and Upper Klamath Lake (Moyle 1976). As with the above species, the working hypothesis of hybridization with other species, specifically the shortnose sucker, as a mechanism of endangerment has led to both state and federal listing of the Lost River sucher.

Recent estimates show that both the shortnose sucker and the Lost River sucker have had severe declines in spawning runs with little or no recruitment (Bienz and Ziller ms, Scoppettone 1986). If populations continue to decline, these species may cross below the minimum viable population threshold and be lost. Recovery efforts must focus on those populations which are most likely to truly represent the pure species' genetic makeup, thus an effort to determine genetic diagnostics for the shortnose sucker and the Lost River sucker is of high priority.

Although not of primary conservation importance, the systematics of the Klamath Basin suckers is of interest. On the basis of morphological data, Miller and Smith (1961) hypothesized that the genus Chasmistes was derived

from the more primitive Catostomus state and that Deltistes was intermediate. Ferris and Whitt (1978) used gene duplication data to argue that certain members of Catostomus were advanced over Chasmistes brevirostris, Deltistes, and the rest of Catostomus. These hypotheses and perhaps the taxonomic validity of Deltistes may be tested with genetic data.

Six objectives were identified to be completed under CDFG contract #FG-8143: 1) establish a state-of-the-art electrophoretic laboratory dedicated to genetic studies of threatened and endangered species; 2) develop an internal catostomid genetic standard using the widespread and secure Sacramento sucker as reference; 3) characterize the genetics of presumed pure populations of Modoc sucker, shortnose sucker, and Lost River sucker; 4) determine genetic status of presumptive hybrid sucker populations; 5) assess systematic relationships of Chasmistes, Deltistes, and Catostomus; and 6) quantify correlation of meristic and genetic data for Modoc sucker populations.

MATERIALS AND METHODS

Populations of suckers were sampled at 9 localities in California and Oregon (Table 1, Figure 1). Shortnose suckers were collected from upper Klamath Lake (SNSK), Clear Lake Reservoir (SNS_{CL}), and Copco Reservoir (SNS_{COP}). Additional species collected were Sacramento sucker (SAC), Klamath smallscale sucker (KSS), Klamath largescale sucker (KLS), Lost River sucker (LRS), Tahoe sucker from Eagle Lake (EAG), and suckers from Cedar Creek, Moon Reservoir (CCMR).

Electrophoretic methods outlined in Aebersold et al. (1987) were followed. Tissues sampled were muscle, heart, eye, and liver. Tissues were mechanically homogenized in PTP buffer (0.05 M PIPES, 0.05: Triton X-100, 0.2 mM pyridoxal-5-phosphate, pH 6.8), centrifuged at 30,000 g for 10 min. and either used immediately or stored at -80°C until use. Histochemical staining techniques generally followed Busack et al. (1979) with modifications. Protein systems examined are listed on Table 2. The peptidase protocol was that of Harris and Hopkinson (1976) with each peptidase specifically identified by substrate specificity and differential tissue distribution (Frick 1983).

Enzyme nomenclature followed recommendations of the International Union of Biochemistry (1984). Electrophoretic patterns were interpreted according to established inheritance models. Individual alleles were identified by their electrophoretic mobility relative to the most common allele found in Sacramento suckers. No implication of relationship among alleles is intended.

Summary statistics included average heterozygosity within each population, H, and proportion of polymorphic loci, $\%P_L$. A locus was

considered polymorphic if any variant allele was observed. Relative gene diversity among populations within brevirostris (G,t.) were estimated as (Nei 1973)

where

$$G_T = \qquad (2)$$

As described by Nei et al. (1977), G_{st} may be equated to F_{st} (Wright 1943) allowing an estimate of historical gene flow among populations, Nm, according to Wright (1969) where

$$Fst = 1 / (4Nm + 1). \qquad (3)$$

Hybridization was quantified depending on the apparent level of occurrence. Level I hybridization is indicated by the presence of complete allelic differences at any locus between samples of presumed parental populations. The maximum estimate of hybridization occurring under level I is given by

$$q = {}^{1} - \qquad (4)$$

where q = minimum detectable allele frequency = maximum estimate of undetected hybridization, α = acceptable error rate = 0.05, n = sample size of hypothesized introgressed population, and l = number of loci which show

complete allelic differences. The estimate, q, obtained by (4) is a measure of sampling error and thus a maximum estimate with its confidence interval including the value zero.

Level II hybridization is indicated by low frequency (<0.10) allelic overlap at loci expected to show complete allelic difference. The maximum estimate of hybridization occurring under level II is the greater of the observed frequency of overlap (Buth et al. 1987) or q estimated by equation (4) with the variable l set to one. Standard error, S_r, of observed frequency overlap estimate is given by the square root of the allele frequency variance, v,, where v, is calculated by

$$v_p = (p * (1 - p))/(2n - 1), \qquad (5)$$

and p = the observed frequency overlap, and n = sample size of the potentially introgressed population.

Level III hybridization is indicated by moderate to high frequency (>0.10) of allelic overlap at loci expected to show complete allelic difference. The estimate of hybridization occurring under level III is estimated by the genotype index method of Campton (1987).

Between population genetic distance estimates were compiled using Rogers genetic distance index (Rogers 1972). These genetic distance values were used to estimate systematic relationships among species by a modification of the distance Wagner method (Farris 1972). The goodness-of-fit criteria of Nei et al. (1983) was used. Systematic relationships were also estimated by using frequency-restricted presence/absence coding of individual alleles as

input for construction of a Wagner tree (Farris 1970). Under the frequency—restricted presence/absence procedure, input data is limited to only those phylogenetically informative alleles (Ferris et al. 1981) occurring at frequency equal to or greater than the q value estimated by (4) for the smallest sample size of included populations. The Wagner tree was assessed by the patristic/phenetic ratio. Cladograms were rooted by mid—point estimation.

RESULTS

Electrophoretic analysis of 9 catostomid populations detected 53 alleles segregating at 19 polymorphic loci (Table 3). Ten loci were monomorphic: Ldh-A, Ldh-B1, sMdh-2, mMdh-1, Pgdh-2, Ck-1, Ck-3, Tpi-2, Cpi-1, and Gpi-2. Thirteen private alleles were detected. Private alleles are those which occur only in a single population or taxon. The most interesting allozyme finding was the Pgm-1,2 rediploidization event in Cedar Creek, Moon Reservoir suckers (CCMR) and the Tahoe suckers from Eagle Lake (EAG). This finding calls for investigation of additional populations of Tahoe sucker and those sucker species which are presumed to be closely related to Tahoe sucker such as the Owens sucker (Catostomus fumeiventris Miller), the Warner Valley sucker (Catostomus warnerensis Snyder), and, perhaps, the undescribed Wall Canyon sucker (Catostomus sr.).

Within any particular population, approximately 1/5 of all loci were found to be polymorphic (Table 3). Percent polymorphic loci ranged from 17.2 in CCMR 34.5 in Sacramento sucker (SAC). Within population heterozygosity estimates, H, ranged from 0.03 in Lost Rive sucker (LRS) to 0.11 in (EAG). These heterozygcsity values are well within the range for teleosts (Nevo et al. 1984), indicating robust populations.

The relative gene diversity estimate among the three shortnose sucker (SNS) populations, G_{ST}, was 0.069 (Table Equating G_{ST} and F , applying equation (3), and solving for Nm yields an estimate of historical gene flow between populations > 3 individuals per generation.

No clear evidence of hybridization between any (SNS) and Klamath smallscale sucker (KSS) or Klamath largescale sucker (KLS) was found. Two

cases of possible level II hybridization were found. No level III hybridization was detected (Table 5). Maximum estimates of hybridization between the sucker populations studied ranged from 1 to 151. and are listed on Table 5. These estimates are largely statistical effects of the limited sample sizes, especially in those estimates involving the small LRS sample.

Systematic analyses are summarized in Figures 2 and 3. Both analyses cleanly separated the CCMR and the EAG from the other species. The genetic differences between CCMR and EAG may indicate that each is a distinct species. The genetic distance cladogram (FIG. 2) had a patristic/phenetic deviation of 0.02. This value is analogous to a standard error in branch lengths. Thus, confidence in Figure 2 is not high. Confidence in Figure 3 is higher. Approximately 1/2 of all included characters showed homoplasy yet four conclusions may be drawn from this analysis. The Pgm-1,2 rediploidization event diagnoses the CCMR and EAG lineage. Further investigation of this lineage may reveal the need for formal nomenclatural action. Certain species were further distinquished by private alleles such as the sAat (110) allele that is restricted to EAG. The lineage including the other five species is diagnosed by the Icdh (100) allele. The correct phylogenetic positions of KLS and KSS need additional analysis. The placement of SAC as well differentiated from *SS*, LRS, *KSS*, and KLS is justified by several characters (Table 3) including the fixed allele difference seen at Ada. Linkage of *SNS* and LRS as sister taxa is validated by the Ldh—B2 (95) allele.

DISCUSSION

As discussed in earlier Progress Reports under contract FG-8143, an electrophoretic laboratory has been set-up and an internal catostomid genetic standard using Sacramento suckers as reference has been established. This report focuses on contract objectives 3), 4), and 5) as outlined in the Cntroduction. Since no Modoc suckers were collected prior to writing this draft final report, contract objective 6) will be completed at a later date

Each of the nine sucker populations sampled were found to have moderate levels of genetic diversity as quantified by heterozygosity and proportion of polymorphic loci. These values indicate that the populations, have not reached census levels where genetic extinction components are imminent. Within the individual shortnose sucker populations approximately 93% (1 - = 1 - 0.069) of the species total genetic diversity. This suggests that each population is a good rand equal) representative of the genetic characteristics of extant brevirostris. Obviously, we cannot assess what the shortnose sucker's genetic status was in the past, but we can say that it was probably not significantly different than it is now.

The principal cause for the declining status of the catostomid species we studied is human modification and destruction of their habitat (Williams et al. I989). We would do well not to forget that habitat alteration of a rate or magnitude greater than species' adaptive abilities is the overwhelmingly common component of both historical and recent extinction events (Donovan 1989, Miller et al. 1989). The secondary threat, secondary onlyin time not in potential impact, is presumed interspecific hybridization leading the lOss of species-specific characters. This study was done to obtain genetic

evidence concerning the hybridization hypotheses.

Discussion of hybridization for each species follows.

Chasmistes brevirostris Cope

The hypotheses concerning shortnose suckers addressed by this research were stated by Miller and Smith (1981):

> "The suckers passing under the name Chasmistes brevirostris . . from Copco Reservoir, Siskiyou Co„ California, are an introgressed population with traits of Catostomus rimiculus." (op. cit. p. 22) and;
>
> "Recently—collected specimens (from the Klamath Lakes region) examined by us have . . traits distinct from brevirostris but clearly characteristic of Catostomus snyderi, indicating introgression with that species." (op. cit. pp. 22 & 24).

Miller and Smith (1981) indicate that the proportion of individuals which are products of hybridization is high: 30% (11 of 27) Lake of the Woods, OR (op. cit. p. 24), and 557. (? of 7) Copco Reservoir (op. cit. p. 25). These individuals were purported to represent both first generation hybrids (Fis) and backcrosses. In spite of the 557. hybrid estimate, they regarded (op. cit. p. 25) the Copco Reservoir population as a "relatively intact gene pool of Chasmistes brevirostris (that] deserves protection and management." This hybridization hypothesis also extends to the shortnose suckers of Clear Lake

Reservoir which have been reported to show evidence of introgression with Catostomus snyderi (Williams et al. 1985).

To sum the hybridization argument: "We have not, however, seen any recently-collected specimens from Klamath Lake [nor from anywhere else) that are the same as brevirostris" (Miller and Smith 1981, p. 23).

Something which must be kept in mind is that hybridization is in and of itself not a risk to a species' integrity if the produced hybrids are sterile. If Fis are produced and they are infertile genetic introgression cannot occur. Introgressive hybridization is the incorporation of genes of one species into the gene pool of another and can only happen if Fis are fertile and successfully backcross (breed with one or both parental species). Without introgression, species-specific characters will not be compromised by the hybridization event.

Certainly, interspecific hybridization and introgression do take plaCe. Campton (1987) cites the presence of thousands of references concerning natural and artificial hybridi ation of fishes. As discussed by Allendorf and Leary (1988), genetic introgression can be a threat to species integrity and may be widespread in certain trout. But the vast majority of the viable individuals produced by hybridization must either be infertile or at a significant fitness disadvantage. Perhaps the most familiar example of extensive interspecific hybridization occurring without a breakdown in parental species characteristics is the existence of millions of mules over thousands of years with only a single case of fertility ever being substantiated (Jones and Johnsen 1985). ETo date, there are two offspring from this single fertile mule, the offspring's names are Blue Moon and Lightening Strikes.)

Population genetic theory shows that very low levels of genetic introgression will result in populations becoming genetically uniform. Gene flow levels as low as a single individual per generation are sufficient to overcome even moderate selection and prevent divergence of populations. Surly a rate of hybridization of 557. would result in the complete loss of species specific characters.

Andreasen (1975) stated "Hybridization is common in suckers (Hubbs et al. 1943) but introgression has not been reported." Andreasen's analyses of shortnose suckers based on morphological characters revealed certain individuals which may have been zhe first generation (i.e., an Fl) result of hybridization but no evidence was available which indicated "mass hybridization" and introgression. The introszression hypothesis was rejected (Andreasen 1975).

Holden and Stalnaker (1975) pointed out, in a discussion of more than 75 years of presumed hybridization between flannlmouth sucker, Catostomus latininnis, and humpback suckers (more widelv known as razorback suckers), Xvrauchen texanus, that no fertile hybrids had ever been reported. Thus, it is not surprising that genetic analysis revealed a maximum of 37. introgression between these species (Buth et al. 1987).

Recently, Bartley et al. (in prep.) examined specimens of cui—ui sucker, Chasmites cujus, Tahoe sucker, Catostomus tahoensis, and their presumptive hybrid from Pyramid Lake, Nevada. Numerous genetic loci were found which distinguished the parental forms. In every case, all of the presumptive hybrid suckers were genotypically identical to "pure" cui—ui suckers. The. maximuM probability of hybridization being the cause of the unusual morphology seen in the presumed "hybrids" is less than 0.5%.

Restating the primary objective of this phase of the study: Is Chasmistes brevirostris extant in pure form or are all shortnose sucker populations hybridized as suggested above? This concern is of substantial import as the shortnose sucker is federally listed as an endangered species and recovery efforts hinge on efficient identification of individuals and populations which may be considered most pure".

The short answer to this question is that no genetic evidence strongly supportive of hybridization between shortnose suckers and either Klamath smallscale suckers or Klamath largescale suckers was found. The allelic overlap at the Ldh-B2 locus is a weak indicator of introgression between SNSci.. and KLS. The Ldh-B2 (100) allele is fixed in KLS, apparently absent in SNS_{Ic} and SNS_{COP}, and occurs at the frequency of 0.03 in SNSou (Table 3, top data line). This observation cannot be completely disregarded. The estimates of maximum level of undetected hybridization which may be taking place between these species is set by possible sampling error. Thus, statistical limitations prescribe estimates of und d hybridization involving these taxa range from 2 to 57. (Table 5). Increasing sample sizes would reduce these estimates but we are confident in asserting that the three shortnose sucker populations tested in this study are "pure".

Catostomus microns Rutter

The Modoc sucker, Catostomus microps, is a small, fine scaled sucker with a very restricted natural range: the Turner-Hulbert-Washington Creeks drainage and the Rush-Johnson Creeks system (Moyle 1974). Mills (1980) reported that the Modoc sucker *was* being experiencing introgressive

hybridization with Sacramento sucker (SAC) which had been allowed access to the spawning habitat of the former through erosion of stream habitats. The combination of restricted natural range and the presumed introgression of Sacramento suckers, led to the Modoc sucker being both state and federally listed as an endangered species.

An objective of this study was to characterize the genetics of pure Modoc suckers and access the level of genetic status of populations of presumed hybrid Modoc/Sacramento suckers. Unfortunately, the continuing drought conditions in California have precluded collection of any populations of Modoc sucker. Reassessment of the status of the Modoc sucker will be done this Spring and if a sufficient census is discovered, samples may then be taken. One option under discussion is to collect young—of—the—year and raise them at the aquaculture facility at UC Davis. If this is done, then this brood may be used for reestablishing native populations and if enough are successfully raised, genetic study.

One population of sucker which as initially postulated to be close to Modoc suckers was sampled for genetic analysis. The site of this population is Cedar Creek, Moon Reservoir (CCMR). This population was found to be most similar to Tahoe suckers from Eagle Lake (EAG). In fact, CCMR and EAG were found to be very different from the other studies species (Table 3 & Fig. 3). Four fixed allele differences were found between CCMR and SAC. Assessment of hybridization between CCMR and SAC yielded a maximum estimate of 17.. The differences between CCMR and EAG are more subtle, yet the maximum estimate of hybridization between these forms was 57. (Table 5).

Deltistes luxatus (Cope)

Originally described as a member of Chasmistes (Cope 1979), Seale (1896) erected a new genus, Deltistes, for the Lost River sucker (LRS). Miller (1959) later assigned luxatus to Catostomus, a conclusion supported by the American Fisheries Society (Robins et al. 1980). We retain the use of Deltistes following Williams et al. (1989).

The concern with LRS is that, at least in Clear Lake Reservoir, genetic introgression may have occurred with *SNS*. This study found no indication of introgression from LRS into SNS_{CL} (sampling error calculated to 0.04) but could not exclude a 15% chance of introgression from SNS_{CL} into LRS (Table 5). This estimate is a direct function of the very small (n = 9) LRS sample size. If we were willing to assume that LRS "should" be fixed for the Ck-2 (105) allele, a position not supported by the data, the 87. frequency of the C1;-2 (100) allele may be an indication of Level II hybridization. Although this possibility is listed on Table 5, it is unlikely to be valid. The Ck-2 (100) allele is probably the ancestral state for this locus and simply is retained as a polymorphism in LRS. Future collections are anticipated and results, if available, will be incorporated into the final report under this contract.

Systematics

A secondary objective of this work was to shed light on the phylogenetic relationships between Catostomus Le Sueur, Chasmistes Jordan, and Deltistes Seale. Is Chasmistes the primitive form of western sucker as hypothesized by Ferris and Whitt (1978) or is it the most derived form as suggested by Miller

and Smith (1981) and is LRS appropriately considered the sole representative of a monotypic genus?

Figure 3 summarizes the systematic analysis. Of the species examined in this study, LRS is the sister group to SNS but this does not solve the problem. If KSS is indeed a member of the LRSISNS lineage and is retained under Catostomus, then Chasmistes is monophyletic, LRS may be a member of Chasmistes or Deltistes, but Catostomus is paraphyletic and is therefore invalid. Whether LRS is sufficiently differentiated to merit its own genus is arguable. Mo objective criteria for genus level taxa has been accepted [illegible] even a majority of zoologists, but on the basis of the available genetic data LRS may not qualify for monotypic status. Additional samples of LRS will shed light on this discussion by increasing cur knowledge of LRS and by allowing a [illegible] data set to be used in the analysis.

The degree of differentiation between the CCHR/EAG lineage and the rest of the species suggests that if any lineage deserves nomenclatural distinction it is this Tahoe—like group.

A final comment on hybridization

Why are there so many reports of hybridization in catostomid species? A quick reading of the morphometric literature e.g., Hubbs et al. 1943. Smith 1966, Miller and Smith 1981) leaves the reader with the impression that virtually every population of western suck-er has, is, or will experience interspecific or intergeneric hybridization. These hybridization events are postulated to include significant backcrossing even between species which have not had a common ancestor for millions of years. If hybridization was so

rampant, it seems that [illegible] species involved would become completely homogenized and recognizable as catostomid fish but not as a particular taxon.

The genetic evidence to date argue that hybridization has not occurred at an appreciable rate. The 37. hybridizatien rate obtainedby Buth et [illegible]. (1987) required an assumption of selection against allozymes which were expected to be detected but were not. [These [illegible] were [illegible] found if the initial assumption of hybridization was correct.] Given that..few studies aimed at specifically finding selection coefficients for allozymes have been successful, the 37. rate of hybridization between razorback suckers and flannelmouth suckers must be considered as a maximum estimate. Results from this study and that of Bartley [illegible]. ([illegible] prep.) indicate that the rate of undetected hybridization between the several tested catostomid species-pairs must be very low, ranging from (0.5 to 8%.

How then may we compare the results from morphometric and genetic analyses? [Keep in mind that not all morphometric studies have argued for the hybridization hypothesis: Andreasen (1975) stated that he found individual suckers which may have been Fl hybrids but did not find morphological evidence for genetic introgression.] Those studies which accept hybridization as a [illegible] explanation may have either missed the implication of Ford (1964) and, more recently, Carson 1990), or been too restricted (typological?) in their view of observed morphological variation.

Miller and Smith (1981) briefly entertained (then rejected) the [illegible] F[illegible] (1964) that swift reduction in population census, perhaps brought on by an environmental crisis, may be followed by new morphological states. These new morphological states are not truly 'new' but are "a hybrid-like combination of characters" (Miller and Smith 1981 p.17),

They felt that the novel (as opposed to new) morphological states were most likely to have been derived as the sum of input from two distinct species. An alternate view is that the genes for the novel states were within the species all the time and merely needed the opportunity to be expressed.

Three examples of substantial morphometric differences derived from single gene pools are to be found in the life histories of the Warner sucker'," Catostomus warnerensis Snyder, the rainbow trout, Oncorhynchus mykiss Walbaum, and the Cuatro Cienegas cichlid, Cichlasoma minckleyi Kornfield and Taylor. The Warner sucker is endemic to the endorheic Warner Basin of southeast Oregon. The life history of this sucker is one of facultative potamodromy - (Berg 1991). Large (>350 mm SL) suckers spend most of their life in the shallow basin lakes ascending the lower creek reaches only to spawn. Bigher in the creeks are resident populations of smaller (<200 mm SL) suckers. The basin lakes have become completely dry during historical times (as they probably will again this summer), eliminating the lake form. With the return of high water, the resident form "reseed" the lakes by being washed downstream. Once in the lake environment, the small resident sucker's offspring the adults probably cannot make the transition) will develop into the larger lake form.

Steelhead trout and resident rainbow trout are genetically indistinguishable Berg and Gall 1988) yet morphologically, physiologically, and behaviorly very different. It is sufficient to point out that the large, ocean-going steelhead trout is but a form derived by the same overall genotype that results in the small, brightly colored, paedomorphic resident rainbow trout. These two forms of the same fish are so different that they have been repeatedly given formal taxonomic names.

A third example of substantial diversity being obtained from a single population is the Cuatro Cienegas cichlid. Four discrete morphologies have been described (Minckley 1969). These forms are sufficiently distinct that one researcher stated chat he could tell them apart while they were in a bag and he wore gloves and a blindfold (W. Minckley, pers. comm.). Not only are these fish genetically indistinguishable (Sage and Selander 1975), but they may be obtained from single broods. These four forms are now recognized as different e::pressions of a single species (Kornfield and Taylor 1983).

In each case, the Warner sucker, the rainbow trout and the Cuatro Cienegas cichlid possess all the genetic information needed to produce these very different forms. The trigger(s) for these specific forms are environmentally induced. These fish express phenotypic plasticity - the ability to produce alternate morphologies, behaviors, and/or physiologies in response tc environmental cues (West-Eberhard 1989).

Smith (1967) described the argument that many of the novel characters found in populations that are interpreted as being derived through hybridization are polygenic. That means that there are multiple genes which work in concert each being expressed as a small individual effect to produce the final phenotypic (morphologic) result. This is probably true. It is also probable that these polygene complexes are variable within each species and they could be the source for novel combinations of expressions resulting in novelmorphological characteristics given novel environmental conditions.

Under 'normal' conditions, a population's census is near its defined carrying capacity. Selection for fitness characters is most strict in these situations, resulting in reduced phenotypic variation. If a population e;:periences an environmentally induced census reduction, and survives,

selection may be reduced. The individuals which made it though the tough times must have the abilities to cope with the stress which caused the census reduction. They will be the founders of the new stock. The population may begin to expand in numbers and to adapt (readapt) to its novel environment. These conditions are those which would enhance phenotypic variability especially in those characters involved with fitness parameters such as feeding apparatuses. [Note: feeding apparatuses are characters of utmost importance in catostomid taxonomy.] Fluctuating environmental conditions result in local population variability through adaptation. These are the conditions found in the watery environs of the western United States.

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TABLE 1. Species, contracted, collected, and received under CDFG contract FG 8143.

Species sample sizes	contracted	collected	received
Pure species			
Sacramento sucker	150	96+	96+
American River			
Modoc sucker			
Washington Creek	30	0	0
Johnson Creek	30	0	0
Shortnose sucker			
Upper Klamath Lake	30	78	78
Lost River sucker			
Upper Klamath Lake	30	0	0
Clear Lake Reservoir	30	9	9
Klamath smallscale sucker			
Lower Klamath River or Rogue River (Scott R.)	30	25	25
Copco Reservoir	0	25?	0
Klamath largescale sucker			
Williamson River or Sycan River	30	30	30
Unknown taxonomic affinity			
Modoc X Sacramento sucker			
Rush Creek	30	0	0
Shortnose X Klamath smallscale sucker			
Copco reservoir	30	31	31
Shortnose X Klamath largescale sucker			
Clear Lake reservoir	30	38	38
?Modoc/Tahoe/Sacramento?			
Cedar Creek, Moon Reservoir	0	30	30
Additional species			
Tahoe sucker			
Eagle Lake	0	-50	-50

TABLE 2. Protein systems studied [abbreviation, Enzyme Commission code number), number of loci resolved, and quaternary structure.

Protein [abb., EC #)	# Loci resolved	Quaternary structure
Lactate dehydrogenase [Ldh, 1.1.1.27]	3	tetramer
Malate dehydrogenase [Mdh, 1.1.1.37]	4	dimer
Isocitrate dehydrogenase [Icdh, 1.1.1.42]	1	dimer
Phosphogluconate dehydrogenase CPgdh, 1.1.1.44]	2	dimer
Aspartate aminotransferase [Aat, 2.6.1.1]	3	dimer
Creatine kinase [Ck, 2.7.3.2]	2	dimer
Adenylate kinase CAk, 2.7.4.3)	2	monomer
Esterase, non-specific [Est,	1	monomer
Adenosine deaminase CAda, 3.5.4.4]	1	tetramer
Triose-phosphate isomerase ETpi, 5.3.1.1]	3	diner
Glucose-6-phosphate isomerase [Gpi, 5.3.1.9]	3	dimer
Phosphoglucomutase Ugm, 5.4.2.2)	3	monomer

TABLE 3. Allele frequencies observed at 19 polymorphic loci in Sacramento sucker (SAC); shortnose sucker from Klamath Lake Basin (SACK); Clear Lake Reservoir (SNScu), and Copco Reservoir (SNS_{COP}); Klamath smallscale sucker (KSS); Klamath largescale sucker (KLS); Lost River sucker (LRS); Tahoe suckers from Eagle Lake (EAG); and Cedar Creek, Moon Reservoir sucker (CCMR). An additional Ten loci were fixed for the same allele in these species. Rediploidization status of Pgm-1,2 loci indicated. Mean heterczygosity, H, and percentage of polymorphic loci, %L, are listed at bottom. Alleles used in frequency-restricted presence/absence coding for Wagner tree indicated by asterisk. No data indicated by n.d.

locus	(allele)	SAC	*SNSK*	*SNSct.*	SNS_{COP}	*KSS*	*KLS*	LRS	EAG	CCMR
Ldh-B2	(100)*	0.99		0.03		1.00	1.00		1.00	1.00
	(95)*	--	1.00	0.97	1.00			1.00		
	(90)	0.01								
sMdh-1	(120)*		--	--			—	--	0.58	0.20
	(100)	0.78	0.97	1.00	1.00	1.00	1.00	0.94	0.42	0.80
	(95)	0,22	0.03	--	--		—	0.06		
mMdh-2	(-100)	0.94	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	(-165)	0.06								
Icdh	(150)	0.01								
	(100)*	0.99	1.00	1.00	1.00	1.00	1.00	1.00	--	--
	(55)*		--	--		--	--	--	0.97	1.00
	(20)	--		--			--	--	0.03	--
Pgdh-1	(100)	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	(85)	0.01								
sAat	(110)								0.25	--
	(100)	0.98	0.97	1.00	1.00	0.94	1.00	0.89	0.75	1.00
	(85)	0.02	0.03	--	--	0.06	--	0.11	--	
mAat-1	(-150)			0.02	0.02	0.02				
	(-100)	1.00	0.96	0.83	0.98	0.57	0.95	0.50	0.33	
	(-60)*	--	0.04	0.15		0.41	0.05	0.50	0.67	1.00
mAat-2	(-100)	1.00	0.78	1.00	0.74	1.00	0.95	1.00	1.00	1.00
	(-85)	--	0.22		0.26		0.05			

TABLE 3 cont.

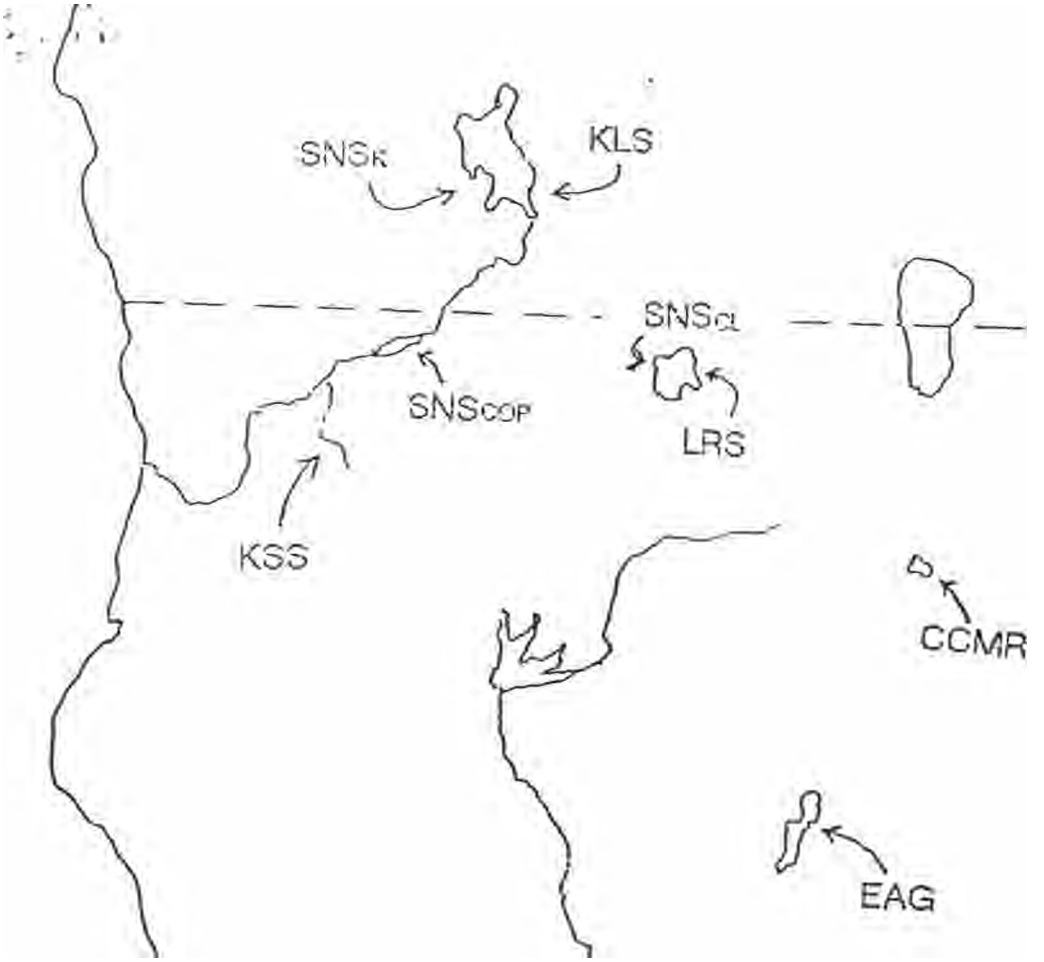
locus	(allele)	SAC	SNSK	SNSCL	SNScop	KSS	KLS	LRS	EAG	CCMR
Ck-2	(105)*	--	0.18	0.11	0.14	1.00	0.07	0.92		
	(100)*	1.00	0.82	0.89	0.86		0.93	0.08	1.00	1.00
Ak-1	(100)	1.00	1.00	1.00	1.00	0.94	0.97	1.00	1.00	1.00
	(55)					0.06	0.03			
Ak-2	(100)	1.00	1.00	1.00	1.00	0.99	0.94	1.00	0.91	0.97
	(65)					0.01	0.06		0.09	0.03
Est-3	(105)	0.44	1.00	1.00	1.00	0.61	1.00	1.00	0.56	1.00
	(100)*	0.56	--	--	--	0.30	--	--	--	--
	(90)	--	--	--	--	0.09	--	--	0.44	
Ada	(371)		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	(100)	1.00								
Tpi -1	(100)	1.00	1.00	n.d.	n.d.	1.00	n.d.	1.00		
	(-440)								1.00	1.00
Tpi-3	(100)	1.00	1.00	n.d.	n.d.	1.00	n.d.	1.00		
	(90)								1.00	1.00
Gpi-3	(110)*	0.05	1.00	1.00	1.00	1.00	1.00	1.00		
	(100)*	0.95							1.00	0.90
	(85)									0.10
Pgm-1,2	(135)*	—							0.44	0.50
	(120)	0.04	0.03	0.17	--	0.01	--		--	
	(100)*	0.54	0.74	0.83	0.98	0.99	0.75	1.00	0.07	—
	(70)*	0.42	0.17	--	0.02	--	0.17	--	--	--
	(60)								0.40	—
	(35)		0.07		—	--	0.08	--	0.09	0.50
Pgm-3	(120)	--	—	--	--		—	—	0.06	
	(115)*								0.44	0.50
	(110)	—		—		--	—	--	0.44	
	(105)	0.25	—	—						
	(100)	0.63	0.85	0.68	0.27	0.42	0.94	1.00	0.06	0.50
	(95)*	0.06	0.15	0.32	0.73	0.58	0.06			
	(90)	0.06							—	
Pgm-1,2 loci diverged?		no	no	no	no	no	no	no	yes	yes
	H	0.08	0.05	0.05	0.04	0.06	0.04	0.03	0.11	0.06
	P1..	34.5	24.1	18.5	18.5	24.1	25.9	13.8	27.6	17.2

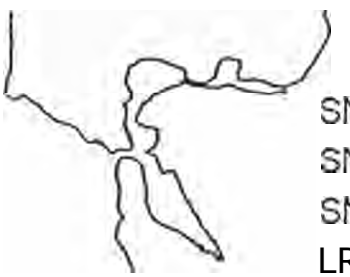
TABLE 4. Summary of gene diversity estimates at eight polymorphic loci in shortnose sucker. Mean G_{pt} = 0.069 indicates historical gene flow > 3 individuals per generation between the three shortnose sucker populations.

locus	G_{pt}
Ldh-B2	0.020
sMdh-1	**0.020**
sAat	**0.020**
mAat-1	**0.059**
mAat-2	**0.097**
Ck-2	**0.007**
Pgm-1,2	**0.082**
Pgm-3	**0.247**
Mean	**0.069**

TABLE 5. Maximum probability of gene introgression under hybridization levels I, II, and III between species (population) pairs. Species A genes assumed introgressed into species B. Underlined value taken as maximum probability. Standard errors of level II estimates, $S_{,}$, are in parentheses. Species abbreviations as given in text.

species pairs		hybridization level		
A	B	I	II	III
KLS	$SNS_{.}$	0.02	n.a.	**n.a.**
KLS	$SNS_{ct.}$	0.04	0.03 (+ 0-02)	**n.a.**
KSS	SNS_{CCP}	0.05	n.a.	**n.a.**
SNSOL	LRS	0.15	0.08 (+ 0.07)	**n.a.**
LRS	SNS	0.04	n.a.	**n.a.**
SAC	CCHR	0.01	n.a.	**n.a.**
EAG	CCHR	0.05	n.a.	**n.a.**





SNS_K shortnose sucker from Klamath Basin
SNS_{CL} : shortnose sucker from Clear Lake Reservoi
SNS_{COP}: shortnose sucker from Copco Reservoir
LRS : Lost River sucker from Clear Lake Reservoir
KSS Klamath smallscale sucker from Scott River
KLS : Klamath largescale sucker from Klamath Bas
SAC : Sacramento sucker from American River
EAG : Tahoe sucker from Eagle Lake
CCMR : Cedar Creek, Moon Reservoir sucker

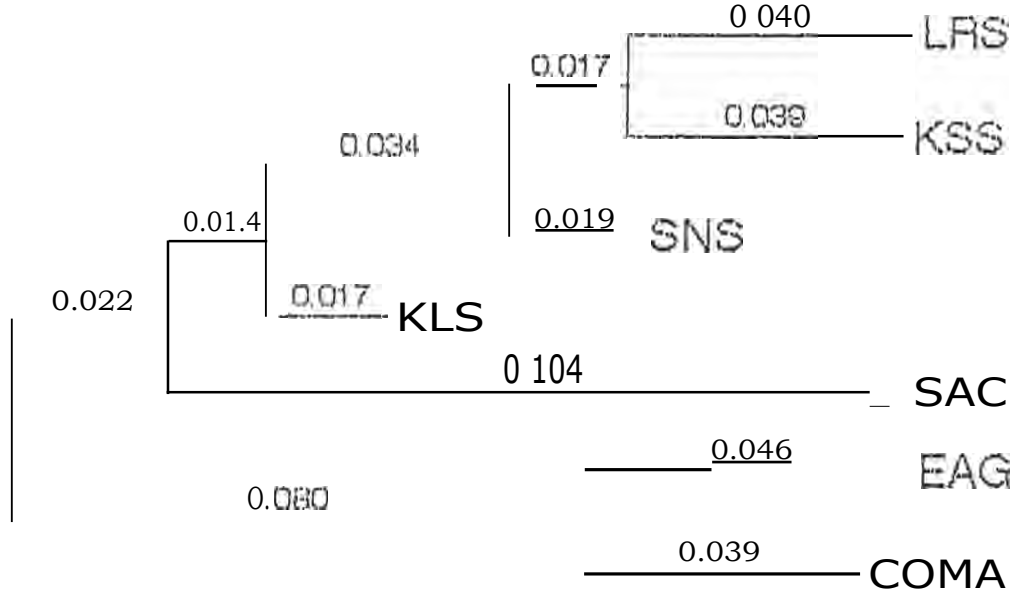


FIGURE 2 Cladogram of seven catostomid species based on Rogers' genetic distance estimates. Horizontal branch lengths indicate relative genetic distance. Vertical branch lengths are meaningless. Average patristic/phenetic deviation = 0.02. Species are Lost River sucker (LRS), Klamath smallscale sucker (KSS), shortnose sucker (SNS), Klamath largescale sucker (KLS), Sacramento bucker (SAC), Tahoe sucker from Eagle Lake (EAG), and Cedar Creek, Moon Reservoir sucker (CCMR).

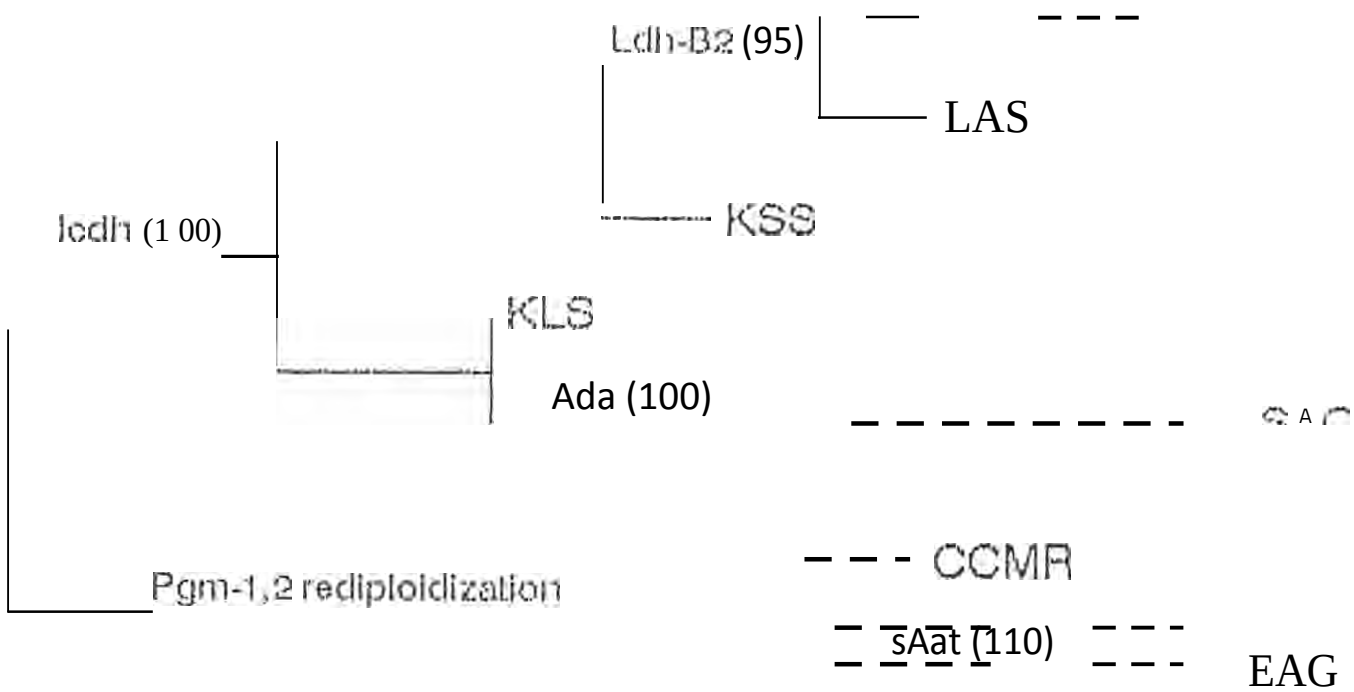


FIGURE 3. Cladogram of seven catostomid species based on frequency-restricted presence/absence coding of genetic alleles and duplicate gene rediploidization data. Horizontal branch lengths indicative of relative genetic divergence. Dashed branches indicate presence of private alleles. Vertical branch lengths are meaningless. Patristic/phenetic ratio 0.74. Genetic data mentioned in text listed. Species are shortnose sucker (SNS), Lost River sucker (LRS), Klamath smallscale sucker (KSS), Klamath largescale sucker (KLS), Sacramento sucker (SAC), Cedar Creek, Moon Reservoir sucker, and Tahoe sucker from Eagle Lake (EAG).