SPATIAL AND TEMPORAL PATTERNS IN THE COVARIANCE OF GENETIC AND MORPHOLOGIC CHARACTERS IN A PUPFISH HYBRID SWARM

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PREFACE

I have written this dissertation in three chapters, each of which is intended to stand alone for submission for publication. I take the opportunity here to anticipate and address two potential questions. First, formats for literature citations and other stylistic elements vary between chapters because each is written for submission to a different journal. The intended journal for each chapter is: Chapter 1- Transactions of the American Fisheries Society; Chapter 2- Southwestern Naturalist; and Chapter 3- Copeia. Second, in writing each chapter, I sometimes found it necessary to refer to other chapters of the dissertation. Where necessary, I have referred to other chapters in the dissertation as: Wilde (1994).

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CHAPTER I

GENETIC STATUS OF PECOS PUPFISH POPULATIONS AFTER ESTABLISHMENT OF A HYBRID SWARM INVOLVING AN INTRODUCED CONGENER

Loss of native fishes through hybridization with introduced species is emerging as a major challenge to conservationists. Nowhere is this problem more evident than in the western United States. Hybridization and genetic introgression following introductions of hatchery-reared rainbow trout *Oncorhynchus mykiss* and cutthroat trout *O. clarki* have led to local losses of native trout populations throughout a large portion of the western United States (Campton and Johnston 1985; Allendorf and Leary 1988). In Arizona and New Mexico, introduced rainbow trout hybridized with Apache trout *O. apache* and Gila trout *O. gilae*, and the resulting hybrids have replaced Gila and Apache trout over large portions of their natural ranges (Loudenslager et al. 1986). A similar replacement occurred on the Edwards Plateau of Texas (Whitmore 1983), where introduced smallmouth bass *Micropterus dolomieu* hybridized with the endemic Guadalupe bass *M. treculi*.

The above examples are associated with large state or federal stocking programs and involve multiple introductions of thousands of fish over long periods. However, large genetic changes can be caused by less conspicuous introductions. In several instances, hybridization between native and introduced species has resulted from apparent releases of bait fish (Hubbs and Miller 1943; Miller 1973; Stevenson and Buchanan 1973; Kennedy 1977; Echelle and Connor 1989) that most likely involved the release of small numbers of fish in localized areas. The potential effects of such introductions are dramatically illustrated by events following the introduction of the sheepshead minnow Cyprinodon variegatus into the range of the Pecos pupfish C. pecosensis, which is endemic to the Pecos River drainage of southeast New Mexico and west Texas (Echelle and Connor 1989). After possibly less than 5 years, and apparently beginning with a single, local introduction, all Texas populations of pupfish in a 430-km reach of the Pecos River were replaced by a hybrid swarm. The affected area encompassed over half the original geographic range of Pecos pupfish.

Hybrid populations, once established, present formidable problems for conservation of natural patterns of genetic diversity. Restoration of genetically introgressed populations to the native form is virtually impossible except in restricted local situations (e.g., Hubbs 1980;

Hubbs et al. 1978; Allendorf and Leary 1988). Furthermore, the presence of hybrid populations threatens remaining native populations. Hybrids may disperse naturally from original sites of introduction or they may be transported by humans, or other means, across barriers to dispersal (dams, stream divides, etc.) into waters in which they can genetically influence additional native populations. For example, pupfish are often used as bait by anglers in the Pecos River (Echelle and Connor 1989) and human transport of hybrids is a major concern of state and federal agencies attempting to protect the remaining genetically pure populations of Pecos pupfish (J. E. Brooks, U. S. Fish and Wildlife Service, personal communication; D. L. Probst, New Mexico Department of Game and Fish, personal communication).

In this paper, I provide further data on occurrences of hybrids between Pecos pupfish and sheepshead minnow in the Pecos River and peripheral waters. My data indicate that: 1) hybrids are more widely distributed than previously reported (Echelle and Connor 1989); and 2) the spread of hybrids represents dispersal within the Pecos River rather than multiple introductions of sheepshead minnow.

Study Area And Sample Sites

The Pecos pupfish is endemic to the Pecos River drainage in a region extending approximately 650 km south-southeast from near Roswell, New Mexico, to the mouth of

Independence Creek (Site 13, Figure 1). In New Mexico, the species occurs most abundantly in two regions: 1) in the vicinity of Roswell, in both the Pecos River and in saline springs, oxbows, and sinkholes in or near the Pecos River floodplain; and 2) in a saline stretch of the Pecos River from Malaga downstream to the New Mexico-Texas boundary. In Texas, prior to establishment of the hybrid swarm, Pecos pupfish occurred abundantly in Salt Creek, Red Bluff Reservoir, Imperial Reservoir, and in the Pecos River from the New Mexico-Texas boundary to Sheffield (Site 12, Figure 1). Pupfish were uncommon downstream from Sheffield because freshwater inputs to the Pecos River decreased salinity and allowed the river to support a relatively diverse fish fauna.

I collected pupfish from a total of 25 sites (Figure 1). The following 12 sites were also sampled by Echelle and Connor (1989; their site numbers in parentheses): 1 (5), 2 (7), 3 (8), 5 (10), 6 (11), 7 (13), 8 (14), 9 (16), 10 (17), 11 (19), P1 (2) and P10 (12). My sample sites in the Pecos River are numbered 1-14, and extend from 44 km downstream from Red Bluff Reservoir to Pandale (Figure 1). Samples from other, "peripheral", waters are numbered P1-P11. These include one sample from the Pecos River near Malaga, New Mexico (P1), and samples from all permanent bodies of water I could find between Red Bluff Reservoir and Pandale, Texas.

I collected pupfish at two locations (P2 and P3) in Red

Bluff Reservoir and at four locations (P4-P7) in Salt Creek, a tributary of the Pecos River that discharges into the river approximately 2.5 km downstream from Red Bluff Reservoir. P4 is at the base of a series of small (< 0.5 m), natural waterfalls located 2.4 km upstream from the confluence with the Pecos River. P5 and P6 are approximately 1.2 km upstream from the waterfalls, and 0.5 km downstream from the spillway of Red Bluff Reservoir that discharges into Salt Creek. P7 is located 12 km upstream from the spillway outlet.

Between sites 1 and 6 in the Pecos River, a series of dams diverts water from the river into a network of irrigation canals (Figure 1). The canals are typically dry; however, pupfish apparently move into them when they are filled. I made one collection of pupfish (P8) at the head of this system of canals. I also collected pupfish from Imperial Reservoir (P11) and from two water-filled, commercial gravel pits: one gravel pit is on property owned by Phipps Gravel Company (P10; 6 km SW of Grandfalls, Ward County, Texas), and the other is at the north end of property owned by Porter's Gravel Company (P9; 6 km W of Grandfalls, Ward County, Texas).

Methods

I made collections in August and November, 1986, and June through August, 1988. Pupfish collected in August 1986 and August 1988 were placed on dry ice in the field, transported to the laboratory, and stored at -70°C; fish collected in other months were transported live to the laboratory and were then frozen and stored at -70°C. The liver and right eye of each fish were removed and homogenized separately in equal volumes of distilled water to obtain extracts of water-soluble proteins. Fish smaller than 20 mm (total length) were decapitated and head and body portions were treated as described for liver and eye samples. Tissue homogenates were centrifuged for 15 minutes at 4000g and stored at -70°C. Specimens were individually tagged, preserved in formalin, and deposited in the Oklahoma State University Collection of Vertebrates (OSUS).

I used standard methods of horizontal starch gel electrophoresis (Selander et al. 1971; Siciliano and Shaw 1976) to examine the products of four presumptive gene loci: alcohol dehydrogenase-1 1.1.1.1.1 (ADH-1), esterase-1 3.1.1.1 (EST-1), glucose-6-phosphate-isomerase-A 5.3.1.9 (GPI-A), and proline-dipeptidase-1 3.4.13.9 (PEPD-1). These loci exhibit complete, or nearly complete, differences between Pecos pupfish and sheepshead minnow (Echelle et al. 1987). Tissue specificities and other details of scoring are presented in Echelle and Connor (1989). In this paper, I employ Barton and Hewitt's (1985) use of the word hybrid to include individuals of F_1 and all subsequent backcross generations.

Genotypic proportions were tested for agreement with Hardy-Weinberg equilibrium expectations using an exact test (Haldane 1954) as implemented in BIOSYS-1 (Swofford and Selander 1981). Gametic phase (linkage) disequilibria between loci were assessed with r, the correlation between alleles at different loci corrected for deviations from Hardy-Weinberg proportions (Weir 1979; Campton 1987). The sample statistic $\underline{N}(\underline{r})^2$ is distributed as a chi-square variate with 1 degree of freedom and can be used to test the null hypothesis of no correlation between loci (Weir 1979). Echelle and Connor (1989) reported significant excesses of coupling gametes (= positive values of r) in hybrid pupfish from the Pecos River. I used a one-tailed binomial test (Siegel 1956) to determine whether excesses of positive correlations existed, for each locus-pair, in my samples. I interpreted significant results as evidence of an association (linkage disequilibrium) between loci.

Across all sample sites, I evaluated a total of 100 (4 loci x 25 locations) individual tests for agreement with Hardy-Weinberg proportions and 150 correlations among loci. To control the probability of falsely rejecting null hypotheses, I used the sequential-Bonferroni test as described by Rice (1989), with a tablewide significance of 0.05, to evaluate test statistics. Results for Pecos River locations (sites 1-14) and those for peripheral waters (P1-P11) were treated as separate analyses. I used SYSTAT

(Wilkinson 1988) to calculate critical values of chi-square for sequential tests of correlations among loci. Individual genotypes of all fish reported on herein are presented in Appendix A.

Results

Alleles diagnostic of sheepshead minnow showed a clinal pattern of variation in the Pecos River (Figure 2; Table 1). Mean frequencies, over four loci, of sheepshead minnow alleles were greatest at site 3 (mean 0.87) and decreased upstream to site 1 (mean 0.33) and downstream to site 8 (mean 0.39). Farther downstream, the frequency of sheepshead minnow alleles increased to a mean of 0.62 at site 14. This pattern was not a result of local differences in the relative abundance of sheepshead minnow and Pecos pupfish. No more than 27% (mean over all sites, 7%) of the specimens in my samples were homozygous at all loci for alleles of only one parent species. As argued by Echelle and Connor (1989), the probability that any individual in these samples was a pure Pecos pupfish or sheepshead minnow across its entire genome is extremely low.

There was little evidence of deviation from Hardy-Weinberg proportions in the Pecos River. Four individual tests indicated significant ($\underline{P}< 0.05$) deviations (Table 1); however, none was significant based on the sequential Bonferroni test. Except for the EST-1* x GPI-A* and EST-1* x PEPD-1* locus-pairs, there was no evidence of linkage disequilibrium in pupfish from the Pecos River. There were seven significant ($P < 0.05$) correlations for the EST-1* x GPI-A* locus-pair, but none was significant for any other locus-pair (Table 2). For both the EST-1* x GPI-A* and the EST-1* x PEPD-1* locus-pairs there were significant ($P < 0.05$) excesses of positive correlations, indicating an excess of coupling gametes for each of these locus-pairs.

Pecos pupfish from the Pecos River at Malaga, New Mexico (site P1), showed no evidence of hybridization with sheepshead minnow. Hybrids were present in upstream (P2) and downstream (P3) areas of Red Bluff Reservoir (Figure 2; Table 1) where the frequency of alleles diagnostic of sheepshead minnow (mean over four loci) was 0.42 and 0.25, respectively. Frequencies of alleles diagnostic of sheepshead minnow were greater at P3 than at P2 for all loci, although only the difference in PEPD-1* was significant ($P < 0.05$). There was also a significant difference in the magnitude of interlocus correlations, across all locus-pairs (signed-ranks test, $P < 0.05$), in samples from P2 (sampled in 1988) and P3 (1986). Differences in allele frequencies and interlocus correlations between P2 and P3 may reflect spatial heterogeneity in pupfish populations in Red Bluff Reservoir, but more likely result from a lakewide increase in alleles diagnostic of sheepshead minnow and an approach to linkage equilibrium as is occurring downstream in the Pecos River (Wilde 1994).

Hybrids were present at three sites in Salt Creek (P4-P6) in 1988, but were not observed there in 1984 or 1985 (Echelle et al. 1987; Echelle and Connor 1989). The mean frequency of alleles of the sheepshead minnow was only 0.10 at P4, but 23 of 53 fish examined (43%) had hybrid genotypes. I also found fish with hybrid genotypes in small numbers at P5 and P6. Echelle and Connor (1989) reported that alleles for the EST-1* and PEPD-1* loci may be shared between Pecos pupfish and sheepshead minnow at a low frequency. Individuals in samples from sites P5 and P6 were either homogyzous for Pecos pupfish alleles across all four loci or they were heterozygous at one locus; however, the latter included heterozygotes for ADH-1* and GPI-A*, loci at which no sharing of alleles is known. Significant inter-locus correlations at P5 and especially P4 (Table 2) suggest a recent establishment of hybrids at these sites.

My one allozymically assayed sample (site P8) from the irrigation system consisted of 30 specimens, all of which had hybrid genotypes. A preserved sample of 10 specimens from a canal at the southern-most end of the system (OSUS 18346; 8 km W of Grandfalls, Ward County, Texas) was not assayed for allozymes, but all specimens had morphologic traits (Echelle and Connor 1989) indicative of influence by sheepshead minnow.

Mean frequencies of alleles diagnostic of sheepshead minnow at Porter's gravel pits (P9) and Imperial Reservoir (P11) were 0.80 and 0.74, respectively. Echelle and Connor (1989) reported a potentially pure population of Pecos pupfish in Phipps gravel pit (P10) in 1986; in 1988, frequency of alleles diagnostic of _C_. _pecosensis_ remained the same (100%) for _ADH-1*_ and _GPI-A*_ and increased for _EST-1*_ (from 90% to 100%) and _PEPD-1*_ (from 90 to 97%).

Discussion

Sheepshead minnow have been introduced into the Pecos River drainage on three separate occasions over the past three decades. In the 1960s and 1970s, sheepshead minnow were introduced into two isolated bodies of water in the basin: a springfed section of Leon Creek (Kennedy 1977) and Lake Balmorhea (Stevenson and Buchanan 1973). Hybridization with endemic species, Leon Springs pupfish _C_. _bovinus_ and Comanche Springs pupfish _C_. _elegans_, respectively, occurred in both locations. Rapid spread of hybrids in Leon Creek threatened the genetic integrity of Leon Springs pupfish; however, an intensive eradication effort involving several state and federal agencies was successful in removing the introduced genome (Hubbs 1980; Echelle et al. 1987). The success of this program was facilitated by the small size of the affected habitat in Leon Creek (<5 km of stream).

Lake Balmorhea has supported a dense population of sheepshead minnow since the introduction of the species in the 1960s. Physical barriers have prevented sheepshead minnow from invading the springfed waters inhabited by Comanche Springs pupfish. Hybrids between the two species commonly occur in irrigation canals leading into Lake Balmorhea, but recent genetic data indicate stringent postmating reproductive isolation between the two species (A. F. Echelle and A. A. Echelle, unpublished data), suggesting that there is little danger of genetic introgression. However, interspecific competition still represents a potential threat, should the locally abundant sheepshead minnow be transported into the spring habitats of Comanche Springs pupfish. In addition, the potential for transport of sheepshead minnow from Lake Balmorhea threatens other endemic pupfishes in the area: Lake Balmorhea could have been the source of sheepshead minnow introduced into Leon Creek or the Pecos River proper, although I cannot exclude the possibility that sheepshead minnow was introduced into these waters from elsewhere.

Echelle and Connor (1989) concluded that sheepshead minnow was introduced into the Pecos River sometime between 1980 and 1984 and that, by 1985, pupfish populations in the Pecos River comprised panmictic admixtures of Pecos pupfish and sheepshead minnow. My results suggest that pupfish populations in Red Bluff Reservoir (P2 and P3), Porter's gravel pit (P9) and Imperial Reservoir (P11) represent similar admixtures.

The clinal distribution of alleles diagnostic of sheepshead minnow, and their predominance in the vicinity of Pecos, Texas, suggest the initial introduction of sheepshead minnow into the Pecos River probably occurred near that locality (Echelle and Connor 1989). At least three additional introductions of sheepshead minnow or hybrids are indicated by my data for peripheral waters in the Pecos River drainage. Hybrids in Red Bluff Reservoir and Imperial Reservoir probably represent separate introductions, possibly as a result of baitfish transport. Both reservoirs are impounded by dams impassable by pupfish. The presence of hybrids in Porter's gravel pit probably has a similar explanation, as there seems to be no surface connection with other waters. Dispersal of hybrids within the Pecos River itself has also apparently been facilitated by human transport (Echelle and Connor 1989). The irrigation-diversion dam between sites 1 and 2 would almost certainly be impassable upstream by pupfish; the relatively low frequency of alleles diagnostic of sheepshead minnow at site 1 suggests that hybrids have only recently gained access to that area.

I believe most, if not all, of the hybrid populations in the Pecos River proper and its associated waters (Salt Creek, Porter's gravel pit, and Red Bluff and Imperial reservoirs) have resulted from intra-basin dispersal and artificial transport of hybrids rather than multiple introductions of sheepshead minnow. Throughout the Pecos River, and in all peripheral waters except Porter's gravel pit, the frequency of alleles diagnostic of sheepshead minnow was significantly lower at the GPI-A* locus than at the other three loci examined (Kruskal-Wallis one-way analysis of variance of mean allele frequencies, $P < 0.05$), possibly as a result of genetic drift early in the development of the hybrid swarm. Absence of this "marker" from Porter's gravel pit may be a founder effect or the result of an introduction of sheepshead minnows, rather than hybrids, at that site.

The magnitude of correlations among loci throughout the Pecos River and in peripheral waters indicate a recent origin of hybridization as suggested by Echelle and Connor (1989). In the Pecos River, correlations among loci increased upstream and downstream from Pecos, Texas. This is consistent with an initial introduction of sheepshead minnow in the Pecos area, and subsequent dispersal of hybrids from that site. Compared with most sites in the Pecos River, correlations among loci (Table 2) were relatively high in lower Salt Creek (P4-P6), Red Bluff Reservoir (P2-P3) and Imperial Reservoir (P11), suggesting more recent introductions of hybrids or sheepshead minnow into these waters.

Until my survey, hybrids had not been detected upstream from site P4 in Salt Creek (Echelle and Connor 1989). A series of small waterfalls immediately upstream from P4 apparently prevented hybrids from invading areas farther upstream. However, in 1987 and 1988, high stream flows resulted in frequent spillway discharge from Red Bluff Reservoir into Salt Creek at site P6. This may account for the presence of hybrid genotypes in my samples from sites P5 and P6, which are upstream from the waterfalls. Four fish from those samples were heterozygous for alleles diagnostic of Pecos pupfish and sheepshead minnow; however, there was no obvious morphologic evidence of sheepshead minnow in these specimens. Large collections (N= 63-559) of pupfish made in August 1989 at P6 and two sites farther upstream (OSUS 18351-18353) revealed no morphologic evidence of sheepshead minnow, and my allozyme data showed no evidence of hybrids still farther upstream at site P7. Thus, the level of introgression apparently remains low in Salt Creek upstream from site P4.

My results indicate that hybrids are now common in downstream areas of the Pecos River, well outside the recorded range of Pecos pupfish. Prior to my study, there was only one record of pupfish downstream from Sheffield (Echelle and Echelle 1978): a single specimen of Pecos pupfish from my site 13, at the mouth of Independence Creek. Otherwise, that site produced no pupfish during repeated, intensive sampling in years prior to 1986 (A. A. Echelle, unpublished data; C. Hubbs, University of Texas, personal communication; R. D. Suttkus, Tulane University, personal communication). In contrast, I found hybrids of Pecos pupfish and sheepshead minnow to be common in 1986 at site 13 and 55 km farther downstream at Pandale Crossing (site 14), a site where previous collecting produced no pupfish (A. A. Echelle, unpublished data; C. Hubbs, personal communication).

The range extension of Pecos pupfish x sheepshead minnow hybrids in the Pecos River may reflect heightened ecologic amplitude as a result of added genetic variation due to introgression (Lewontin and Birch 1966). This effect may be especially important for Pecos pupfish, as its original genetic variation was well below the average for fish (Echelle et al. 1987). Alternatively, the range extension may be an adventitious result of an extensive fish kill that occurred in the lower Pecos River in the fall of 1985 (James and De La Cruz 1989), prior to my collections (August 1986) from sites 13 and 14. Martin (1972) and Echelle et al. (1972) found that sheepshead minnow and Red River pupfish _C_. _rubrofluviatilis_, both of which are closely related to Pecos pupfish, are abundant only in environments supporting few other fish species. Thus, the expanded range of pupfish may be a response to the low abundance of other fishes following the 1985 fish kill rather than a result of heightened genetic variation.

To date, the distribution of hybrids in New Mexico is restricted to headwaters of Red Bluff Reservoir (site P2), except for a single collection of 29 pupfish (OSUS 18349) from the mouth of Delaware River (4.5 km N of the New Mexico-Texas boundary, Eddy County, New Mexico), all of which had belly scalation and color patterns indicative of genetic influence by sheepshead minnow. My genetic data for site P1 in 1986, and the morphology of specimens collected by J. E. Brooks in 1988 and 1989 at that locality (OSUS 18355, 18356) and elsewhere throughout the geographic range of the species in New Mexico (University of New Mexico, uncataloged) indicate that the remaining New Mexico populations are largely unaffected by hybrids.

Hybridization with sheepshead minnow has reduced the range of Pecos pupfish by approximately 60%. In Texas, genetically pure populations of Pecos pupfish occur only in Salt Creek and Phipps gravel pit. Pure populations in New Mexico are virtually restricted to portions of the Pecos River near Malaga and Roswell and to isolated springs and sinkholes near Roswell (Sublette et al. 1990). Available habitat in the Roswell area has declined as a result of excessive groundwater withdrawal and a consequent loss of spring and sinkhole habitat (Williams et al. 1985).

In combination, habitat loss and introgressive hybridization threaten the Pecos pupfish throughout its entire range. Of these threats, introgressive hybridization is the most immediate cause for concern. The potential for rapid change in the genetic status of remaining populations is considerable, given the rate of change that occurred in Texas populations. Dispersal of hybrids in Texas waters has apparently been facilitated by intra-basin transport by human activities. Additionally, the distribution of hybrids in Texas waters suggests hybrids may be able to occupy areas in the Pecos River drainage previously unavailable to pupfish, thereby facilitating their spread into areas now occupied by genetically pure populations of Pecos pupfish.

Addendum

Since completion of this chapter, Childs (1993) has reported the presence of a cryptic allele at the GPI-A* locus. This allele is diagnostic of *C. variegatus* but is generally uncommon; however, it is present in Pecos River pupfish populations in relatively high abundance. This cryptic allele has an electrophoretic mobility similar to that of a common allele that is characteristic of *C. pecosensis* and was coded as such in my study. The results of this miscoding do not appear to qualitatively affect any inferences or conclusions reached in this chapter, although it may explain my observation that the frequency of alleles characteristic of *C. variegatus* was significantly lower at the GPI-A* locus than at the other loci examined.

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Table 1. Genotypic arrays for four loci in pupfish samples from the Pecos River, New Mexico-Texas. Locality numbers are as in Figure 1. Alleles are given letters in alphabetic order of decreasing anodal mobility. Allele assignments follow Echelle and Connor (1989) and Echelle et al. (1987): P = loci diagnostic of Pecos pupfish; S = loci diagnostic of sheepshead minnow.

	Locus			
Site	ADH-1*	EST-1*	GPI-A*	PEPD-1*
1	a/a:31	a/a:31	c/c: 3	b/b: 8
	a/c:29	a/b:33	c/d:25	b/c:39
	c/c:11	b/b: 7	d/d:43	c/c:24
2	a/a: 5	a/a: 5	c/c:17	b/b:34
	a/c:32	a/b:28	c/d:35	b/c:36
	c/c:39	b/b:43	d/d:24	c/c: 6
3	a/a: 1	a/b: 5	c/d:32	b/b:58*
	a/c:10	b/b:82	d/d:39	b/c:17
	c/c:68		d/e:16	c/c: 7
4	a/a: 1	a/b: 9	c/c:24	b/b:38
	a/c:10	b/b:40	c/d:22	b/c: 9
	c/c:38		d/d: 3	c/c: 2
5	a/a: 6	a/a: 2	c/c:31	b/b:65
	a/c:36	a/b:21	c/d:54	b/c:30
	c/c:60	b/b:79	d/d:17	c/c: 7
6	a/a:11	a/a: 8	c/c:15	b/b:31
	a/c:29	a/b:31	c/d:44	b/c:33
	c/c:25	b/b:33	d/d:14	c/c:12

Table 1. (Continued)

	Locus			
Site	ADH-1*	EST-1*	GPI-A*	PEPD-1*
7	a/a:19* a/c:21 c/c:23	a/a:18 a/b:28 b/b:17	c/c: 9 c/d:32 d/d:22	b/b:14 b/c:23 c/c:25 c/d: 1
8	a/a:32 a/c:51 c/c:25	a/a:30 a/b:56 b/b:21	c/c:10 c/d:40 d/d:58	b/b:20* b/c:35 c/c:49
9	a/a:32 a/c:33 c/c:15	a/a:28 a/b:32 b/b:20	c/c:10 c/d:27 d/d:43	b/b:16 b/c:37 c/c:27
10	a/a:12 a/c:35 c/c:11	a/a:20 a/b:27 b/b:11	c/c: 4 c/d:27 d/d:27	b/b:10 b/c:28 c/c:20
11	a/a:22 a/c:43 c/c: 9	a/a:18 a/b:35 b/b:20	c/c: 5 c/d:37 d/d:32	b/b:15 b/c:33 c/c:26
12	a/a:23 a/c:35 c/c:24	a/a:20 a/b:34 b/b:28	c/c: 5 c/d:39 d/d:38	b/b:15 b/c:41 c/c:26
13	a/a:12* a/c:18 c/c:23	a/a: 8 a/b:30 b/b:15	c/c: 7 c/d:27 d/d:19	b/b: 8 b/c:24 c/c:21
14	a/a: 2 a/c:14 c/c:34	a/a: 4 a/b:20 b/b:26	c/c: 3 c/d:19 d/d:28	b/b:27 b/c:16 c/c: 7
P1	a/a:36	a/a:36	d/d:30 d/e: 6	c/c:36

Table 1. (Continued)

	Locus			
Site	ADH-1*	EST-1*	GPI-A*	PEPD-1*
P2	*a/a*:13 *a/c*:13 *c/c*: 7	*a/a*:10 *a/b*:20 *b/b*: 3	*c/c*: 3 *c/d*:13 *c/e*: 1 *d/d*:15 *d/e*: 1	*b/b*: 7 *b/c*:17 *c/c*: 9
P3	*a/a*:37 *a/c*:28 *c/c*: 4	*a/a*:25* *a/b*:42 *b/b*: 2	*c/c*: 2 *c/d*:20 *c/e*: 1 *d/d*:41 *d/e*: 4 *d/f*: 1	*b/b*: 3 *b/c*:23 *c/c*:43
P4	*a/a*:44 *a/c*: 8 *c/c*: 1	*a/a*:42 *a/b*:11	*c/d*: 7 *d/d*:44 *d/e*: 2	*b/b*: 1 *b/c*:10 *c/c*:42
P5	*a/a*:23 *a/c*: 1	*a/a*:23 *a/b*: 1	*d/d*:22 *d/e*: 2	*c/c*:24
P6	*a/a*:30	*a/a*:29 *a/b*: 1	*c/d*: 1 *d/d*:29	*b/c*: 1 *c/c*:29
P7	*a/a*:30	*a/a*:30	*d/d*:29 *d/e*: 1	*c/c*:30
P8	*a/a*: 6 *a/c*:14 *c/c*:10	*a/a*: 3 *a/b*:20 *b/b*: 7	*c/c*: 2 *c/d*:12 *d/d*:16	*b/b*: 7 *b/c*:10 *c/c*:13
P9	*a/a*: 1 *a/c*: 3 *c/c*:26	*b/b*:30	*c/c*:14 *c/d*:14 *d/d*: 2	*b/b*: 6* *b/c*:22 *c/c*: 2
P10	*a/a*:30	*a/a*:30	*d/d*:30	*b/c*: 2 *c/c*:28

Table 1. (Continued)

	Locus			
Site	ADH-1*	EST-1*	GPI-A*	PEPD-1*
P11	a/a: 1 a/c:13 c/c:22	a/a: 3* a/b: 5 b/b:28	c/c: 9 c/d:20 d/d: 7	b/b:24 b/c:10 c/c: 2
Allele assignments:	P = a S = c	P = a S = b	P = d-f S = c	P = c-d S = b

* significant ($P < 0.05$) deviation from Hardy-Weinberg expectations based upon single-locus tests.

Table 2. Correlations between alleles of diagnostic loci in hybrid pupfish from the Pecos River, New Mexico-Texas, and peripheral waters. Locations are as in Figure 1.

Site	ADH-1* x EST-1*	ADH-1* x GPI-A*	ADH-1* x PEPD-1*	EST-1* x GPI-A*	EST-1* x PEPD-1*	GPI-A* x PEPD-1*
			Pecos River			
1	0.038	0.128	-0.047	0.509**	0.020	-0.039
2	0.242	0.063	0.324*	0.424**	0.204	-0.041
3	0.032	0.125	0.123	0.063	0.009	-0.071
4	0.088	0.010	0.148	0.075	0.162	-0.091
5	-0.060	0.014	-0.071	0.291*	0.175	-0.070
6	-0.112	-0.126	-0.061	0.479**	0.194	0.296*
7	0.237	-0.063	-0.056	0.375*	0.160	0.138
8	0.025	-0.041	0.079	0.336*	-0.045	-0.083
9	0.139	0.072	0.086	0.666**	0.111	0.111
10	0.109	0.027	0.111	0.567**	0.154	0.082
11	0.011	0.045	-0.087	0.525**	0.189	0.122
12	0.231*	-0.177	0.026	0.139	0.164	0.192
13	-0.017	0.090	-0.045	0.423**	0.156	0.084
14	-0.117	-0.236	-0.010	0.052	0.139	0.091
			Peripheral waters			
P1	0.000	0.000	0.000	0.000	0.000	0.000
P2	0.131	-0.141	-0.022	0.557*	-0.105	-0.188
P3	0.272*	0.064	0.078	0.236*	0.270*	0.050
P4	0.007	-0.169	0.183	0.786**	0.712**	0.713**
P5	1.000**	0.000	0.000	0.000	0.000	0.000
P6	0.000	0.000	0.000	-0.030	1.000**	-0.030
P7	0.000	0.000	0.000	0.000	0.000	0.000
P8	-0.375*	-0.085	-0.129	0.371*	-0.090	0.218

Table 2. (Continued)

Site	ADH-1* x EST-1*	ADH-1* x GPI-A*	ADH-1* x PEPD-1*	EST-1* x GPI-A*	EST-1* x PEPD-1*	GPI-A* x PEPD-1*
P9	0.000	0.446	-0.049	0.000	0.000	0.044
P10	0.000	0.000	0.000	0.000	0.000	0.000
P11	-0.296	-0.166	0.100	-0.026	-0.098	-0.157

* $\underline{P} < 0.05$, based on single locus-pair comparisons.

** $\underline{P} < 0.05$, table-wide significance based upon sequential Bonferroni test; results for sites 1-14 and P1-P11 were treated separately.

Figure 1. Map of the Pecos River, Texas, showing the locations of sampling sites. Sites 1 to 14 are located in the Pecos River. Sites P2 and P3 are located in Red Bluff Reservoir, New Mexico-Texas, an impoundment of the Pecos River. Sites P4 to P7 are located in Salt Creek, a small tributary to the Pecos River, and represent an upstream (P7)- downstream (P4) series. Site P8 is an irrigation canal located just downstream from an irrigation diversion dam at Site 2. Site P11 is Imperial Reservoir; sites P9 and P10 are commercial gravel pits owned by Phipp's Gravel Company and Porter's Gravel Company, respectively. Inset shows the locations of Roswell (R) and Malaga (P1), New Mexico, Lake Balmorhea (LB) and Leon Creek (LC), Texas, and Falcon Reservoir (FR) on the border between the United States and Mexico.

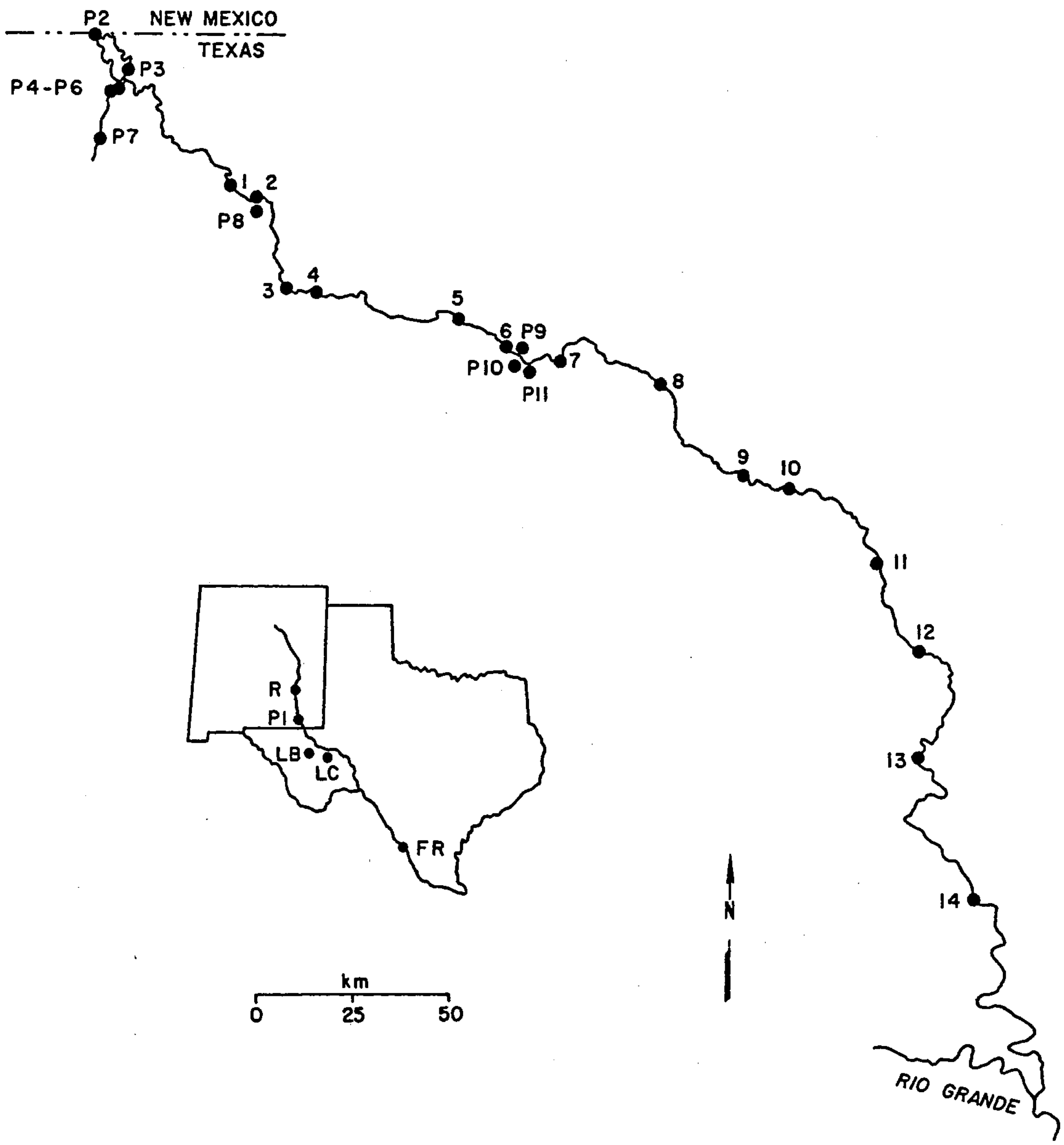
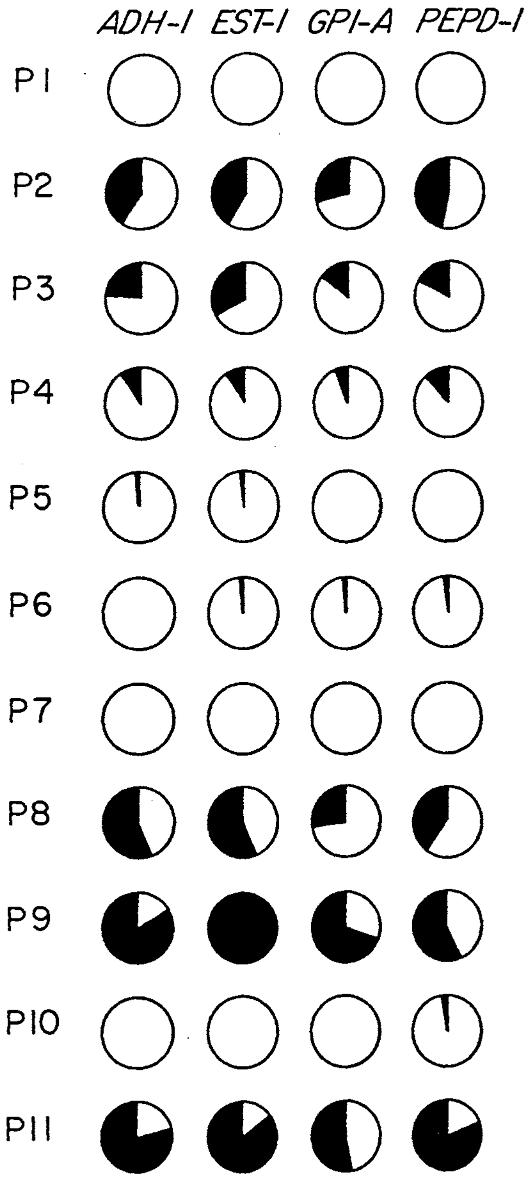
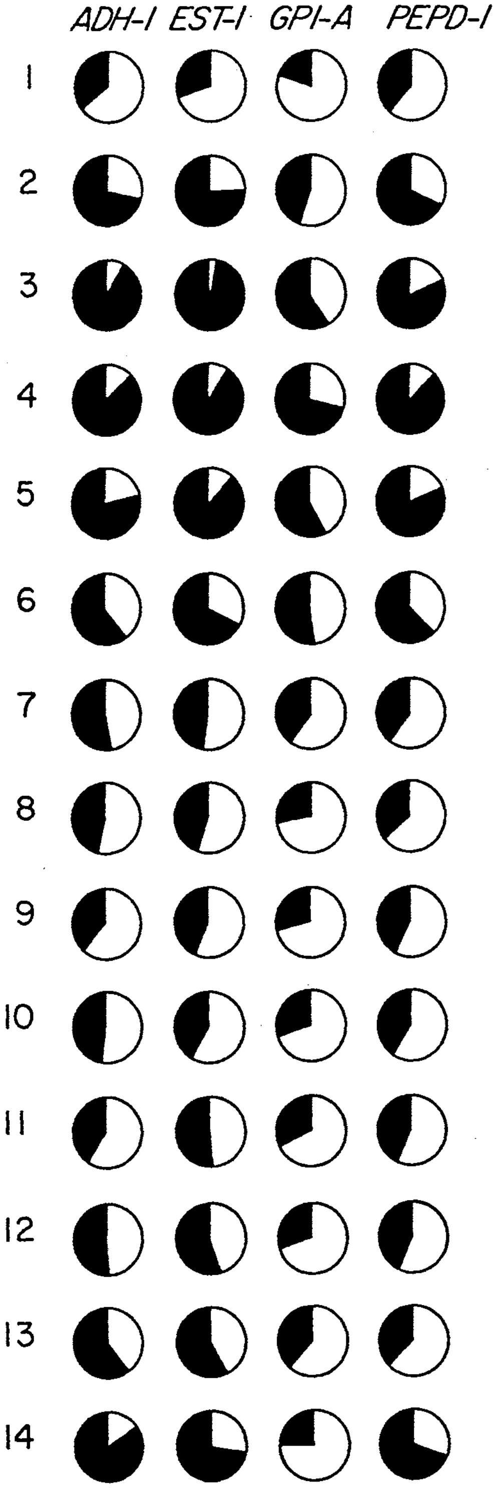

P2
NEW MEXICO
TEXAS
P3
P4-P6
P7
1
2
P8
3
4
5
6
P9
P10
P11
7
8
9
10
11
12
13
14
RIO GRANDE
R
P1
LB
LC
FR
km
0
25
50
N

Figure 2. Frequencies of alleles diagnostic of Pecos pupfish (light) and sheepshead minnow (shaded) in pupfish populations from the Pecos River, New Mexico-Texas, and associated waters.


ADH-1
EST-1
GPI-A
PEPD-1
P1
P2
P3
P4
P5
P6
P7
P8
P9
P10
P11


ADH-1
EST-1
GPI-A
PEPD-1
1
2
3
4
5
6
7
8
9
10
11
12
13
14

CHAPTER II

MORPHOLOGICAL VARIATION IN INTERGRADE PUPFISH POPULATIONS (CYPRINODONTIDAE: CYPRINODON) FROM THE PECOS RIVER

The sheepshead minnow, *Cyprinodon variegatus*, was introduced into the Pecos River of eastern New Mexico and southwest Texas between 1980 and 1984 (Echelle and Connor 1989). In 1984, specimens showing evidence of hybridization between sheepshead minnow and an endemic species, the Pecos pupfish, *C. pecosensis*, were collected from two sites in Texas portions of the river (Echelle et al. 1987). An allozyme survey conducted in 1985 (Echelle and Connor 1989) found no evidence of hybridization or of *C. variegatus* in New Mexico portions of the Pecos River. However, panmictic admixtures of *C. variegatus* and *C. pecosensis* were found throughout some 430 kilometers of the Pecos River in Texas, about half the original range of *C. pecosensis* (Echelle and Echelle 1978). There was pronounced geographic variation in the genetic structure of pupfish populations in Texas portions of the Pecos River; alleles diagnostic of *C. variegatus* represented about 85% of the pupfish genome in the vicinity of Pecos, Texas, and decreased clinally to 18%

in areas upstream from Pecos and to 40-45% in areas downstream from Pecos (Echelle and Connor 1989). Geographic variation in a single morphological character, belly scalation, roughly paralleled that observed in allozymes (Echelle and Connor 1989).

In 1986, I sampled the Pecos River from the New Mexico-Texas boundary downstream to Pandale, Texas, and extended the known distribution of genetically mixed pupfish "intergrade" populations approximately 100 kilometers (Wilde 1994). The geographic pattern of allozymic variation in 1986 generally was unchanged from that seen in 1985, but there was evidence of a decline in the magnitude of linkage disequilibrium (correlations among gene loci) throughout the river (Wilde 1994). The purpose of this paper is to describe inter- and intrapopulational morphologic variation in intergrade pupfish in the Pecos River.

METHODS

I collected pupfish from 14 locations in the Pecos River in Texas (Fig. 3) during August 1986. Fish were frozen on dry ice in the field, transported to the laboratory, and stored at -70°C. After removal of liver and eye tissues for electrophoresis (Wilde 1994), fish were individually tagged, fixed in 40% formalin, and later transferred to 50% isopropyl alcohol. All specimens are deposited in the Oklahoma State University Collection of

Vertebrates (OSUS 26718-26731). I made 12 measurements on each specimen (Fig. 4); eight measurements were arranged in a truss network (Bookstein et al. 1985) and the others included standard length (SL) and lengths of the dorsal, anal, and pectoral fins. Measurements were made with Helios dial calipers and recorded to the nearest 0.1 mm. Specimens occasionally lacked fins or were otherwise damaged so that all measurements could not be made. If only one character was missing or damaged, I replaced the missing value with the mean for that character of all specimens of the same size (± 1-3 mm SL) and sex from that collection. Specimens were not used if more than one character could not be measured. Measurements were estimated for no more than seven specimens per location (both sexes combined) and, overall, for less than five percent of all individuals reported on here.

I also coded belly scalation and color pattern (depth and width of vertical bars) in reference samples of C. pecosensis and C. variegatus and in intergrade samples. The belly is incompletely scaled in C. pecosensis, whereas in C. variegatus it is completely scaled (Echelle and Echelle 1978); I coded this character 0 (naked) to 6 (fully scaled) as shown in Fig. 4. Color patterns of C. pecosensis, C. variegatus, and genetic intergrades are shown in Echelle and Connor (1989). I coded this character 0 for the pattern typical of C. pecosensis (vertical bars wide, usually failing to reach the ventral edge of the lateral profile) and 6 for patterns typical of C. variegatus (vertical bars thin, extending to the ventrum). Color patterns perceived as being intermediate were assigned a value of 3; usually, such patterns consisted of wide, triangular bars that extended to the venter, a pattern that occasionally occurs in "pure" C. pecosensis, but did not occur in any of my reference samples.

Allozyme data (Echelle and Connor 1989; Wilde 1994) suggest that no pure individual of either parental species occurs in Texas portions of the Pecos River. I used collections of C. pecosensis deposited in the University of Texas Memorial Museum (TNHC 4812, 4816, 4820, and 4854) from the lower Pecos River as reference specimens to describe morphological variation in the original pupfish populations of the lower Pecos River. These collections were made at the following locations (Fig. 3) (number of male and female specimens examined, respectively, in parentheses): site 1 (Fig. 3; 12 males, 7 females), site 9 (16 males, 17 females), site 10 (17 males, 21 females), and site 11 (5 males, 5 females). The exact source of C. variegatus introduced into the Pecos River is unknown, but two sources are most likely: 1) Lake Balmorhea (Fig. 3), into which C. variegatus was introduced in the 1960s (Stevenson and Buchanan 1973); and 2) the Texas Gulf Coast where C. variegatus is widespread and abundant. I used a collection from Galveston Island, Texas (OSUS 26751), as reference specimens of this species.

I treated males and females separately in all analyses because of the pronounced sexual dimorphism characteristic of Cyprinodon (Miller 1948). Morphometric data were $\log_{10}$-transformed to stabilize variances. I used the first principal component of the pooled within-group covariance matrix for reference specimens as an estimate of within-group general-size allometry (Bookstein 1989) and adjusted the $\log_{10}$-transformed data for both reference specimens and intergrade samples for this size factor using Burnaby's (1966) method as recommended by Rohlf and Bookstein (1987). I performed a second set of principal components analyses on the size-adjusted data for reference specimens. Variable loadings from the first principal component of the size-adjusted data (BPC1, Table 3) were used to calculate a morphometric "hybrid" index score for each specimen. Scores for the morphometric index were standardized so that means for reference specimens of C. pecosensis and C. variegatus were 0.0 and 6.0, respectively.

I assessed significance of geographic variation in size-adjusted variables and the morphometric index with one-way analyses of variance (ANOVA). Relationships among morphological variables (morphometric index, belly scalation, and color pattern) were assessed with Spearman's rank correlation (r_S). Within-sample variability was evaluated on the basis of univariate (CV) and multivariate (MCV) coefficients of variation (Sokal and Rohlf 1981; Van Valen 1978) and the sample variance ($\underline{s}^2$) for color pattern and belly scalation. If intergrade populations and the parental populations exhibit equal variability, I would expect 50% of intergrade CVs for each character to be greater, and 50% less, than CVs for the more variable parental species. I tested for departures from these proportions, for each character, with a one-tailed binomial test (Siegel 1956) and interpreted significant results as evidence of greater morphological variability in intergrades. MCVs were tested in a similar manner. I evaluated table-wide significance of ANOVA results, correlations, and binomial tests by the sequential Bonferroni test (Rice 1989). All statistical analyses, except binomial tests, were performed using SAS (SAS Institute 1985).

RESULTS

Morphological Comparisons Between Parental Species and Intergrade Populations

Females.--There were significant ($\underline{P} < 0.05$) differences between C. pecosensis and C. variegatus in all size-adjusted morphometric characters except m8 and m9. C. pecosensis and C. variegatus were completely separable by their scores on the first principal component (BPC1) of the size-adjusted data (Fig. 5). Loadings of six morphometric characters were greater than 0.290 on BPC1 (Table 3) and accounted for most of the morphometric differentiation between species (Table 4). Compared with C. variegatus, C. pecosensis is relatively longer (m1) and more shallow bodied (m7 and m10) and has a longer anal fin (m3) and more posteriorly placed dorsal (m5) and anal (m6) fins. Scores for color pattern were invariant, 0.0 and 6.0, in reference collections of C. pecosensis and C. variegatus, respectively. Belly scalation was reduced in C. pecosensis (mean 1.22; range 1 to 4), but was complete (mean 6.0) in all specimens of C. variegatus.

Among the six morphometric characters that most differentiated the parent species, sample means for two (m7 and m10) were generally intermediate in the intergrade populations, whereas means of three characters (m1, m5, and m6) were shifted toward C. pecosensis, and means for m3 were generally shifted toward C. variegatus (Table 4). Three of the remaining morphometric characters (m2, m11, and m12) were intermediate to the parent species and three (m4, m8, and m9) were generally more extreme in the intergrade populations than in either C. pecosensis or C. variegatus. Sample means for color pattern and belly scalation were shifted toward C. variegatus in all intergrade populations. Mean scores of color pattern and belly scalation ranged from 4.74 to 6.00 and from 3.95 to 6.00, respectively.

Males.--Males of *C*. *pecosensis* and *C*. *variegatus* differed significantly ($P < 0.05$) in all size-adjusted morphometric characters except m1, m6, and m12. BPC1 scores separated almost completely male *C*. *pecosensis* from *C*. *variegatus* (Fig. 5). The greatest morphometric differences between these species were in five characters that had loadings greater than 0.250 on BPC1 (Tables 3, 5). *C*. *pecosensis* is more shallow bodied (m7 and m10), and has longer anal fins (m3), shorter pectoral fins (m4), and a longer caudal peduncle (m9) than does *C*. *variegatus*. There was no variation in scores for color pattern in the reference samples; all scores were 0 in *C*. *pecosensis* and 6 in *C*. *variegatus*. Scores for belly scalation ranged from 1 to 4 in *C*. *pecosensis* (mean = 1.06), but did not vary in *C*. *variegatus* (mean = 6.0).

Samples of males from the intergrade populations were intermediate to *C*. *pecosensis* and *C*. *variegatus* in most characters (Table 5). Among the five characters that most differentiated the parent species, sample means of m3 and m7 were intermediate to the parent species; means of m4 and m10 tended toward *C*. *pecosensis*, whereas means of m9 tended toward *C*. *variegatus*. Means for the remaining morphometric characters were intermediate to *C*. *pecosensis* and *C*. *variegatus*, except for m2, m6, and m12 which were generally more extreme than in either parent. Sample means of color pattern and belly scalation were shifted toward *C*.

variegatus in all intergrade populations. Mean scores of color pattern and belly scalation ranged from 4.06 to 6.00 and from 3.96 to 6.00, respectively.

Geographic Variation in Intergrade Populations

There was significant ($P < 0.05$) geographic variation in all size-adjusted morphometric characters in males (Table 5) and in all except m2, m5, and m8 in females (Table 4). In both sexes, morphometry was most like that of *C. variegatus* at sites 3 and 4 and generally was shifted toward that of *C. pecosensis* in areas upstream and downstream from these sites.

Distributions of morphometric-index scores of intergrade populations were significantly different ($P < 0.05$) from those for the parent species except in male pupfish at sites 1 and 14 (Fig. 5). At most sites, intergrade populations spanned much of the range of variation encompassed by both parental species. Modal index scores were intermediate to the parental species, but were generally shifted toward one parent. Male scores were shifted toward *C. variegatus* upstream from Site 11 and toward *C. pecosensis* downstream from that site. Female scores were shifted toward *C. pecosensis* at all sites except 3 and 4. Frequency distributions of morphometric-index scores generally were unimodal at all sites.

Correlations Among Characters

Geographic variation in means of the morphometric index, belly scalation, and color pattern (Fig. 6) was congruent in females; correlations ($\underline{r}_s$) among these characters ranged from 0.71 to 0.87 and were significant in every case ($\underline{P} < 0.005$). In males, geographic variation in morphometric-index scores, belly scalation, and color pattern was similar at sites 1 to 8; downstream from Site 8, morphometric-index scores exhibited an opposite trend from belly scalation and color pattern. Across all sites, belly scalation and color pattern were highly correlated in males ($\underline{r}_s = 0.63$; $\underline{P} = 0.015$), but there was no significant correlation between morphometric-index score and belly scalation ($\underline{r}_s = 0.36$; $p = 0.212$) or color pattern ($\underline{r}_s = 0.14$; $p = 0.644$). Within sites, only 6 of 168 correlations (2 sexes x 6 character combinations x 14 stations) among morphometric-index scores, belly scalation, and color pattern were significant ($\underline{P} < 0.05$) suggesting independent assortment of these characters.

Within-Sample Variability in Intergrade Populations

For both sexes, intergrade populations were more variable than the parental species (Tables 4 and 5). Coefficients of variation (CV) for four characters (m2, m3, m6, and m9) were significantly greater ($\underline{P} < 0.05$; one-tailed binomial test) in females from intergrade populations than in the parental species; in males, CVs of nine characters (m1-m4, m6, m8, m11, and m12) were significantly greater than in the parental species. None of the characters showed greater variation in the parental species than in intergrade populations. Multivariate coefficients of variation (MCV) for females were 6.47 and 6.86, respectively, in _C. variegatus_ and _C. pecosensis_ and ranged between 7.85 and 10.17 in females from intergrade populations; for males, MCVs were 5.31 and 5.33 in _C. variegatus_ and _C. pecosensis_, respectively, and ranged from 7.17 to 9.38 in intergrade populations (Fig. 7). In both sexes, MCVs for the Pecos River populations were significantly greater ($P < 0.005$) than for the parental species.

Intergrade populations expressed greater variation than either parent species in both belly scalation and color pattern. Color pattern was fixed in reference specimens of both parent species ($s^2 = 0.0$), but s^2 for intergrade populations ranged from 0.00 to 6.15 in females and 0.00 to 8.23 in males. Belly scalation was fixed in _C. variegatus_ and exhibited low variability in _C. pecosensis_ ($s^2 = 0.51$ in females and 0.42 in males); in intergrade populations, s^2 for belly scalation ranged from 0.00 to 32.41 in females and from 0.00 to 2.59 in males.

DISCUSSION

My results show that extensive morphological change has accompanied the genetic changes previously documented in studies of allozyme variation in pupfishes of the Pecos River in Texas (Echelle and Connor 1989; Wilde 1994). Morphological and allozyme character sets agree in several aspects. Intergrade populations generally are intermediate to the parental forms, there has been a rapid approach to random assortment among characters, and the intergrade populations exhibit greater variability than originally occurred in C. pecosensis. These observations and the lack of consistent bimodality in morphometric-index scores support Echelle and Connor's (1989) conclusion that pupfish populations in the Pecos River represent panmictic admixtures of C. pecosensis and C. variegatus.

The morphological effects of hybridization and introgression are evident in pupfish populations throughout some 500 km of the Pecos River, from the New Mexico-Texas boundary downstream to Pandale, Texas. Historically, C. pecosensis was widespread and abundant as far downstream as Site 10, but was known to occur downstream as far as Site 12 (Echelle and Echelle 1978). Since the introduction of C. variegatus, individuals resembling that species in morphometry, color pattern, and belly scalation, including some that are morphologically indistinguishable from C. variegatus, have become common throughout this area, and now occur as far downstream as Site 13, beyond the historic range of C. pecosensis. Additionally, pupfish with color patterns, belly scalation, or allozymes characteristic of C. variegatus are found in virtually all aquatic habitats along Texas portions of the Pecos River, including irrigation canals, water-filled gravel pits, and reservoirs isolated by dams that pupfish would be incapable of traversing (Wilde 1994). The occurrence of intergrade populations in these habitats is likely the result of a combination of natural dispersal and intrabasin transport of pupfish by humans (Wilde 1994).

The overall pattern of geographic variation in morphology of the intergrade populations generally agrees with patterns revealed in studies of allozyme and mitochondrial DNA (mtDNA) variation (Echelle and Connor 1989; Childs 1993; Wilde 1994). The molecular studies demonstrate high frequencies (approaching 90%) of introduced genetic elements in the vicinity of Pecos, Texas (sites 2 to 4) and lower frequencies in areas upstream and downstream from that area, except at the downstream-most site (site 14), where there was a tendency (Childs 1993; Wilde 1994) toward increased frequencies of elements typical of C. variegatus. The morphological data roughly correspond with this pattern (Fig. 6). Male morphometry at site 14 deviated from the tendency for the morphological indices at that site to be shifted toward the condition typical of C. variegatus, possibly as a result of a founder effect. Historically, pupfish were absent from this site and appear to have become established only after a recent fish kill in the lower Pecos River (Wilde 1994).

The morphological changes documented herein appear to have occurred in less than five years. Echelle and Connor (1989) examined museum specimens of pupfish collected in 1980 from three locations between my sites 7 and 12; none of these samples showed any morphological evidence of hybridization with _C_. _variegatus_ based on color pattern and belly scalation. However, pupfish collected in 1984 from two widespread locations, sites 3 and 11, showed morphological (Wilde 1994) and allozyme (Echelle et al. 1987) traits characteristic of _C_. _variegatus_.

Based on frequencies of introduced mtDNA relative to introduced allozymes, Childs (1993) suggested that the frequencies of introduced genetic elements in the intergrade pupfish populations are not a result of competitive displacement of native elements. His mtDNA and allozyme data were best explained by the hypothesis that the existing frequencies of introduced genetic elements at each site are similar to the original starting frequencies at the time when hybridization was initiated between _C_. _pecosensis_ and _C_. _variegatus_ or intergrades. This implies extremely low abundances of _C_. _pecosensis_ at sites where the frequency of introduced genetic elements approaches 90%, for example, in the vicinity of Pecos (sites 2-4). According to this hypothesis, C. variegatus was introduced into the Pecos River, probably in the vicinity of Pecos, at a time when population densities of the native pupfish were extremely low.

Changes in the morphological and genetic structure of pupfish populations in the Pecos River may have been facilitated by population fluctuations associated with fish kills. Since at least the 1950s, landowners adjacent to saline reaches of the Pecos River have reported fish kills that were attributed to high salinities or pollution from oil and gas field operations (Texas Parks and Wildlife Department, unpubl. data; Rhodes and Hubbs 1992). However, both C. pecosensis and a related species, C. rubrofluviatilis, seem highly tolerant of oil and gas field pollution and sometimes occur abundantly in areas where such pollution appears severe and other species are virtually absent (A. A. Echelle, pers. comm.). More recently, toxins produced by blooms of the chrysophyte alga Pyrmnesium parvum have been implicated in several fish kills in the Pecos River (James and De La Cruz 1989). These kills occurred over hundreds of kilometers of the river in the fall months of 1985, 1986, and 1988 (James and De La Cruz 1989; Rhodes and Hubbs 1992). Although P. parvum cannot be implicated in earlier fish kills, W. L. Minckley (pers. comm.) noted that, during a fish kill in the 1960s, the water in the Pecos

River had attributes similar to those associated with the algal-induced kills described by Rhodes and Hubbs (1992). Field observations made by Rhodes and Hubbs (1992) suggest that pupfish are susceptible to toxins produced by *P. parvum*, but not as greatly as other fish species. However, at the time of their study, no genetically "pure" individuals of *C. pecosensis* occurred in the affected portions of the Pecos River (Echelle and Connor 1989; Wilde 1994). It is possible that *C. variegatus* and the intergrades are more resistant than *C. pecosensis* to toxins produced by *P. parvum*.

Thus, the introduction of *C. variegatus* into the Pecos River might have coincided with a fish kill that nearly eliminated the native species in the vicinity of Pecos. Irrigation diversion dams upstream and downstream from the Pecos area would have limited recolonization by *C. pecosensis*, allowing the development of a local pupfish population genetically dominated by *C. variegatus*. This would explain the rapidity of the extensive morphological and genetic changes that developed in the Pecos River pupfish population between 1980 and 1984. Subsequent fish kills, together with dispersal of introduced genetic elements, might have contributed to the rapid changes that occurred throughout the river. The presence of pupfish downstream from Independence Creek (Site 12), the former downstream limit of distribution of *C. pecosensis*, appears to have been the result of colonization by pupfish following a fish kill (Wilde 1994). Morphological shifts toward character states more typical of *C. variegatus* in this area may have resulted from a founder effect.

Except for geographic scale, hybridization and subsequent changes in pupfish morphology in the Pecos River are remarkably similar to events in Leon Creek, Texas, following the introduction of *C. variegatus* in the 1970s. Leon Creek is an isolated, springfed watercourse in the Pecos River drainage that supports an endemic species of pupfish, *C. bovinus*, that appears to be closely related to *C. pecosensis* (Echelle and Echelle 1992). Within two years after discovery of *C. variegatus* in Leon Creek, putative hybrids were common, pupfish with morphological traits characteristic of *C. variegatus* were dispersed throughout an isolated 4-km portion of the creek, and an extensive eradication program was required to protect the genetic integrity of *C. bovinus* (Kennedy 1977; Hubbs et al. 1978; Hubbs 1980). No genetic studies were performed on Leon Creek pupfish populations, but, as in the Pecos River, there seems to have been a rapid increase in the frequency of intergrades between *C. variegatus* and *C. bovinus*.

Non-anthropogenic contact and hybridization appear to have played a significant role in the evolution of a variety of North American fishes, as evidenced by both morphological (Miller and Smith 1981) and biochemical studies (Rosenfeld and Wilkinson 1989; Echelle and Dowling 1993; Echelle and Echelle 1993). The changes occurring after the introduction of _C_. _variegatus_ into the range of _C_. _pecosensis_ illustrate that both molecular and morphological change can proceed rapidly over large geographic areas once two previously allopatric species have been brought into contact. In this instance, the rate and magnitude of change may have been enhanced by a decline in the abundance of the native species that occurred prior to, or coincident with, the introduction of _C_. _variegatus_.

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Table 3. Character loadings on PC1 and PC2 of the $\log_{10}$ transformed data and PC1 of the size-adjusted data (BPC1). Percentage of total variance explained by PC1 and PC2 and the percentage of residual variance (after removal of general-size-allometry) explained by BPC1 are given at the bottom of table.

	females			males		
	PC1	PC2	BPC1	PC1	PC2	BPC1
m1	0.277	0.304	0.292	0.262	0.048	0.036
m2	0.312	-0.184	-0.196	0.339	0.109	0.097
m3	0.150	0.508	0.500	0.172	0.634	0.629
m4	0.288	-0.127	-0.139	0.271	-0.237	-0.252
m5	0.265	0.444	0.433	0.253	0.108	0.099
m6	0.286	0.356	0.345	0.259	-0.082	-0.092
m7	0.335	-0.291	-0.304	0.349	-0.229	-0.242
m8	0.307	-0.018	-0.031	0.301	-0.102	-0.120
m9	0.247	0.091	0.078	0.245	0.550	0.532
m10	0.351	-0.397	-0.412	0.351	-0.360	-0.375
m11	0.308	-0.099	-0.111	0.314	-0.081	-0.098
m12	0.288	-0.123	-0.137	0.297	0.090	0.073
% of variance	90.1	5.2		87.7	5.1	
% of residual variance			53.3			42.0

Table 4. Back-transformed means and coefficients of variation (CV) of size-adjusted variables in female _C. pecosensis_, _C. variegatus_, and intergrade pupfish populations from the Pecos River, Texas.

Sample	N	m1		m2		m3		m4		m5		m6	
		$\bar{X}$	CV	$\bar{X}$	CV	$\bar{X}$	CV	$\bar{X}$	CV	$\bar{X}$	CV	$\bar{X}$	CV
C. pecosensis	50	2.75	1.85	0.61	4.20	1.57	4.24	0.65	4.16	1.66	3.21	1.76	2.73
1	23	2.71	1.94	0.60	7.43	1.43	7.45	0.60	6.04	1.61	3.50	1.78	3.81
2	24	2.68	2.45	0.61	5.43	1.37	6.37	0.65	6.52	1.60	3.27	1.78	3.37
3	24	2.68	1.74	0.62	3.92	1.33	5.96	0.63	4.50	1.60	3.34	1.76	2.76
4	44	2.70	2.41	0.62	4.63	1.34	8.51	0.67	6.37	1.59	2.63	1.77	3.55
5	59	2.70	2.38	0.61	5.01	1.32	8.27	0.61	6.86	1.61	3.13	1.77	3.56
6	37	2.72	2.75	0.62	6.53	1.38	7.37	0.63	6.01	1.60	4.26	1.75	4.35
7	25	2.72	2.50	0.62	5.07	1.39	8.79	0.64	7.91	1.62	3.36	1.78	3.25
8	62	2.75	2.24	0.62	4.46	1.42	7.27	0.64	6.96	1.62	3.08	1.80	3.34
9	38	2.70	2.23	0.62	4.69	1.39	9.02	0.63	6.75	1.60	4.11	1.76	4.55
10	33	2.73	2.30	0.62	5.07	1.42	8.53	0.63	4.74	1.63	3.41	1.79	3.34
11	38	2.74	2.65	0.62	4.20	1.39	7.75	0.65	5.53	1.63	3.39	1.79	4.04
12	53	2.72	2.18	0.63	4.49	1.40	7.62	0.63	5.48	1.59	4.12	1.77	3.89
13	24	2.70	1.80	0.62	5.02	1.39	5.67	0.66	3.92	1.58	3.70	1.78	3.88
14	21	2.68	1.48	0.64	5.25	1.35	6.97	0.67	4.44	1.59	3.67	1.77	3.50
C. variegatus	50	2.56	1.48	0.64	3.69	1.40	6.27	0.68	4.00	1.49	3.17	1.60	2.03

Table 4. Extended.

Sample	m7		m8		m9		m10		m11		m12	
	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV
<u>C</u>. <u>pecosensis</u>	0.72	4.60	1.05	4.06	1.11	5.87	0.29	4.24	1.20	2.59	1.04	3.32
1	0.73	4.86	1.07	6.03	1.13	8.59	0.31	4.01	1.25	2.87	1.08	4.45
2	0.73	3.57	1.04	5.20	1.10	7.86	0.31	4.49	1.23	3.09	1.06	3.60
3	0.74	2.94	1.06	4.84	1.12	6.98	0.31	4.21	1.24	2.82	1.06	3.83
4	0.74	3.72	1.07	5.77	1.07	6.80	0.31	3.55	1.23	2.07	1.05	3.12
5	0.76	3.67	1.07	6.11	1.10	6.94	0.31	4.33	1.25	2.42	1.05	4.65
6	0.72	4.08	1.06	5.80	1.16	8.58	0.30	3.40	1.24	2.83	1.07	5.79
7	0.73	5.00	1.05	6.27	1.12	7.59	0.30	4.48	1.23	3.25	1.07	5.19
8	0.71	4.59	1.04	4.87	1.13	7.34	0.30	4.94	1.21	3.55	1.06	3.74
9	0.73	4.28	1.06	5.53	1.11	6.50	0.31	4.36	1.25	3.39	1.08	4.25
10	0.73	5.83	1.05	6.64	1.12	7.39	0.30	6.18	1.23	2.99	1.06	3.22
11	0.73	5.50	1.05	5.45	1.09	7.62	0.31	4.30	1.22	3.03	1.04	4.50
12	0.72	3.79	1.06	6.00	1.14	7.71	0.30	5.03	1.24	3.07	1.08	4.81
13	0.71	3.73	1.05	4.96	1.14	8.29	0.31	4.32	1.21	3.49	1.08	4.45
14	0.73	3.57	1.05	5.05	1.10	6.25	0.31	3.79	1.21	3.22	1.03	4.24
<u>C</u>. <u>variegatus</u>	0.77	2.88	1.05	2.23	1.10	3.91	0.32	3.19	1.23	2.11	1.09	2.01

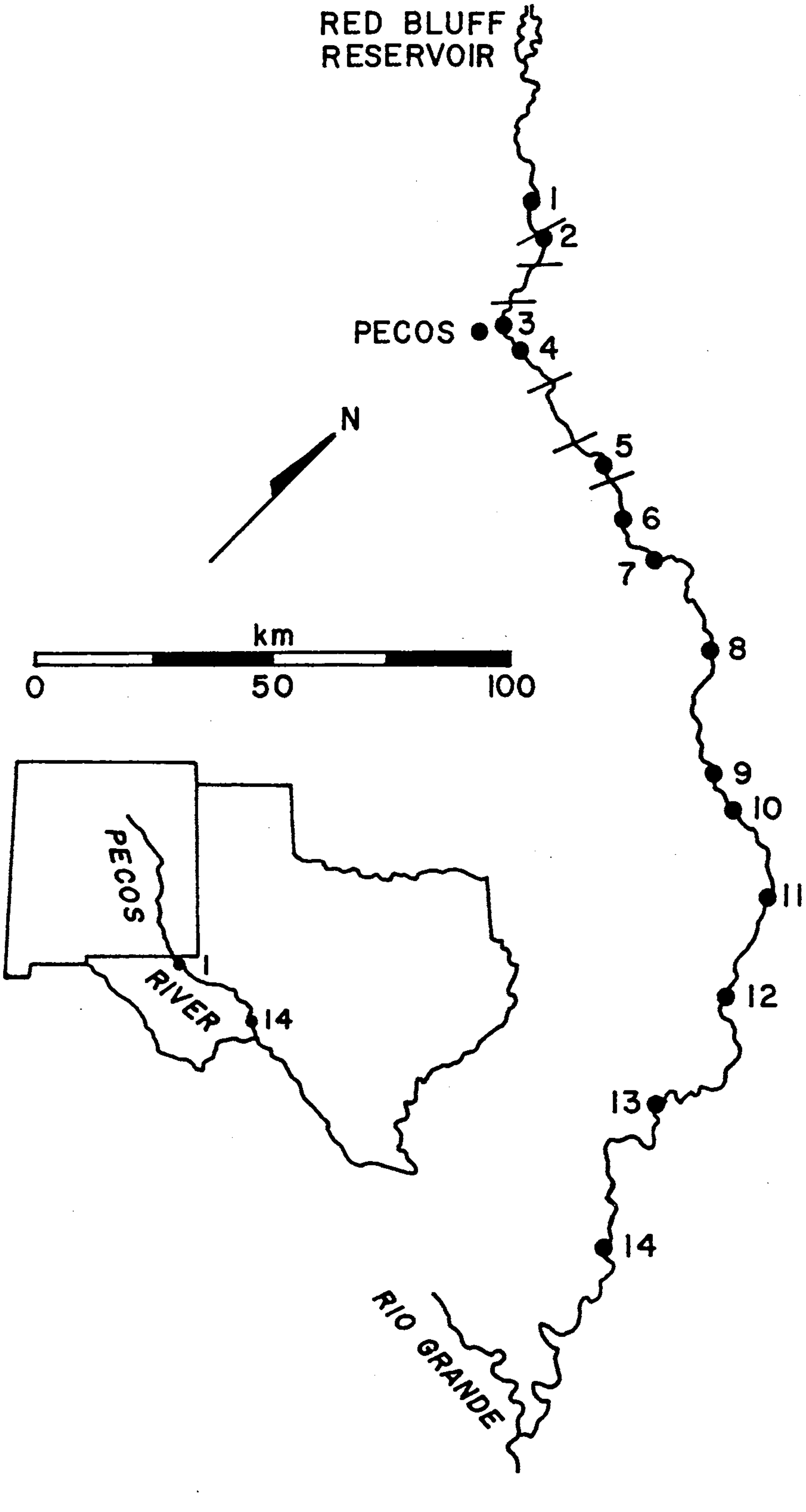
Table 5. Back-transformed means and coefficients of variation (CV) of size-adjusted variables in male _C_. _pecosensis_, _C_. _variegatus_, and intergrade pupfish populations from the Pecos River, Texas.

Sample	N	m1		m2		m3		m4		m5		m6	
		$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV
_C_. _pecosensis_	50	3.19	1.55	0.49	4.26	1.37	3.28	0.82	3.48	1.83	3.15	2.34	2.80
1	48	3.18	2.41	0.51	4.75	1.32	6.76	0.77	6.99	1.79	3.52	2.37	3.79
2	52	3.11	2.47	0.53	6.79	1.27	7.90	0.86	5.31	1.76	3.28	2.42	3.65
3	23	3.13	2.03	0.51	6.75	1.25	6.18	0.83	6.71	1.81	3.14	2.38	3.12
4	41	3.19	2.22	0.50	5.62	1.26	6.01	0.85	6.54	1.83	3.51	2.45	3.78
5	42	3.16	2.67	0.53	7.79	1.28	6.65	0.81	6.65	1.79	4.68	2.41	3.40
6	39	3.25	2.93	0.50	5.50	1.25	8.73	0.85	5.25	1.85	5.00	2.48	3.96
7	38	3.21	2.67	0.51	5.19	1.25	6.67	0.84	6.48	1.85	4.77	2.46	3.78
8	53	3.25	2.86	0.50	6.78	1.28	5.85	0.86	6.91	1.86	3.82	2.50	3.60
9	42	3.20	2.78	0.51	7.38	1.30	5.84	0.82	7.24	1.83	3.66	2.47	4.02
10	25	3.22	2.65	0.49	5.37	1.28	7.05	0.81	6.57	1.82	2.86	2.49	3.94
11	36	3.21	2.95	0.50	5.63	1.27	6.38	0.83	5.23	1.85	2.90	2.47	3.85
12	29	3.28	3.04	0.49	7.16	1.28	5.41	0.79	7.41	1.86	3.70	2.48	4.39
13	16	3.23	1.58	0.49	4.83	1.32	5.99	0.81	6.59	1.82	4.36	2.44	2.62
14	29	3.15	2.29	0.51	3.73	1.34	5.11	0.81	5.67	1.80	3.65	2.42	3.50
_C_. _variegatus_	50	3.17	1.61	0.48	3.94	1.23	4.15	0.86	3.45	1.78	3.80	2.36	2.51

Table 5. Extended.

Sample	m7		m8		m9		m10		m11		m12	
	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV
C. pecosensis	0.67	3.41	1.16	3.10	1.00	5.29	0.31	3.15	1.17	2.36	0.95	2.43
1	0.66	4.33	1.19	5.67	1.01	6.02	0.32	3.54	1.18	3.50	0.96	3.86
2	0.68	3.46	1.15	5.32	0.93	7.46	0.32	3.49	1.17	3.15	0.93	3.51
3	0.69	2.98	1.18	5.44	0.94	6.73	0.32	3.42	1.19	3.17	0.94	3.85
4	0.68	4.42	1.19	5.70	0.93	9.09	0.31	4.60	1.20	2.87	0.92	4.38
5	0.68	4.03	1.16	6.25	0.95	9.11	0.32	4.44	1.18	2.98	0.92	5.38
6	0.66	3.40	1.17	5.73	0.97	8.42	0.31	4.09	1.18	2.67	0.93	4.63
7	0.67	4.62	1.17	7.05	0.95	8.72	0.31	4.65	1.18	2.96	0.93	3.69
8	0.66	5.81	1.15	6.16	0.98	9.86	0.31	4.11	1.16	3.52	0.94	4.90
9	0.66	4.14	1.16	5.15	0.97	6.85	0.31	4.55	1.18	3.16	0.95	4.15
10	0.67	4.31	1.16	6.42	0.98	7.03	0.31	4.58	1.18	2.69	0.95	3.85
11	0.67	4.55	1.16	5.57	0.97	7.88	0.32	4.12	1.18	2.98	0.94	4.05
12	0.66	4.41	1.21	5.59	1.00	8.72	0.30	5.02	1.20	3.52	0.96	4.76
13	0.64	3.66	1.19	5.82	0.99	7.29	0.31	2.52	1.20	3.47	0.96	4.44
14	0.67	3.72	1.12	4.85	0.99	6.51	0.32	4.23	1.16	3.26	0.95	4.44
C. variegatus	0.69	3.28	1.19	3.08	0.93	3.97	0.33	3.45	1.20	2.05	0.95	2.26

Figure 3. Map of the Pecos River from Red Bluff Reservoir, Texas, to the confluence of the Pecos River and the Rio Grande. Solid circles indicate sampling sites; slashes (/) between sites 1 and 6 show the locations of irrigation-diversion dams. Locations of sites 1 and 14 are shown in the inset.


RED BLUFF RESERVOIR
1
2
PECOS
3
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RIO GRANDE
N
km
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PECOS
RIVER
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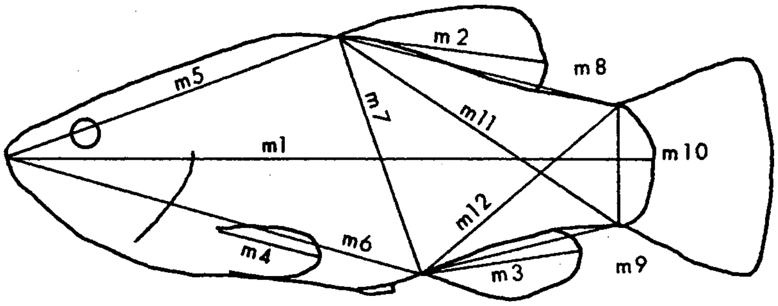
14

Figure 4. Morphometric measurements (above) and the scheme used to score belly scalation (below). Scores 5 and 6 for belly scalation differ in the greater degree of imbrication of the scales in 6.


m 2
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m5
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m11
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m12
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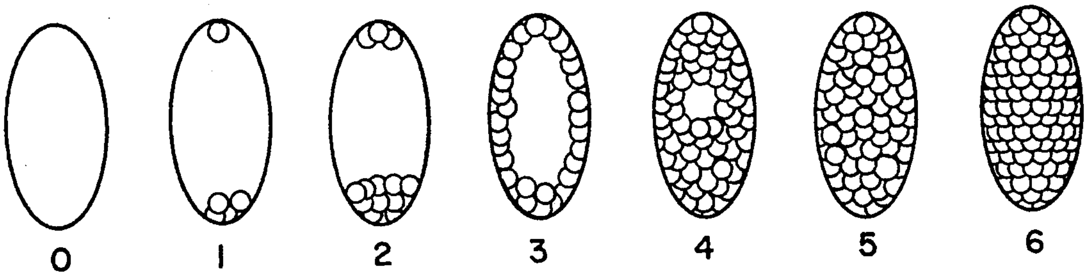
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4
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6

Figure 5. Frequency distributions of morphometric index scores for _C_. _pecosensis_, _C_. _variegatus_ and intergrade samples from the Pecos River, Texas. Station numbers are as in Fig. 3.

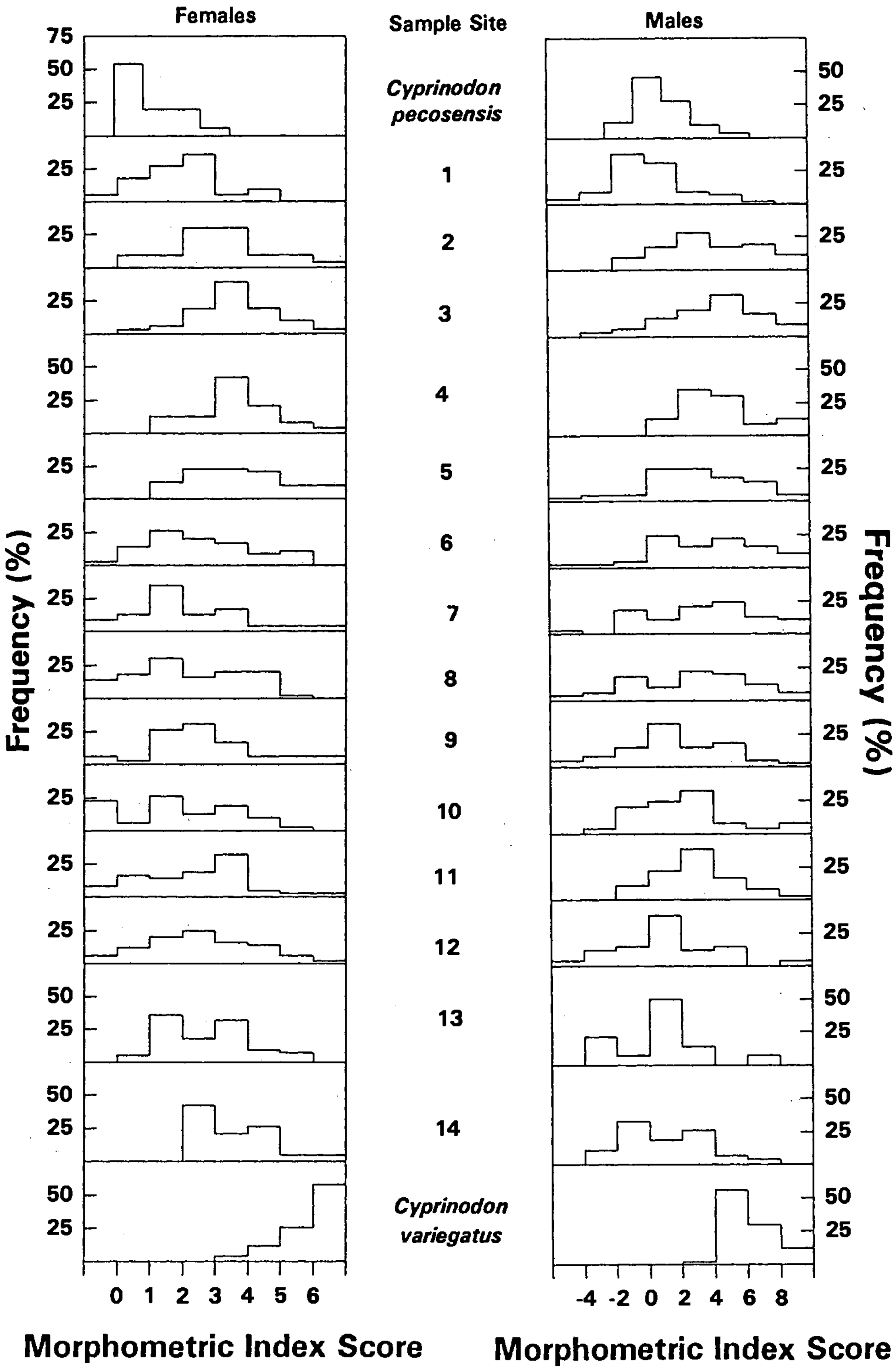
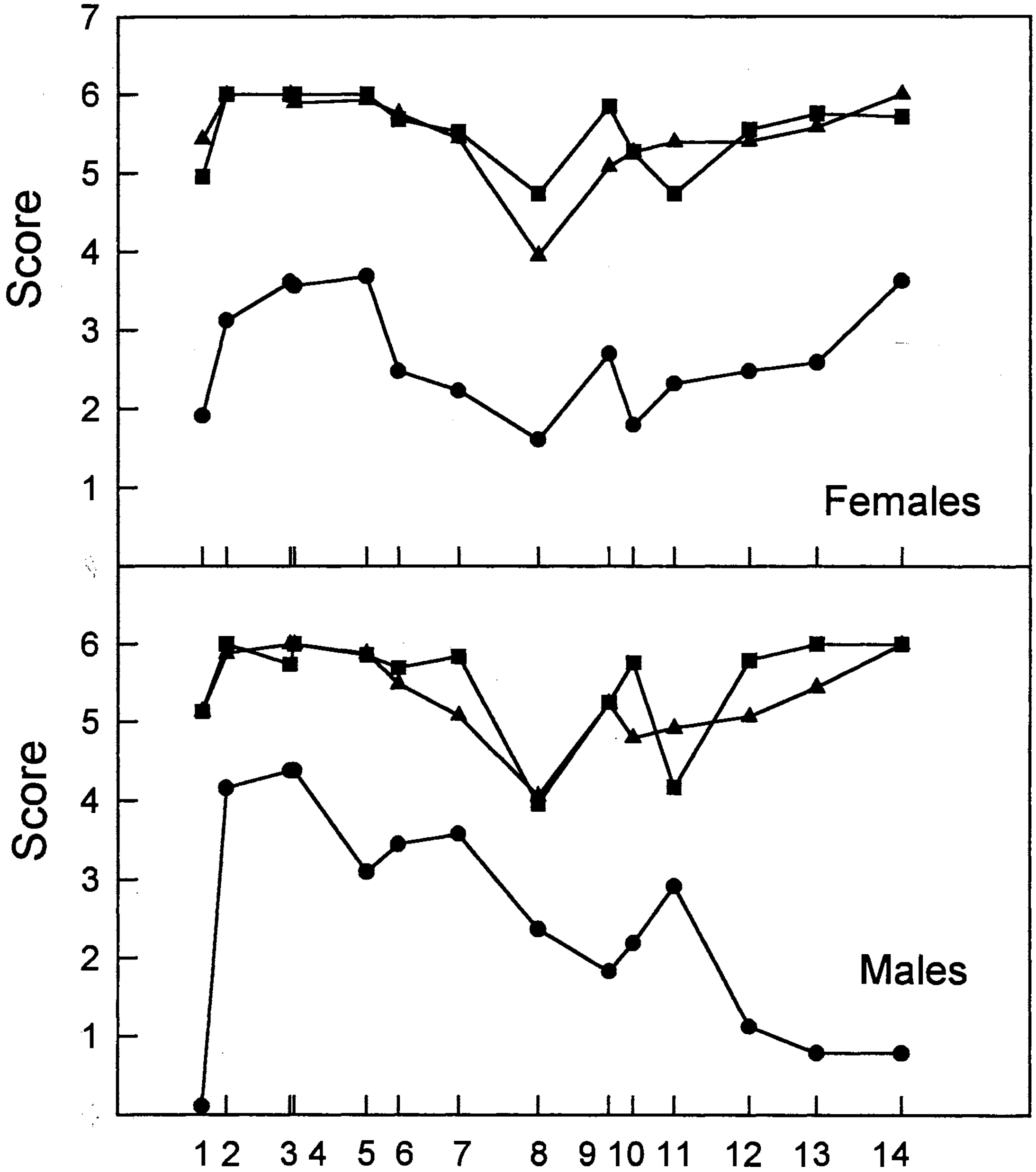
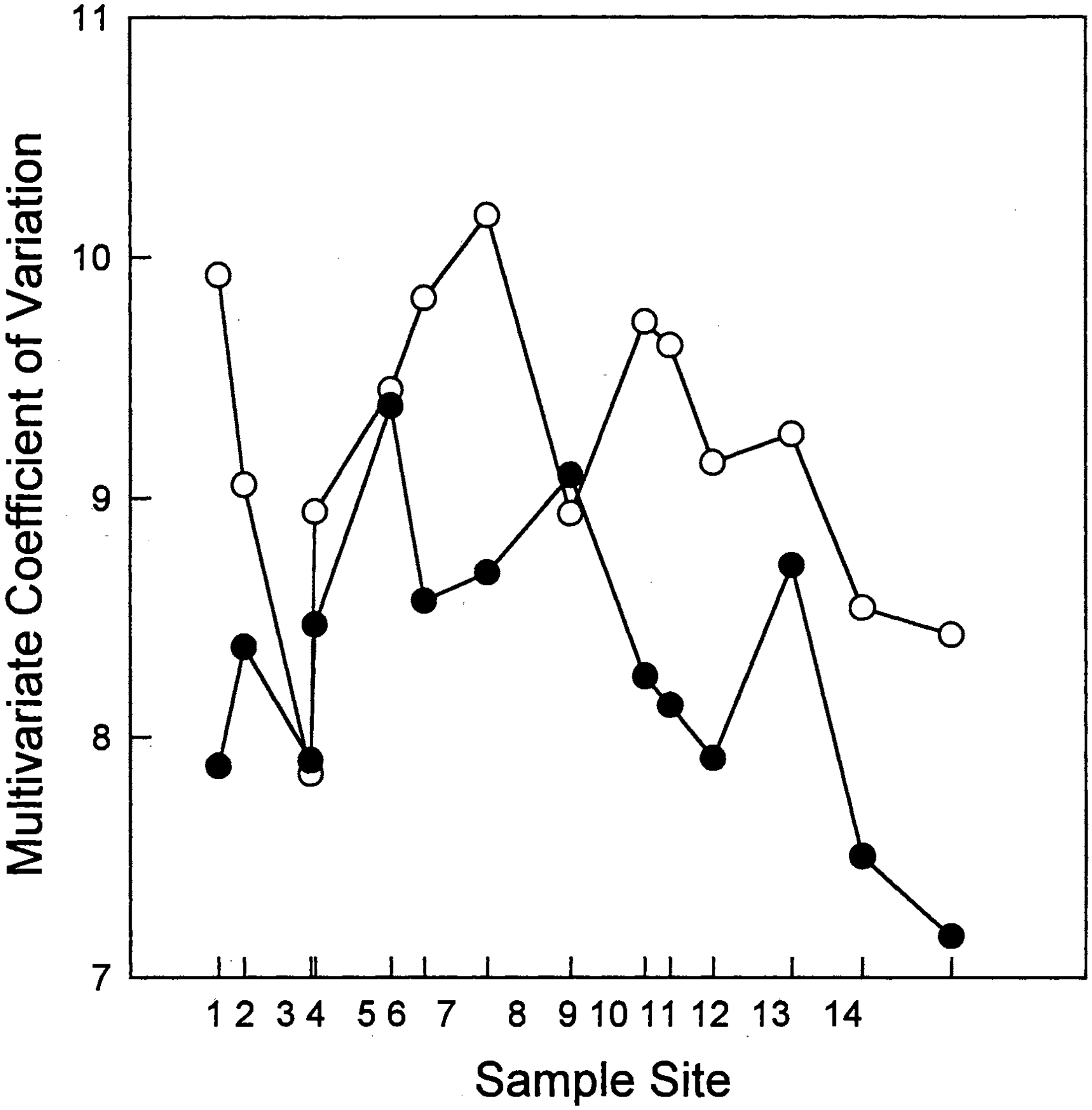

Females
Sample Site
Males
Frequency (%)
Frequency (%)
75
50
25
Cyprinodon pecosensis
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Cyprinodon variegatus
0 1 2 3 4 5 6
-4 -2 0 2 4 6 8
Morphometric Index Score
Morphometric Index Score

Figure 6. Population means of morphometric index scores, belly scalation and color pattern in intergrade pupfish from the Pecos River, Texas. Key to symbols: morphometric index (●), color pattern (■), and belly scalation (▲). Station numbers are as in Fig. 3, scaled to river distance.



7
6
5
4
3
2
1
Score
Females
Score
Males
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Sample Site

Figure 7. Multivariate coefficients of variation (MCV) for intergrade pupfish from the Pecos River, Texas. MCVs for female pupfish are indicated by open circles; closed circles indicate male MCVs. Station numbers are as in Fig. 3, scaled to river distance.


11
10
9
8
7
Multivariate Coefficient of Variation
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Sample Site

CHAPTER III

GEOGRAPHIC AND TEMPORAL PATTERNS IN THE COVARIANCE OF GENETIC AND MORPHOLOGIC CHARACTERS IN INTERGRADE PUPFISH (CYPRINODONTIDAE: *CYPRINODON*) POPULATIONS

The sheepshead minnow, *Cyprinodon variegatus*, was introduced into the Pecos River of eastern New Mexico and southwestern Texas between 1980 and 1984 (Echelle and Connor, 1989). In 1984, putative hybrids between *C. variegatus* and the endemic Pecos pupfish *C. pecosensis* were collected from two widely separated sites in Texas portions of the river (Echelle et al., 1987). An allozyme survey conducted in 1985 found no evidence of hybridization or *C. variegatus* in New Mexico portions of the Pecos River; however, panmictic admixtures of *C. variegatus* and *C. pecosensis* were found throughout some 430 kilometers of the Pecos River in Texas (Echelle and Connor, 1989), about half the original range of *C. pecosensis* (Echelle and Echelle, 1978). Subsequent allozyme surveys revealed that intergrades between *C. variegatus* and *C. pecosensis* had dispersed downstream in the Pecos River beyond the historic range of Pecos pupfish and were nearly ubiquitous in waters peripheral to the river, occurring in impoundments of tributary streams, flooded gravel quarries, and irrigation canals (Wilde, 1994).

There was pronounced geographic variation in the genetic structure and morphology of pupfish populations in Texas portions of the Pecos River. Allozymes diagnostic of *C. variegatus* represented about 85% of the pupfish genome in the vicinity of Pecos, Texas, and decreased clinally to 18% in areas upstream from Pecos and to 40-45% in areas downstream from Pecos (Echelle and Connor, 1989). In samples collected in 1990 and 1991, mitochondrial DNA (mtDNA) haplotypes characteristic of *C. variegatus* represented between 70 and 90% of haplotypes in the vicinity of Pecos and declined to 40 to 50% in downstream areas (Childs, 1993), except for an anomalously high proportion (93%) at a single downstream site outside the historic range of *C. pecosensis*. Geographic variation in several morphological characters (Wilde, 1994) roughly paralleled that observed in allozymes and mtDNA. Overall, the morphology of intergrade populations was shifted toward that of *C. variegatus* in the vicinity of Pecos and progressively shifted toward that of *C. pecosensis* in areas upstream and downstream from Pecos. Allozyme, mtDNA, and morphological character sets are consistent with the hypothesis that there was an initial introduction of *C. variegatus* in the vicinity of Pecos and that this was followed by dispersal of intergrade pupfish upstream and downstream from that site.

The rapid spread of introduced alleles characteristic of _C_. _variegatus_ throughout several hundred kilometers of the Pecos River led Echelle and Connor (1989) to suggest that strong selection was occurring for some components of the introduced genome. Such selection should be manifested in a continuous increase through time in the frequency of genetic (allozyme) and morphologic elements characteristic of _C_. _variegatus_ as well as in a maintenance of within-site correlations (linkage) among these characters. Alternatively, in the absence of selection for the introduced genome, there should be no consistent pattern in temporal variation of genetic and morphologic elements, other than that dictated by neutral gene flow, and there should be a decrease in the magnitude of within-site correlations among characters. The purposes of this paper are to: 1) describe geographic and temporal variation in, and correlations among, genetic and morphologic characters in intergrade pupfish populations in the Pecos River; and 2) determine whether variation in these characters and correlations is consistent with selection for the introduced genome.

METHODS

Pupfish were collected from 11 locations in the Pecos River (Figure 8). Collections were made at sites 4 and 11 during August 1984 (= sites P7 and P8 of Echelle et al. 1987), at sites 1, 2, 4-8, 10, and 11 during March and August 1985 (= sites 5, 7, 9-11, 13-14, 17, and 19 of Echelle and Connor, 1989), at sites 1-11 during August 1986, and at sites 2, 4, 7-9, and 11 in 1988. Pupfish were placed on dry ice in the field, transported to the laboratory, and stored at -70°C. The liver and right eye of each fish were removed and homogenized separately in equal volumes of distilled water to obtain extracts of water-soluble proteins. Fish ≤20 mm in total length were decapitated and the head and body portions were treated as described for liver and eye samples. Tissue homogenates were centrifuged for 15 minutes at 4000g and stored at -70°C. Specimens were individually tagged, preserved in formalin, and deposited in the Oklahoma State University Collection of Vertebrates (OSUS).

Genetic Analyses

I used standard methods of horizontal starch-gel electrophoresis (Selander et al., 1971; Siciliano and Shaw, 1976) to examine the products of four presumptive gene loci: alcohol dehydrogenase-A (Adh-1), esterase-1 (Est-1), glucose-6-phosphate-isomerase-A (Gpi-A), and proline-dipeptidase-1 3.4.13.9 (Pdp-A). These loci exhibit complete, or nearly complete, differences between Pecos pupfish and sheepshead minnow (Echelle et al., 1987).

Tissues, buffer systems employed and genetic interpretations of zymograms followed Echelle and Connor (1989). Subsequent to my scoring of allozymes, Childs (1993) reported a cryptic Gpi-A allele of C. variegatus that was common in the intergrade populations, but not resolved on my gels. In my study, the product of this allele was scored as the Gpi-A allele characteristic of C. pecosensis. Consequently, allele frequencies for Gpi-A presented in this study overestimate the proportion of alleles characteristic of C. pecosensis in intergrade populations.

I used BIOSYS-1 (Swofford and Selander, 1981) to test genotypic frequencies for agreement with Hardy-Weinberg equilibrium expectations. Gametic phase (linkage) disequilibrium between loci was assessed with r, the correlation between alleles at different loci corrected for deviations from Hardy-Weinberg proportions (Weir, 1979; Campton, 1987). The sample statistic $N(r)^2$ is distributed as a chi-square variate with 1 degree of freedom and can be used to test the null hypothesis of no correlation between loci (Weir, 1979). I evaluated table-wide significance of tests for departure from Hardy-Weinberg expectations and r, for each year separately, with a sequential Bonferroni test (Rice, 1989). Significance of geographic and temporal variation in allele frequencies was assessed with logistic regression (Agresti, 1990).

Morphologic Analyses

I made 12 measurements on each specimen (Figure 9); eight measurements were arranged in a truss network (Bookstein et al., 1985) and the others included standard length and lengths of the dorsal, anal, and pectoral fins. Specimens occasionally lacked fins or were otherwise damaged, so that all measurements could not be made. If only one character was missing or damaged, I replaced the missing value with the mean for that character of all specimens of the same size (± 1-3 mm SL) and sex from that collection. Specimens were not used if more than one character could not be measured. Measurements were estimated for no more than seven specimens per location (both sexes combined) and, overall, for less than five percent of all individuals reported on here.

I also coded belly scalation and color pattern (depth and width of vertical bars) in the reference samples and intergrade samples. The belly is incompletely scaled in C. pecosensis, whereas in C. variegatus it is completely scaled (Echelle and Echelle, 1978). I coded this character from 0 when the belly was naked to 6 when it fully scaled (Figure 9). Color pattern on the sides of the body was scored 0 for the pattern typical of C. pecosensis (vertical bars wide, usually not reaching the ventral edge of the lateral profile) and 6 for patterns typical of C. variegatus (vertical bars narrow, extending to the ventrum). Color patterns perceived as being intermediate were assigned a value of 3.

Male and female pupfish were treated separately in all morphological analyses because of the pronounced sexual dimorphism characteristic of Cyprinodon (Miller, 1948). Morphometric data were $\log_{10}$-transformed to stabilize variances. I used the first principal component of the pooled within-group covariance matrix for reference specimens as an estimate of within-group general-size-allometry (Bookstein, 1989) and adjusted the $\log_{10}$-transformed data for both reference specimens and introgressed samples for this size factor using Burnaby's (1966) method as recommended by Rohlf and Bookstein (1987). I performed a second set of principal components analyses on the size-adjusted data for reference specimens. Variable loadings from PC1 were multiplied against size-adjusted data for both reference specimens and intergrade populations to calculate a morphometric "hybrid" index. Scores for this morphometric index were standardized so that means for reference specimens of C. pecosensis and C. variegatus were 0.0 and 6.0, respectively.

I assessed significance of temporal and geographic variation in the morphometric index, color pattern, and belly scalation with two-way analyses of variance (ANOVA). Relationships within sites among morphological variables (morphometric index, belly scalation, and color pattern) and among morphological and genetic (allozyme) variables, were assessed with Spearman's rank correlation ($\underline{r}_s$). For correlation analyses, allozymes were coded 0 (homozygous for alleles diagnostic of C. pecosensis), 1 (heterozygous for alleles of both species), and 2 (homozygous for alleles diagnostic of C. variegatus). I used a one-tailed binomial test (Siegel, 1956) to determine whether excesses of positive correlations existed, for each character pair. I evaluated table-wide significance of ANOVA results, correlations, and binomial tests for each year separately with the sequential Bonferroni test. All statistical analyses were performed using SAS (SAS Institute, 1985).

RESULTS

From 1984 to 1988, pupfish populations throughout the Pecos River, from just south of the New Mexico-Texas boundary downstream to Iraan, Texas (site 11), were segregating for alleles of C. pecosensis and C. variegatus at the four loci examined (Table 6). There was no evidence of any difference in allele frequencies between males and females; 8 of 112 individual tests for intersexual differences, across all sites and years, were significant ($0.05 \geq \underline{P} \geq 0.01$), but none was significant based on the sequential Bonferroni test ($\underline{P} > 0.05$); therefore, genetic data for both sexes were combined. Pupfish populations throughout the study area consisted primarily of individuals of mixed (hybrid) genetic background. Except in one sample, fewer than 12% of the pupfish collected from any location consisted of individuals homozygous for alleles of _C. pecosensis_ at all loci; the single exception was a sample collected from site 1 in 1985 in which 23% of the specimens had genotypes expected of _C. pecosensis_. At sites 2 to 5, 18 to 61% of the pupfish had genotypes expected of _C. variegatus_. Such genotypes represented only 0 to 7% of the sample at the remaining sites.

Despite the presence of genetic admixtures of _C. pecosensis_ and _C. variegatus_ at all sites sampled, there was little evidence of departures from Hardy-Weinberg equilibrium expectations. Of a total of 112 single-locus tests, only nine indicated significant ($\underline{P} \leq 0.05$) departures from expectations; however, none was significant ($\underline{P} > 0.05$) based on the sequential Bonferroni test. Regardless of statistical significance, there was a slight bias toward heterozygote deficiencies with 63% of tests indicating fewer heterozygotes than expected from Hardy-Weinberg ratios.

There was significant ($\underline{P} < 0.0001$) geographic and temporal heterogeneity in the genetic structure of intergrade pupfish populations (Figure 10). Although the geographic pattern of variation in Gpi-A differed somewhat from that exhibited by Adh-1, Est-1, and Pdp-A, the general pattern shown by all loci was that of a bi-directional cline centered in the vicinity of Pecos, Texas (sites 3 and 4).

The mean frequency, over all loci and years, of alleles characteristic of *C. variegatus* (introduced alleles) was 82% at sites 3 and 4. This frequency decreased in both upstream and downstream directions, reaching minima of 30% at site 1 and 42% at site 10, respectively. Differences between adjacent sites in allele frequencies at any locus generally were <10%, with greater changes usually occurring between sites separated by irrigation diversion dams (Figures 8 and 10).

Between 1984 and 1988, there was a significant ($P < 0.0001$, logistic analysis) river-wide increase at each locus in the frequency of introduced alleles; however, within sites, there was only weak evidence of temporal variation. Ten of 40 individual tests (10 sites x 4 loci; only 10 sites were included because site 3 was sampled only once) for temporal changes in allele frequencies were significant ($0.046 > P > 0.0001$); only four of these tests were significant ($P < 0.05$) based on sequential Bonferroni tests.

There was no consistent pattern among sites in temporal variation in allele frequencies (Figure 10). At sites 3 to 6, there was little temporal variation in allele frequencies, except for a significant increase in Gpi-A at site 3 ($P < 0.05$, sequential Bonferroni test). Downstream at sites 7 to 11, the frequency of introduced alleles generally decreased from 1985 to 1986, but increased in 1988. This pattern was most pronounced at sites 8 and 9 where there were significant increases in the frequency of introduced alleles at the Est-1 (both sites) and Gpi-A loci (site 9). Upstream, the frequency of introduced alleles decreased at sites 1 and 2 between 1985 and 1986, before increasing again in 1988 (site 2); however, none of these changes were significant.

Within-sample correlations among loci (Figure 11) generally were non-significant, except between the Est-1 x Gpi-A locus pair. Sixty-four percent (18 of 28) of correlations between these loci were significant ($\underline{P} < 0.05$; sequential Bonferroni test). Among the remaining five paired combinations of loci (a total of 140 correlations), there were only three additional significant correlations, two for the Adh-1 x Pdp-A and one for the Est-1 x Pdp-A locus pairs. For each of three locus pairs, Est-1 x Gpi-A (in 1985, 1986, and 1988), Est-1 x Pdp-A (in 1985 and 1986) and Gpi-A x Pdp-A (in 1985), there were significant excesses of positive correlations across all samples ($\underline{P} < 0.05$; one-tailed binomial test) indicating an excess of coupling gametes for each of these locus pairs and possible linkage between the Est-1, Gpi-A, and Pdp-A loci.

Correlations among loci were extremely variable throughout the study period and there was no evidence of any significant ($\underline{P} < 0.05$) directional change in the magnitude of correlations among any pair of loci. However, an overall approach to linkage equilibrium throughout the Pecos River may be indicated by the binomial tests (see above), which indicated significant excesses of positive correlations at three pairs of loci in 1985, at two pairs in 1986, and at only one pair in 1988.

There was significant geographic variation ($\underline{P} < 0.0001$) in morphometric index scores, color pattern, and belly scalation in both male and female intergrade pupfish from the Pecos River (Figure 12). In agreement with allozymes, the general pattern of geographic variation in morphological characters was a bi-directional cline centered in the vicinity of Pecos, Texas (sites 3-4). Overall, morphology of intergrade pupfish populations, as indicated by scores for the morphometric index, most resembled that of C. variegatus at sites 3 and 4 where mean index-scores, across all years, were 3.3 to 4.4 for males and 3.3 to 3.6 for females (on a scale of 0 to 6). The scores decreased upstream to site 1 (males = 0.1, females = 1.9) and downstream to site 10 (males = 1.1, females = 1.6). Similar geographic variation was exhibited by color pattern and belly scalation. Throughout the study area, scores for color pattern and belly scalation were shifted well away from states typical of C. pecosensis (0 to 2 for belly scalation, 0 for color pattern) toward states characteristic of C. variegatus (6 for both characters). Means for intergrade pupfish, both sexes combined and across all years, were 6.0 (color pattern) and 5.9 to 6.0 (belly scalation) at sites 3 and 4; means for both characters decreased upstream to site 1 (color pattern 5.1, belly scalation 5.3) and downstream to site 8 (color pattern 4.7, belly scalation 4.6).

Between 1985 and 1988, there was a significant ($\underline{P} < 0.0001$) river-wide increase in scores for the morphometric index in female intergrade pupfish; however, there was no comparable change in scores for males ($\underline{P} = 0.377$). Female scores generally increased (morphometry shifted toward C. *variegatus*) from year to year at each station (Figure 12). There was relatively little temporal variation in morphology of female intergrades at sites 2 to 5; however, variation was more extensive in downstream areas, particularly at sites 8, 9, and 11 where there was significant ($\underline{P} < 0.05$, sequential Bonferroni test) temporal variation in female scores. In male intergrade pupfish, there was a general increase in scores from 1985 to 1986, followed by a decrease in 1988. Although there was no directional change in male morphology, there was significant ($\underline{P} < 0.05$, sequential Bonferroni test) temporal variation in morphometric index scores at seven sites (sites 2, 5-8, and 10-11).

There were significant ($\underline{P} < 0.05$) increases in scores for color pattern and belly scalation (=shifts toward character states typical of C. *variegatus*) in both female and male intergrade pupfish between 1985 and 1988 (Figure 12). In both sexes, there was little temporal variation in either character in upstream areas (sites 2-5); however, in downstream areas, especially at sites 8-11, scores for both color pattern and belly scalation showed a general increase through time. Within locations, changes in both color pattern and belly scalation for female intergrades were significant ($\underline{P} < 0.05$) at sites 8 and 9; in males, significant changes occurred in color pattern at sites 8, 10, and 11 and in belly scalation at sites 8 and 11.

Within-site correlations among color pattern, belly scalation, and the morphometric index indicate a weak tendency toward positive (within-species) associations among traits. First, all significant correlations (based on sequential Bonferroni tests) were positive in sign; these included six of 54 correlations in females and six of 59 in males (Table 7). Second, although many of the remaining correlations were non-significant, there was an overall excess of positive signs. Seventy-seven (68%) of the 113 correlations were positive in sign, giving a ratio of approximately 2:1 in favor of positive signs. Statistically significant ($\underline{P} < 0.05$, binomial test) excesses of positive signs occurred across samples for the comparisons of morphometric index and color pattern (females, 1985; males, 1986), morphometric index and belly scalation (females, 1986), and color pattern and belly scalation (males, 1985). The distribution of positive signs exhibited no easily discernable pattern with respect to sex, year, or combination of the three variables.

A weak tendency toward positive associations among within-species traits also occurred between the three morphologic variables and allozyme characters (Tables 8 and 9). Fewer than 4% of the individual correlations were statistically significant (9 of 256 in females, 6 of 268 in males). However, all statistically significant correlations were positive in sign and there was generally an excess of positive correlations. There were significant excesses of positive correlations ($\underline{P} < 0.05$, one-tailed binomial test), across samples, for morphometric index and Est-a (females, 1985), color pattern and Gpi-A (females, 1986; males, 1986), and color pattern and Adh-a (females, 1985).

DISCUSSION

Several lines of evidence indicate that hybridization between C. pecosensis and C. variegatus has led to formation of locally panmictic assemblages throughout the Pecos River in Texas. First, specimens from the Pecos River possessing genotypes of either parental species generally occur in very low proportions (Echelle and Connor, 1987; Wilde, 1994) such as might occur randomly as a result of recombination (Barton and Hewitt, 1985). Second, there is a lack of significant deviations from Hardy-Weinberg expectations for genotypic frequencies. Third, frequency histograms of individual scores for allozyme (Echelle and Connor, 1987) and morphometric (Wilde, 1994) hybrid indices are unimodal in almost all samples.

Introduction of C. variegatus into the Pecos River represents at least the third such introduction within the Pecos River drainage system. C. variegatus was introduced into Lake Balmorhea in the 1960s (Stevenson and Buchanan, 1972) and into Leon Springs in the 1970s (Kennedy, 1977; Hubbs, 1980). The Lake Balmorhea population of C. variegatus and intergrade populations in the Pecos River both exhibit unusually high frequencies of an introduced Gpi-A allele that is uncommon in natural populations of C. variegatus; thus the introduced population in Lake Balmorhea probably served as the source for the introduction of C. variegatus into the Pecos River (Childs, 1993).

The introduction of C. variegatus into the Pecos River apparently occurred between 1980 and 1984. Collections of pupfish made in 1980 at three locations between my sites 7 and 12 showed no evidence of morphological traits (belly scalation and color pattern) characteristic of C. variegatus (Echelle and Connor, 1989). However, individuals of hybrid origin were collected in abundance at sites 3 and 11 in 1984 (Echelle et al., 1987). The presence, in 1984, of introgressed pupfish at sites which are separated by approximately 255 km, the absence of departures from Hardy-Weinberg expectations, and the relatively low levels of linkage disequilibrium (only two of 12 interlocus allozyme correlations were significant in 1984), and non-significant associations among morphologic characters suggest that the initial introduction probably occurred early, rather than late in the period between 1980 and 1984.

The rapidity and geographic extent of hybridization between C. variegatus and C. pecosensis led Echelle and Connor (1989) to suggest there might be strong selection for some elements of the introduced genome. Starting with the premise that diagnostic loci in a hybrid swarm would have equal initial frequencies (Forbes and Allendorf, 1991), Childs (1993) suggested that selection should result in within-site heterogeneity in the relative frequencies of introduced mtDNA and allozyme markers. Alternatively, if local frequencies of mtDNA and allozyme markers have remained approximately equal, neutral gene flow was a more parsimonious explanation for genetic changes. Childs (1993) found equivalent frequencies of allozyme and mtDNA markers and concluded that genetic replacement was a more parsimonious explanation for genetic changes in the Pecos River.

The allozyme and morphological data presented herein roughly conform with Childs' (1993) results. The geographical pattern of morphological variation in intergrades generally parallels that of allozymes and mtDNA, and there is no compelling evidence that the rate of change in morphology has differed from that in allozymes and mtDNA.

Although there is some indication in downstream locations of greater amounts of change in belly scalation, and possibly, color pattern, such comparisons are complicated by the qualitative character-states assigned to these characters and their unknown mechanisms of genetic control. Thus, the morphological results do not refute the hypothesis from nuclear (allozyme) and cytoplasmic (mtDNA) genetic elements (Childs, 1993) that the introduction of C. variegatus into the Pecos River had roughly equivalent effects throughout the entire genome of C. pecosensis.

Replacement, without selection, of portions of the genome of C. pecosensis by the introduced genome of C. variegatus would have occurred at a time when C. pecosensis was at extremely low population densities. Fish kills have been reported in the study area since the 1950's (Wilde, 1994), and massive fish kills caused by toxins from the chysophyte alga, Prymnesium parvum occurred in the fall months of 1985, 1986, and 1988 (James and De La Cruz, 1990; Rhodes and Hubbs, 1992). It is possible that C. variegatus was introduced at a locality where C. pecosensis had been extirpated, or effectively so, by a fish kill. Although no fish kills are known to have occurred during the period of the introduction (between 1980 and 1984), the study area is sufficiently remote that kills might go unreported.

The most likely site of the introduction was in the vicinity of Pecos, Texas, where the frequencies of introduced genetic elements are greater than 80% (Echelle and Connor, 1989). If, as suggested by Childs (1993), the present genetic structure reflects the relative abundances of the two species at the time of reproductive fusion, then the introduced species would have been four times more abundant than the native population in the vicinity of Pecos, either at the time of the introduction or at some subsequent time when the two species fused reproductively. Although replacement without selection might explain the present genetic structure, it is possible that selection played a role prior to, or during, reproductive fusion of the two genomes. For example, the introduced population of C. variegatus might have been more resistant to the agent responsible for the hypothesized fish kill, allowing it to expand in abundance at a time when the native species was being decimated or impaired in reproductive performance.

Because of sample-size limitations, significant linkage disequilibrium for unlinked loci is unlikely to be detected in a hybrid swarm that has existed for several generations (Brown, 1975). Nevertheless, weak associations among allozyme and morphologic characters persist in the Pecos River, primarily in the form of excesses of positive correlations. Selection can induce or maintain such correlations among characters (Lewontin, 1974; Lande and Arnold, 1983). However, selection need not be invoked to explain associations among characters observed in Pecos

River intergrade pupfish. First, these associations may be a residual effect of the initially high levels of linkage disequilibrium that would have existed early in the history of the intergrade populations. Even in the absence of selection or close linkage between characters, linkage equilibrium is only approached asymptotically and many generations of random mating may be required before characters become totally disassociated (Hedrick, 1983). Second, correlations among characters in intergrade pupfish can be maintained by gene flow. Erosion of clines in all characters in downstream areas of the Pecos River suggests gene flow from the vicinity of Pecos, where allozyme and morphologic characters typical of _C_. _variegatus_ predominate, into downstream sites where there are higher frequencies of traits characteristic of _C_. _pecosensis_. Admixture of two such stocks could generate linkage disequilibrium in local populations (Forbes and Allendorf, 1991). Support for this alternative is provided by the slightly greater proportion ($\underline{P}$ = 0.0775, chi-square) of heterozygote deficiencies that occurred in downstream areas (sites 7 to 11, 71%) compared with upstream area (sites 1 to 6, 55%). Regardless of whether they are residual phenomena or a result of gene flow, the observed associations among characters should decline with time. Continued gene flow between sites and the apparent lack of assortative mating among intergrade pupfish should cause reduced geographic variation and disassociation of all character states for the allozyme and morphologic characters studied herein (Endler, 1977; Hedrick, 1983).

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Table 6. Genotypic arrays for four loci in pupfish samples from the Pecos River, Texas, 1984 and 1988. (Genotypic data for 1985 and 1988 are presented in Echelle and Connor [1989] and Wilde [1994], respectively.) Locality numbers are as in Figure 8. Alleles are given letters in alphabetic order of decreasing anodal mobility. Allele assignments follow Echelle and Connor (1989) and Echelle et al. (1987): P = loci diagnostic of Pecos pupfish; S = loci diagnostic of sheepshead minnow.

		Locus			
Year	Site	ADH-1	EST-1	GPI-A	Pdp-1
1984	3	aa: 2	ab: 8	cc:15	bb:50
		ac:12	bb:57	cd:34	bc:11
		cc:33		dd:16	cc: 4
1984	11	aa:23	aa:19	cc: 4	bb: 8
		ac:27	ab:33	cd:32	bc:25
		cc: 7	bb:11	dd:28	cc:26
1988	2	aa: 3	aa: 2	cd:28	bb:71
		ac:28	ab:22	dd:56	bc:22
		cc:71	bb:78	de:18	cc: 7
1988	3	aa: 4	ab:12	cc:22	bb:48
		ac:14	bb:53	cd:31	bc:14
		cc:47		dd:12	cc: 3
1988	7	aa:11	aa: 3	cc:10	bb: 8
		ac:12	ab:17	cd:20	bc:14
		cc:17	bb:20	dd:10	cc:17
				de: 1	
1988	8	aa:27	aa: 8	cc:21	bb:25
		ac:42	ab:49	cd:48	bc:41
		cc:27	bb:42	dd:30	cc:33

Table 6. (Continued)

		Locus			
Year	Site	ADH-1	EST-1	GPI-A	Pdp-1
1988	9	aa:10 ac:29 cc:12	aa: 8 ab:23 bb:21	cc:13 cd:18 dd:20	bb:18 bc:21 cc:12
1988	11	aa:29 ac:42 cc:31	aa:18 ab:48 bb:36	cc:17 cd:48 dd:36	bb:28 bc:41 cc:29
Allele assignments:		P = a S = c	P = a S = b	P = d-e S = c	P = c S = b

Table 7. Correlations (r_s) among morphologic characters in female and male intergrade pupfish populations from the Pecos River, Texas. Sample sizes are minimum numbers for each site-sex combination. Missing values (.) indicate samples in which color pattern, belly scalation, or both were fixed within a given site and, consequently, r_s could not be calculated.

Sample	Sample Size		Morphometric Index vrs Color Pattern		Morphometric Index vrs Belly Scalation		Color Pattern vrs Belly Scalation	
	Female	Male	Female	Male	Female	Male	Female	Male
1984								
4	36	23	.	.	.	.	.	.
11	22	27	-0.048	0.027	-0.073	0.074	0.045	-0.070
1985								
2	36	79	0.285	0.194	.	0.000	.	0.703**
4	50	50	.	.	-0.173	-0.035	.	.
5	56	28	0.017	-0.179	0.167	.	-0.042	.
6	24	33	0.215	-0.107	0.000	-0.121	-0.153	0.776**
7	29	37	0.501**	-0.037	0.518**	0.252	0.293	0.202
8	40	20	0.195	0.010	0.421**	-0.048	0.206	0.409
10	32	35	0.292	0.018	-0.113	0.205	0.221	0.244
11	49	47	0.052	0.236	0.351*	0.183	0.326*	0.380**
1986								
1	22	44	0.279	0.104	0.610**	0.031	0.012	-0.152
2	23	47	.	.	.	-0.103	.	.
3	31	35	.	.	0.334	.	.	.
4	24	23	.	0.225	.	.	.	.
5	39	40	.	0.049	0.259	-0.184	.	-0.035
6	35	37	0.280	0.022	0.232	-0.177	-0.071	-0.108
7	23	38	0.023	-0.142	0.138	-0.105	-0.147	0.255
8	50	49	0.489**	0.083	0.169	-0.021	0.088	0.336**
9	34	48	-0.170	-0.273	0.049	0.426**	0.266	-0.230
10	31	25	0.244	0.226	-0.025	0.169	0.000	0.109
11	37	36	-0.142	0.061	0.000	-0.013	-0.059	0.275
1988								
2	51	26	.	.	.	0.136	.	.
4	22	14	.	.	.	.	.	.
8	29	27	0.049	0.172	0.295**	-0.005	0.069	0.324**
9	34	18	0.170	-0.393	.	0.259	-0.160	-0.140
11	20	12	0.154	-0.073	0.209	0.151	0.191	0.267

Table 8. Correlations (r_s) among morphologic characters and allozymes in female intergrade pupfish. Missing correlations indicate samples in which color pattern, belly scalation, or both were fixed within a given sample. Sample sizes for correlations are presented in Table 7.

Sample	Morphometric Index with				Color Pattern with				Belly Scalation with			
	ADH	EST	GPI	PDP	ADH	EST	GPI	PDP	ADH	EST	GPI	PDP
1984												
4	0.056	-0.131	0.219	0.025	.	.	.	.	.	.	.	.
11	0.217	0.197	0.309	-0.310	-0.138	-0.192	-0.227	-0.184	0.367	-0.189	-0.084	0.326
1985												
2	0.335*	0.043	-0.051	0.302	0.286	0.318	0.229	0.279	.	.	.	.
4	0.077	-0.248	0.074	0.057	.	.	.	.	-0.058	-0.036	-0.177	-0.080
5	-0.145	0.234	0.364*	-0.153	0.110	-0.118	-0.160	0.011	0.030	0.125	0.075	-0.115
6	0.249	0.263	0.111	-0.152	0.032	-0.098	0.121	-0.240	0.165	-0.031	0.067	0.237
7	0.317	0.420*	-0.096	0.433*	0.219	0.042	-0.164	0.015	0.616**	0.067	-0.045	0.236
8	0.423*	0.510**	0.496**	0.033	0.462**	0.537**	0.413*	0.276	0.332*	0.488**	0.276	0.064
10	0.152	0.335	-0.068	-0.068	0.235	0.217	0.159	0.067	0.354*	0.543**	0.379*	0.464*
11	-0.031	0.241	0.102	0.292*	0.135	0.027	0.014	0.115	0.082	0.161	0.040	0.144
1986												
1	0.178	0.386	0.536*	0.380	0.456*	-0.106	0.301	-0.140	0.173	0.202	0.343	0.259
2	0.162	0.388	0.500*	0.352	.	.	.	.	.	.	.	.
3	-0.080	-0.073	-0.180	-0.117	.	.	.	.	-0.071	-0.062	-0.072	-0.135
4	-0.482*	-0.524*	-0.128	-0.243	.	.	.	.	.	.	.	.
5	0.061	-0.159	-0.107	-0.090	.	.	.	.	0.155	-0.062	0.033	-0.106
6	-0.219	-0.036	0.138	0.001	-0.202	0.065	0.390*	0.348*	0.140	0.277	0.485**	-0.055
7	0.448*	0.191	-0.099	0.416*	0.022	-0.011	0.377	0.109	0.294	0.237	0.193	0.180
8	-0.216	0.172	0.170	-0.125	-0.097	0.156	0.055	0.286*	0.183	0.230	0.223	-0.182
9	0.122	-0.008	0.015	0.189	-0.070	0.167	0.125	-0.234	0.180	0.469*	0.350*	0.304
10	0.287	-0.282	-0.150	0.093	0.227	0.243	0.249	0.116	-0.055	-0.152	-0.260	0.078
11	0.187	0.112	-0.014	0.122	-0.052	0.077	0.115	0.291	0.114	0.310	0.103	0.195
1988												
2	-0.034	-0.206	-0.168	0.076	.	.	.	.	.	.	.	.
4	-0.360	-0.322	-0.164	-0.158	.	.	.	.	.	.	.	.
8	0.238	-0.023	0.160	-0.144	0.025	0.053	0.040	0.072	0.236	-0.140	-0.068	-0.008
9	-0.287	-0.157	0.180	-0.039	0.218	0.111	-0.116	0.139	0.040	-0.365*	-0.013	-0.171
11	0.084	0.202	-0.205	0.199	-0.059	-0.147	-0.109	0.041	0.335**	0.035	0.152	-0.020

*$\underline{P}$ < 0.05 for individual test **$\underline{P}$ < 0.05 based on sequential Bonferroni test.

Table 9. Correlations (r_s) among morphologic characters and allozymes in male intergrade pupfish populations. Missing correlations indicate samples in which color pattern, belly scalation, or both were fixed within a given sample. Sample sizes for correlations are presented in Table 7.

Sample	Morphometric Index with				Color Pattern with				Belly Scalation with			
	ADH	EST	GPI	PDP	ADH	EST	GPI	PDP	ADH	EST	GPI	PDP
1984												
4	0.254	0.000	0.058	-0.158	.	.	.	.	.	.	.	.
11	-0.008	0.361	0.181	0.192	0.015	0.269	0.223	-0.087	-0.049	-0.199	-0.019	0.089
1985												
2	-0.135	0.317**	0.148	0.105	0.217	0.190	0.163	0.125	0.245*	0.090	0.118	0.029
4	-0.081	-0.038	-0.037	-0.091	.	.	.	.	-0.096	-0.052	-0.066	-0.095
5	0.083	0.084	-0.105	-0.157	0.184	-0.130	0.252	-0.149	.	.	.	.
6	-0.206	0.076	0.321	-0.125	-0.276	0.286	0.149	0.046	-0.164	0.294	0.113	0.057
7	0.318	0.078	0.264	0.280	0.161	0.219	0.057	0.306	0.306	0.444**	0.335*	0.196
8	0.091	0.072	-0.077	-0.367	-0.144	0.301	0.156	0.274	0.207	0.320	0.446*	0.410
10	-0.089	0.139	0.143	0.353*	-0.034	0.079	0.106	-0.085	0.004	0.285	0.085	0.263
11	0.195	-0.014	0.162	0.243	0.259	0.227	0.208	0.350*	0.107	0.134	-0.025	0.141
1986												
1	-0.081	0.273	0.162	-0.029	-0.050	0.034	-0.196	-0.044	0.124	0.142	0.121	-0.053
2	-0.092	0.053	-0.132	0.200	.	.	.	.	0.084	0.278*	0.225	0.059
3	-0.125	0.255	0.178	-0.277	.	.	.	.	.	.	.	.
4	-0.018	-0.064	0.013	0.502*	-0.126	-0.045	0.243	0.577**	.	.	.	.
5	-0.194	-0.200	-0.180	-0.144	-0.140	0.253	0.042	0.281	0.006	0.120	0.204	0.033
6	-0.141	-0.176	-0.101	0.069	-0.232	-0.023	0.012	0.148	0.151	0.283	-0.077	0.094
7	-0.275	0.085	0.140	0.292	0.207	0.000	-0.084	-0.065	0.411*	0.407*	-0.241	0.067
8	-0.093	-0.012	0.031	-0.138	-0.223	0.219	0.190	-0.069	0.194	0.432**	0.153	0.208
9	0.107	-0.280	-0.360*	-0.050	-0.155	0.061	0.203	0.232	0.346*	-0.044	-0.050	-0.040
10	0.074	0.113	0.105	0.013	0.034	-0.124	0.193	0.221	0.021	0.204	-0.192	-0.093
11	0.270	0.263	0.356	-0.107	-0.143	-0.082	-0.099	0.151	0.157	0.515**	0.180	0.191
1988												
2	0.110	0.396	-0.024	0.542*	.	.	.	.	-0.083	0.077	0.233	0.060
4	0.307	-0.480	-0.067	0.000	.	.	.	.	.	.	.	.
8	0.290	0.426**	0.330*	0.294	0.240	0.125	0.067	0.095	0.326*	0.163	0.014	-0.002
9	-0.122	-0.057	0.359	-0.115	0.342	0.059	-0.141	-0.239	0.445*	-0.396	0.201	0.191
11	0.230	0.095	0.156	0.049	-0.185	0.060	0.177	0.214	-0.242	0.041	0.054	0.021

*$P < 0.05$ for individual test **$P < 0.05$ based on sequential Bonferroni test.

Figure 8. Map of the Pecos River from Red Bluff Reservoir, New Mexico-Texas, to the confluence of the Pecos River and the Rio Grande. Solid circles indicate sampling sites; slashes (/) between sites 1 and 6 show the locations of irrigation-diversion dams. Locations of sites 1 and 11 are shown in the inset.

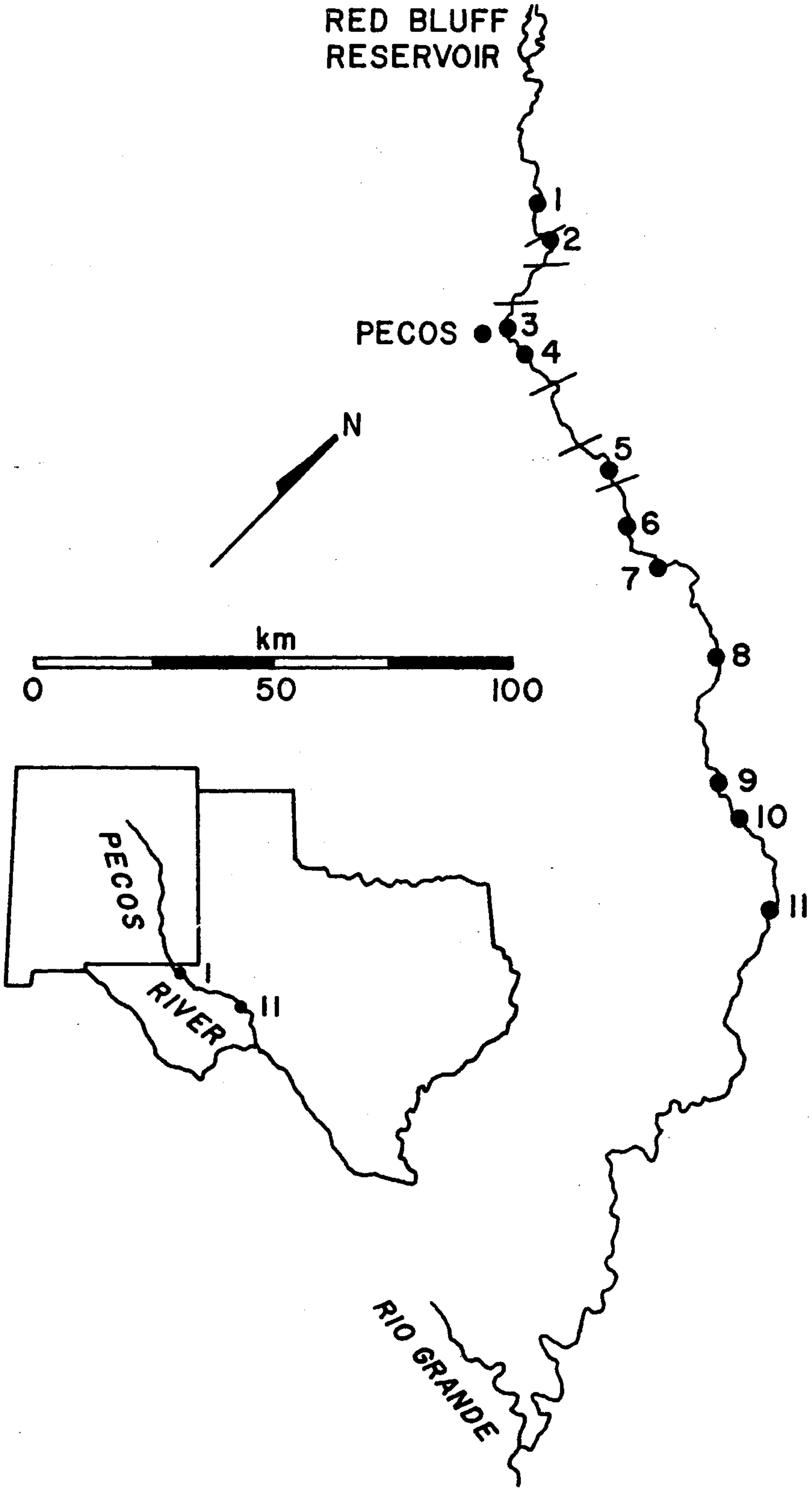
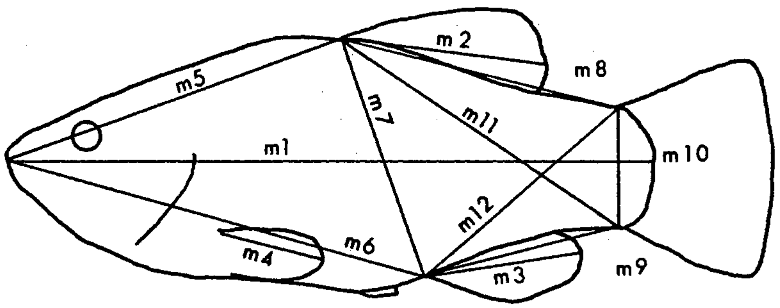

RED BLUFF RESERVOIR
1
2
PECOS
3
4
N
5
6
7
km
0
50
100
8
9
10
11
PECOS
1
RIVER
11
RIO GRANDE

Figure 9. Morphometric measurements (above) and the scheme used to score belly scalation (below). Scores 5 and 6 for belly scalation differ in the greater degree of imbrication of the scales in 6.


m2
m8
m5
m7
m11
m1
m10
m12
m6
m4
m3
m9

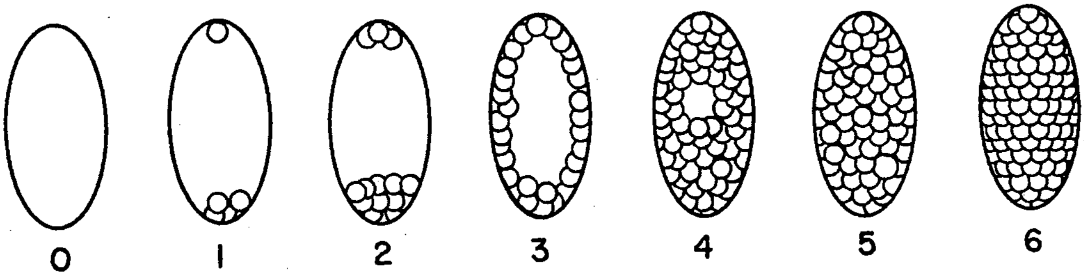
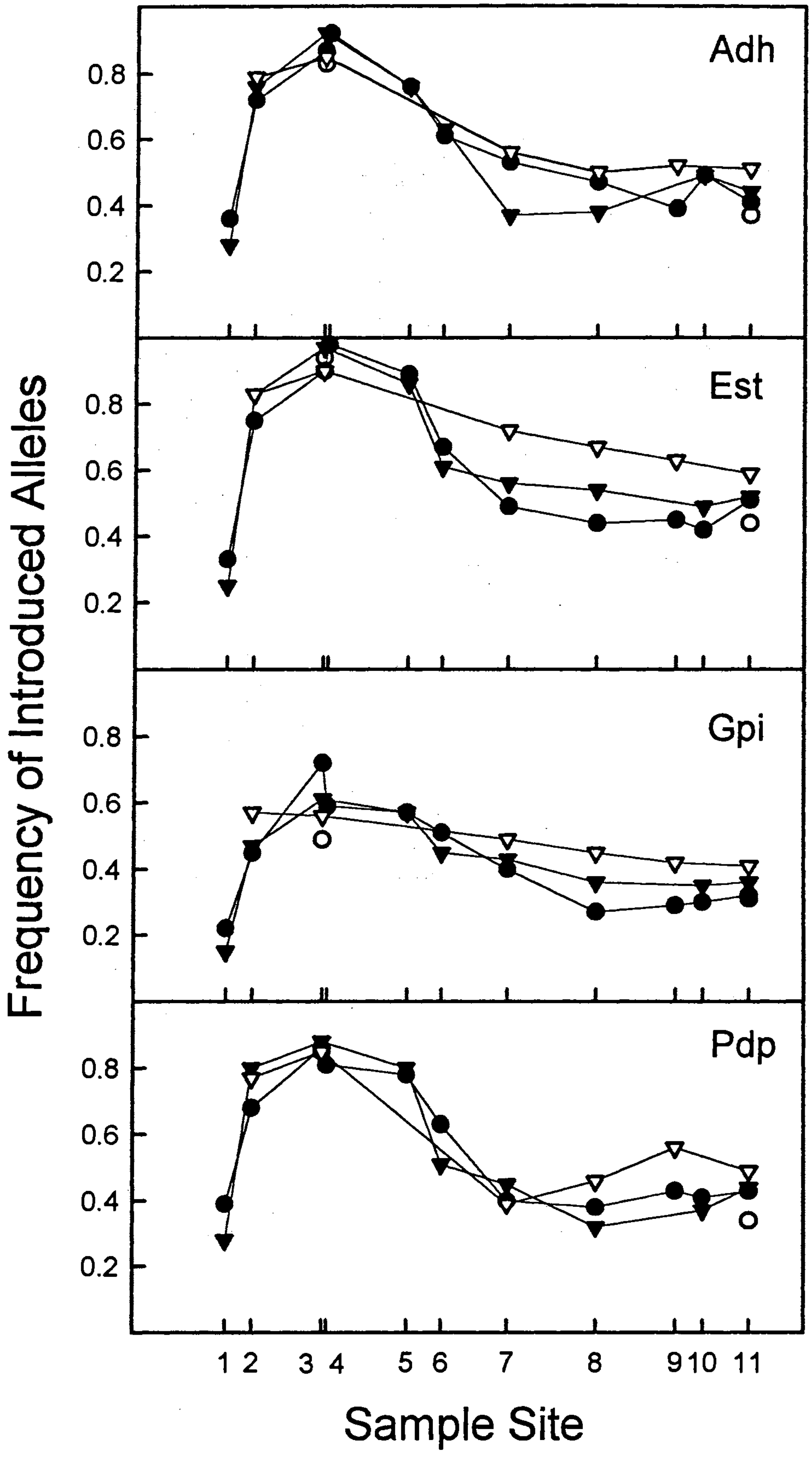

0
1
2
3
4
5
6

Figure 10. Frequencies of introduced alleles, from 1984 to 1988, in intergrade pupfish from the Pecos River, Texas. Sites are as in Figure 8. Key to symbols: ○ - 1984; ▼ - 1985; ● - 1986; and ▽ - 1988.



Adh
Est
Gpi
Pdp
0.8
0.6
0.4
0.2
Frequency of Introduced Alleles
1 2 3 4 5 6 7 8 9 10 11
Sample Site

Figure 11. Correlations among alleles of diagnostic loci in intergrade pupfish from the Pecos River, Texas, 1984-1988. Correlations marked with an asterisk (*) are significant ($\underline{P} < 0.05$) based on sequential Bonferroni tests.

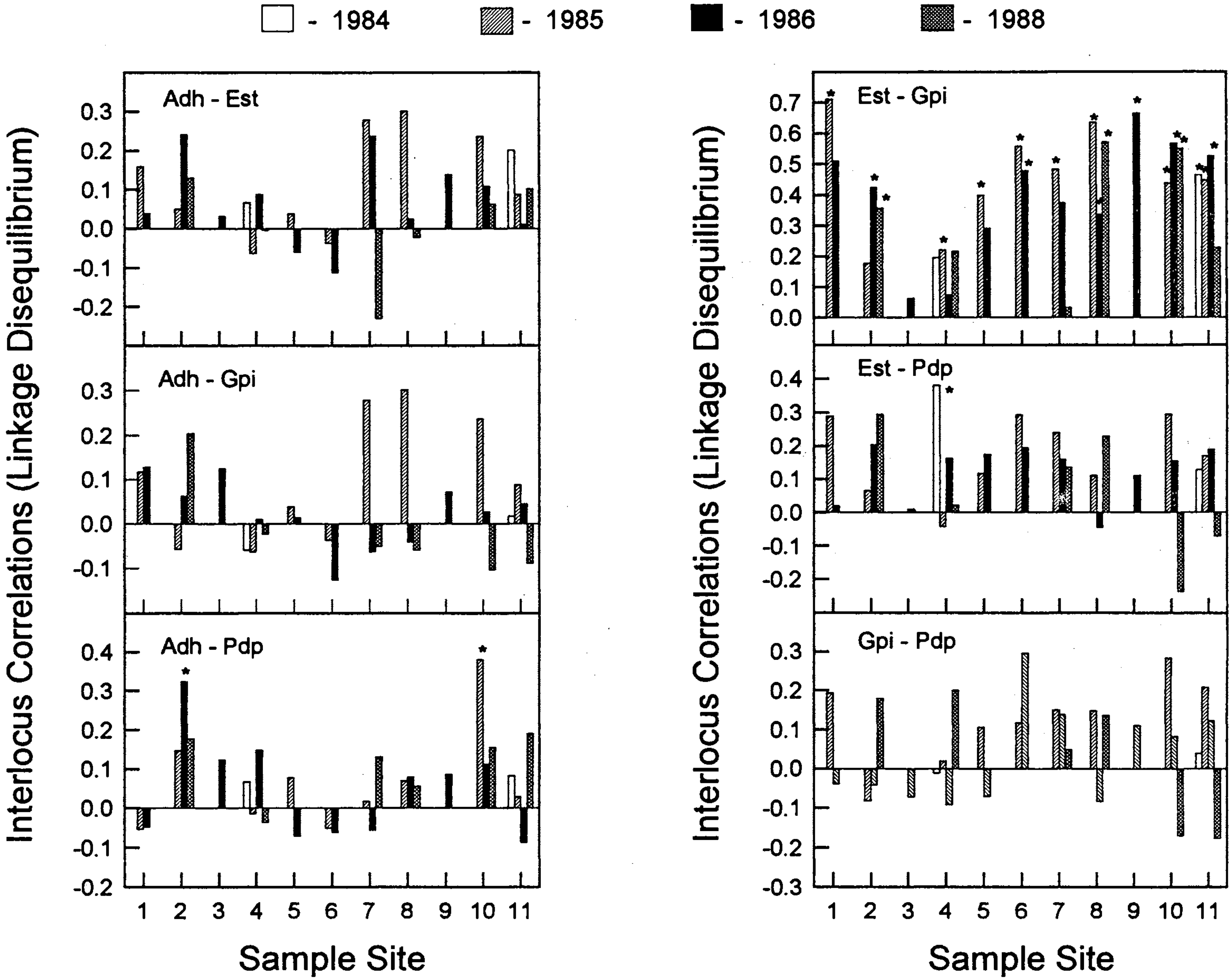
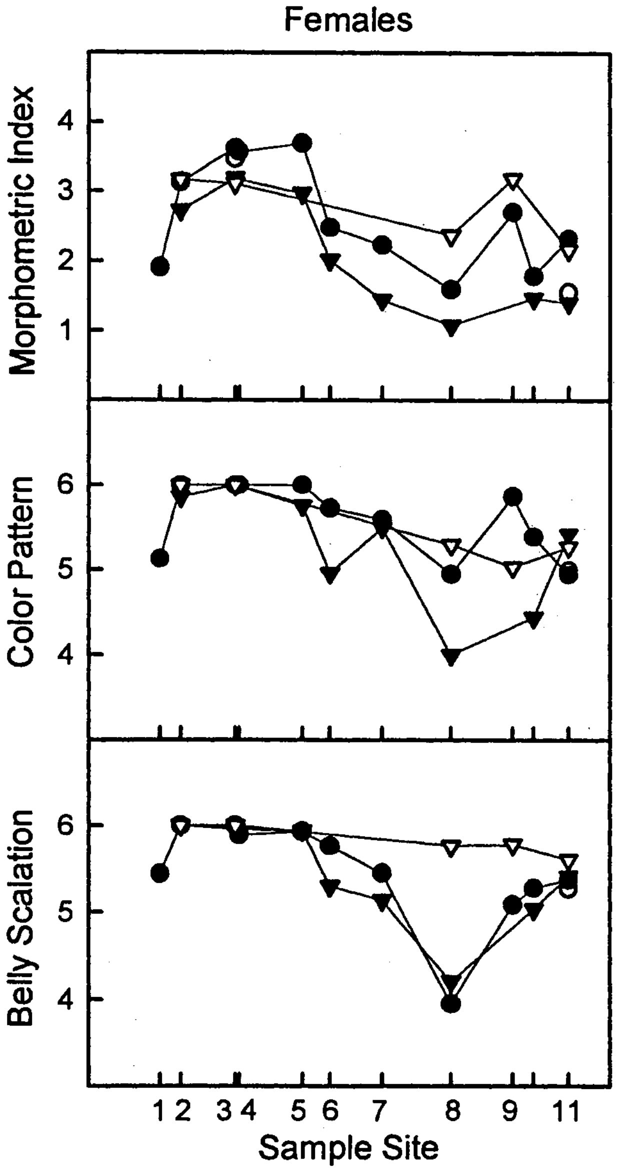
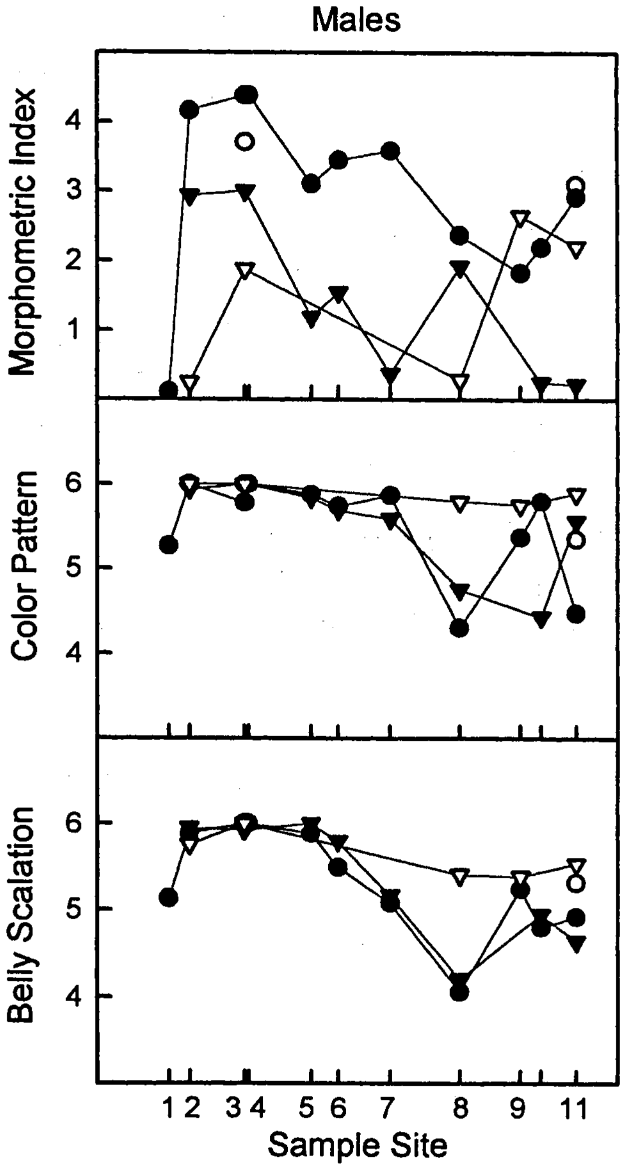

□ - 1984
▨ - 1985
■ - 1986
▩ - 1988
Adh - Est
Adh - Gpi
Adh - Pdp
Est - Gpi
Est - Pdp
Gpi - Pdp
Interlocus Correlations (Linkage Disequilibrium)
Interlocus Correlations (Linkage Disequilibrium)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
1 2 3 4 5 6 7 8 9 10 11
Sample Site
Sample Site
*

Figure 12. Population means of morphometric index scores, belly scalation, and color pattern in intergrade pupfish collected between 1984 and 1988 from the Pecos River, Texas Sites are as in Figure 8. Key to symbols: ○ - 1984; ▼ - 1985; ● - 1986; and ▽ - 1988.


Females
Morphometric Index
4
3
2
1
Color Pattern
6
5
4
Belly Scalation
6
5
4
1 2
3 4
5 6
7
8
9
11
Sample Site


Males
Morphometric Index
4
3
2
1
Color Pattern
6
5
4
Belly Scalation
6
5
4
1 2
3 4
5 6
7
8
9
11
Sample Site

APPENDIX

GENOTYPES OF FISH INCLUDED IN THIS STUDY

List of sampling sites, dates, and museum catalog numbers for fish examined in this study.

Site 3	14 August 1984	OSUS 26716
Site 11	12 August 1984	OSUS 26717
Site 1	11 August 1986	OSUS 26718
Site 2	11 August 1986	OSUS 26719
Site 3	12 August 1986	OSUS 26720
Site 4	12 August 1986	OSUS 26721
Site 5	12 August 1986	OSUS 26722
Site 6	13 August 1986	OSUS 26723
Site 7	13 August 1986	OSUS 26724
Site 8	13 August 1986	OSUS 26725
Site 9	13 August 1986	OSUS 26726
Site 10	13 August 1986	OSUS 26727
Site 11	13 August 1986	OSUS 26728
Site 12	13 August 1986	OSUS 26729
Site 13	14 August 1986	OSUS 26730-26731
Site 14	14 August 1986	OSUS 26732
Site 2	20 August 1988	OSUS 26733
Site 3	20 August 1988	OSUS 26734
Site 7	20 August 1988	OSUS 26735
Site 8	20 August 1988	OSUS 26736
Site 9	20 August 1988	OSUS 26737
Site 11	20 August 1988	OSUS 26738
Site P2	9 September 1988	OSUS 26739
Site P3	11 August 1986	OSUS 26740
Site P4	9 June 1988	OSUS 26741
Site P4	20 August 1988	OSUS 26742
Site P5	9 June 1988	OSUS 26743
Site P6	20 August 1988	OSUS 26744
Site P7	8 September 1988	OSUS 26745
Site P8	20 August 1988	OSUS 26746
Site P9	28 July 1988	OSUS 26747
Site P10	10 August 1986	OSUS 26748
Site P10	20 August 1988	OSUS 26749
Site P11	13 August 1986	OSUS 26750

Site 3. Pecos River at U. S. Highway 80, 1.5 km E of Pecos, Reeves-Ward County line, Texas. 14 August 1984.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	ac	bb	cd	bb
2	aa	bb	cd	bb
3	aa	bb	dd	bb
4		bb	cd	bb
5	ac	ab	cd	bb
6	ac	bb	cc	bb
7		bb	cd	bb
8		bb	dd	bc
9		bb	cc	bb
10		bb	dd	bb
11		bb	cc	bb
12		bb	cd	bb
13		bb	cd	bb
14		bb	dd	bb
15		bb	cc	bb
16		bb	cd	bb
17		bb	cd	bc
18		bb	cd	bb
19	cc	bb	cd	bb
20	cc	ab	cd	bb
21	cc	bb	dd	bb
22	cc	bb	cc	bb
23	cc	bb	dd	bb
24	cc	bb	cd	bb
25	ac	bb	dd	bb
26	cc	bb	dd	bb
27	cc	bb	cd	bb
28	cc	bb	cd	bb
29	cc	ab	dd	bc
30	cc	bb	cd	bb
31	cc	bb	cd	bb
32	cc	bb	dd	bb
33		bb	cc	cc
34	cc	bb	cc	bb
35	cc	bb	cd	bc
36	cc	bb	cd	bb
37	ac	ab	cd	bc
38		ab	cd	cc
39	cc	bb	dd	bb
40	ac	bb	cc	bb
41	cc	bb	dd	bb
42	cc	bb	cd	bb
43	cc	bb	cc	bb
44	ac	bb	cc	bc

Site 3. Pecos River at U. S. Highway 80, 1.5 km E of Pecos, Reeves-Ward County line, Texas. 14 August 1984. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	ac	bb	cd	bb
46	ac	bb	cd	cc
47		bb	cc	bb
48	cc	bb	cd	bc
49	cc	bb	cd	bc
50		bb	dd	bb
51	cc	bb	cc	bb
52		bb	cc	bc
53	cc	bb	cd	bb
54	cc	bb	cd	bb
55	cc	ab	dd	bb
56	cc	bb	cd	bc
57	cc	ab	dd	cc
58	ac	bb	cd	bb
59	ac	bb	cd	bb
60	cc	bb	cd	bb
61	cc	bb	cc	bb
62	cc	bb	dd	bb
63	cc	bb	cc	bb
64	ac	ab	cd	bc
65	cc	bb	cd	bb

Site 11. Pecos River at Texas State Highway 349, 6 km NW of Iraan, Pecos-Crockett County line, Texas. 12 August 1984.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	ac	ab	cd	cc
2	cc	ab	dd	bc
3	ac	ab	cd	bc
4	ac	ab	cd	bc
5	ac	bb	dd	cc
6	ac	aa	dd	bc
7	ac	ab	cc	bb
8	ac	bb	cd	bc
9		ab	cd	
10	ac	ab	dd	bb
11	cc	ab	dd	cc
12	aa	ab	cd	cc
13	ac	ab	cd	bc
14		aa	dd	cc
15	aa	aa	dd	bc
16		aa	dd	cc
17		ab	dd	cc
18	ac	aa	cd	cc
19		bb	dd	bc
20	aa	bb	cd	cc
21	ac	bb	cd	bc
22	aa	bb	cd	bb
23	aa	ab	cd	cc
24	aa	aa	dd	cc
25	aa	ab	dd	bc
26	aa	aa	cd	cc
27	aa	aa	dd	cc
28	ac	ab	cd	bb
29	cc	aa	dd	bc
30	aa	ab	cd	bc
31	cc	bb	cc	cc
32	ac	ab	cd	bb
33	aa	ab	cd	cc
34	ac	bb	cd	cc
35	aa	aa	dd	cc
36	ac	aa	dd	bc
37	cc	ab	cd	bc
38	aa	aa	dd	cc
39	aa	ab	dd	bc
40	ac	bb	cd	cc
41	ac	aa	cd	cc
42	cc	aa	dd	bc
43	ac	ab	cd	bc
44	aa	ab	cd	bc

Site 11. Pecos River at Texas State Highway 349, 6 km NW of Iraan, Pecos-Crockett County line, Texas. 12 August 1984. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	aa	ab	cd	
46	ac	ab	dd	cc
47		ab	cd	
48	ac	ab	dd	bc
49		ab	cd	cc
50	aa	aa	dd	bc
51	aa	aa	dd	bc
52	ac	aa	dd	cc
53	ac	bb	cc	bc
54	aa	ab	cc	bc
55	aa	ab	dd	bb
56	aa	aa	cd	cc
57	ac	ab	cd	cc
58	aa		cd	cc
59	ac	ab	dd	bc
60	ac	ab	dd	
61	ac	ab	cd	
62	cc	bb	cd	bc
63	ac	aa	dd	bb
64	aa	ab	cd	bb

Site 1. Pecos River at Texas State Highway 302, 5.1 km SW of Mentone, Loving-Reeves County line, Texas. 11 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	ac	ab	cd	cc
2	aa	bb	cd	bb
3	aa	aa	dd	bc
4	aa	aa	dd	bc
5	ac	aa	dd	cc
6	ac	bb	cc	bc
7	aa	ab	dd	cc
8	ac	ab	cd	bc
9	ac	ab	cd	bc
10	ac	ab	cd	cc
11	cc	aa	cc	cc
12	ac	aa	dd	cc
13	ac	ab	dd	bc
14	aa	ab	dd	cc
15	cc	aa	dd	bb
16	cc	ab	dd	bc
17	aa	aa	dd	bc
18	aa	aa	dd	bc
19	cc	ab	cd	bc
20	cc	ab	cd	bc
21	ac	ab	dd	cc
22	aa	ab	dd	bb
23	ac	ab	dd	bc
24	aa	aa	cd	bc
25	aa	aa	dd	bc
26	ac	bb	cd	bc
27	aa	ab	dd	bc
28	ac	ab	dd	cc
29	aa	ab	cd	bc
30	aa	ab	cd	cc
31	ac	aa	cd	bc
32	ac	aa	dd	cc
33	aa	bb	cc	cc
34	ac	aa	dd	bc
35	ac	ab	dd	bc
36	aa	ab	cd	bc
37	ac	aa	dd	bb
38	cc	ab	dd	bc
39	aa	aa	dd	bc
40	aa	ab	dd	bc
41	cc	ab	cd	cc
42	cc	ab	dd	bc
43	ac	aa	dd	bc
44	ac	aa	dd	cc

Site 1. Pecos River at Texas State Highway 302, 5.1 km SW of Mentone, Loving-Reeves County line, Texas. 11 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	aa	aa	dd	cc
46	ac	ab	dd	cc
47	ac	aa	dd	cc
48	ac	bb	cd	cc
49	cc	ab	cd	cc
50	ac	aa	dd	cc
51	aa	aa	dd	bc
52	aa	ab	dd	cc
53	aa	aa	dd	bc
54	aa	ab	dd	bb
55	ac	ab	cd	bc
56	aa	ab	cd	bc
57	aa	aa	dd	bc
58	aa	aa	dd	bc
59	aa	aa	dd	bc
60	cc	aa	cd	bc
61	aa	aa	dd	cc
62	aa	bb	cd	bb
63	aa	ab	cd	bc
64	aa	ab	cd	cc
65	ac	aa	dd	bc
66	ac	bb	cd	bc
67	aa	aa	cd	bc
68	ac	aa	dd	bc
69	ac	ab	cd	bb
70	ac	ab	dd	cc
71	cc	aa	dd	bb

Site 2. Pecos River below Reeves County W.I.D. NO. 2 diversion dam (Brush Dam), 10 km SW of Mentone, Reeves-Ward County line, Texas. 11 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	cc	bb	cd	bb
2	cc	ab	cd	bc
3	cc	bb	cd	bb
4	ac	ab	dd	bb
5	cc	ab	cd	bc
6	cc	ab	cd	bb
7	ac	bb	dd	bb
8	ac	bb	cd	bc
9	cc	bb	cd	bc
10	ac	bb	dd	bc
11	ac	bb	cc	bc
12	cc	ab	cd	bb
13	ac	aa	cd	cc
14	ac	bb	cd	bb
15	ac	aa	dd	bb
16	ac	ab	cc	bc
17	ac	ab	cd	cc
18	ac	bb	cd	bb
19	cc	bb	cc	bb
20	cc	bb	cd	bc
21	cc	ab	cc	bc
22	cc	bb	cc	bc
23	ac	ab	cd	bc
24	cc	bb	dd	bb
25	ac	aa	dd	bb
26	cc	bb	dd	bb
27	cc	bb	cd	bb
28	cc	bb	cc	bc
29	cc	bb	cd	bc
30	cc	bb	dd	bb
31	ac	ab	dd	bc
32	cc	ab	cd	bc
33	ac	aa	dd	bc
34	cc	ab	dd	bc
35	cc	ab	dd	bb
36	aa	bb	cc	bb
37	ac	ab	cd	bc
38	cc	ab	dd	bc
39	ac	bb	dd	bc
40	cc	bb	cd	bb
41	cc	ab	cd	bb
42	ac	bb	cd	bc
43	ac	bb	cc	bc

Site 2. Pecos River below Reeves County W.I.D. NO. 2 diversion dam (Brush Dam), 10 km SW of Mentone, Reeves-Ward County line, Texas. 11 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
44	aa	ab	cd	bb
45	aa	ab	cd	cc
46	ac	ab	dd	bc
47	cc	ab	dd	bb
48	aa	aa	dd	cc
49	cc	bb	dd	bb
50	cc	bb	cc	bb
51	ac	bb	cd	bc
52	ac	bb	cc	bc
53	cc	bb	cc	bb
54	ac	bb	cc	bc
55	cc	bb	cd	bb
56	cc	bb	cc	bc
57	ac	bb	cd	bc
58	ac	bb	cd	bc
59	cc	ab	cd	bb
60	cc	bb	cc	bc
61	ac	ab	dd	bc
62	ac	ab	dd	bc
63	cc	bb	cd	bb
64	cc	ab	dd	bb
65	cc	bb	cc	bc
66	cc	bb	cd	bc
67	cc	bb	dd	cc
68	aa	ab	dd	bc
69	cc	bb	cd	bb
70	cc	ab	dd	bb
71	ac	bb	cc	bb
72	ac	ab	cd	cc
73	ac	bb	cd	bb
74	ac	bb	cd	bc
75	ac	bb	cc	bb
76	cc	ab	cd	bb

Site 3. Pecos River at Texas Farm Road 3398, 3.2 km NE of Pecos, Reeves-Ward County line, Texas. 12 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	cc	bb	cc	bb
2	cc	bb	cd	bc
3	cc	bb	cd	bb
4	cc	bb	dd	bb
5	cc	bb	cd	bc
6	cc	bb	cc	bc
7	cc	bb	cd	bb
8	cc	bb	cc	bb
9	cc	bb	dd	bb
10	cc	bb	cd	bb
11	cc	bb	cd	bb
12	cc	bb	cc	bb
13	cc	bb	cc	bb
14	cc	bb	cd	bc
15	cc	bb	cd	bb
16	cc	bb	cd	bb
17	cc	bb	dd	bb
18	cc	bb	cd	bb
19	cc	bb	cd	bc
20		bb	cc	bc
21	cc	bb	cd	bb
22	cc	bb	cd	bb
23		bb	cc	bb
24	cc	bb	cd	
25	ac	bb	dd	bb
26	cc	bb	cc	bb
27	cc	bb	cc	bb
28	cc	bb	cc	bc
29	cc	bb	dd	cc
30	cc	bb	cc	bb
31	cc	bb	cd	bb
32	cc	bb	cd	bb
33	ac	ab	cd	cc
34	cc	bb	cc	
35	cc	bb	cd	
36	cc	ab	cd	bb
37	cc	bb	cc	bc
38	cc	bb	cc	bb
39	cc	bb	cd	bb
40	cc	bb	cd	bb
41	ac	bb	dd	cc
42	cc	bb	dd	bb
43	cc	bb	cc	bb

Site 3. Pecos River at Texas Farm Road 3398, 3.2 km NE of Pecos, Reeves-Ward County line, Texas. 12 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
44		bb	cc	bb
45	cc	bb	cc	bb
46	cc	bb	dd	bc
47	cc	bb	cc	bb
48	cc	bb	cc	bc
49	cc	bb	dd	bc
50	ac	bb	cc	cc
51	cc	bb	cd	bc
52	ac	bb	cd	bb
53	cc	bb	cd	bb
54	cc	bb	cc	cc
55	cc	bb	cd	bb
56		bb	cc	
57	ac	bb	cc	bb
58	cc	bb	cc	bc
59		bb	cd	
60		bb	cd	bb
61	cc	bb	dd	bb
62	cc	bb	cd	cc
63	ac	bb	dd	bb
64	cc	bb	cd	bb
65	cc	bb	dd	bb
66	cc	ab	cd	bb
67	cc	bb	cd	bb
68	ac	bb	cc	bc
69	cc	bb	cc	cc
70	cc	bb	cc	bb
71	cc	bb	cd	bb
72	cc	bb	cd	bb
73	cc	bb	dd	bb
74	cc	ab	cc	bb
75	ac	bb	dd	bb
76	cc	bb	cd	bb
77	cc	bb	dd	bb
78		bb	cd	bc
79	cc	bb	cc	bb
80	ac	bb	cd	bb
81		bb	cd	bb
82	aa	bb	cd	bb
83	cc	bb	cc	bc
84	cc	bb	cc	bb
85	cc	bb	cc	bb

Site 3. Pecos River at Texas Farm Road 3398, 3.2 km NE of Pecos, Reeves-Ward County line, Texas. 12 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
86	cc	ab	dd	bb
87	cc	bb	cd	bc

Site 4. Pecos River at U. S. Interstate Highway 20, 4.5 km E of Pecos, Reeves-Ward County line, Texas. 12 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	cc	ab	dd	bb
2	cc	bb	cd	bb
3	cc	bb	cd	bb
4	ac	ab	cd	bc
5	cc	bb	cc	bb
6	cc	bb	cd	cc
7	cc	ab	cd	bb
8	cc	bb	cc	bb
9	cc	bb	cc	bb
10	cc	bb	cd	bb
11	cc	bb	cd	bb
12	cc	bb	cc	bb
13	aa	bb	cd	bb
14	ac	ab	cd	bc
15	cc	bb	cc	bb
16	cc	ab	cc	bb
17	ac	bb	cc	bb
18	ac	bb	cd	bb
19	cc	bb	cc	bb
20	cc	bb	cd	bb
21	cc	bb	cd	bc
22	cc	bb	cc	bb
23	cc	bb	cd	bb
24	cc	bb	cc	bb
25	cc	bb	cd	bb
26	cc	bb	dd	bb
27	ac	bb	cd	bb
28	cc	bb	cd	bb
29	cc	ab	cd	bb
30	ac	bb	cc	bb
31	ac	bb	cd	bb
32	cc	bb	cc	bb
33	cc	ab	cc	bb
34	cc	bb	cc	bc
35	ac	bb	cc	cc
36	cc	bb	cd	bb
37	ac	bb	cc	bb
38	cc	bb	cd	bb
39	cc	bb	cc	bb
40	cc	bb	cc	bc
41	cc	bb	cc	bc
42	cc	bb	cc	bb
43	cc	bb	cd	bc
44	cc	bb	cc	bb

Site 4. Pecos River at U. S. Interstate Highway 20, 4.5 km E of Pecos, Reeves-Ward County line, Texas. 12 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	cc	ab	cc	bc
46	ac	ab	cc	bc
47	cc	bb	cd	bb
48	cc	bb	dd	bb
49	cc	bb	cc	bb

Site 5. Pecos River at Texas Farm Road 1776, 21 km SE of Pyote, Reeves-Ward County line, Texas. 12 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	ac	bb	cc	bb
2	ac	bb	cd	bb
3	cc	bb	cc	bc
4	ac	bb	dd	bb
5	ac	bb	cd	bb
6	cc	ab	cd	bb
7	ac	bb	cd	bc
8	cc	bb	cd	bb
9	cc	bb	cc	bb
10	cc	bb	cd	bb
11	cc	bb	cc	bb
12	ac	bb	cc	bb
13	ac	bb	cd	bc
14	ac	ab	cd	bc
15	cc	ab	dd	bb
16	cc	bb	cd	bc
17	cc	ab	cd	bb
18	cc	bb	cc	bb
19	cc	ab	cd	cc
20	ac	ab	cd	bb
21	ac	bb	dd	bb
22	ac	bb	cc	cc
23	cc	bb	cd	bb
24	cc	bb	cc	bc
25	cc	ab	cd	bb
26	cc	bb	cc	bc
27	cc	bb	dd	bb
28	ac	bb	cd	bb
29	ac	bb	cc	bb
30	cc	bb	cc	bb
31	cc	bb	cd	bb
32	aa	bb	cc	bb
33	cc	bb	cc	bb
34	cc	bb	cc	bb
35	cc	ab	cd	bc
36	ac	bb	dd	bc
37	ac	bb	cd	bc
38	cc	bb	cd	bb
39	cc	ab	cd	bb
40	ac	bb	cd	bc
41	cc	bb	dd	bb
42	cc	bb	cd	bb
43	cc	ab	dd	cc
44	cc	bb	cc	bc

Site 5. Pecos River at Texas Farm Road 1776, 21 km SE of Pyote, Reeves-Ward County line, Texas. 12 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	cc	bb	cc	bb
46	cc	bb	cd	bb
47	cc	bb	cd	bb
48	ac	bb	dd	bb
49	ac	bb	cd	bb
50	cc	bb	cc	bb
51	cc	bb	cd	bc
52	aa	bb	cc	bc
53	cc	bb	cd	bc
54	cc	bb	cd	bb
55	aa	bb	cd	bb
56	cc	bb	cc	bc
57	ac	ab	dd	bb
58	ac	ab	cd	bb
59	ac	bb	dd	bb
60	cc	bb	cd	bb
61	ac	bb	cd	bb
62	cc	bb	cc	bb
63	ac	ab	cc	bc
64	aa	bb	cc	bb
65	cc	bb	cc	bb
66	aa	bb	cd	bc
67	cc	bb	cc	bb
68	ac	bb	cc	bb
69	cc	bb	cd	bc
70	cc	bb	cd	bc
71	ac	aa	cd	bc
72	cc	bb	cd	cc
73	cc	bb	dd	bb
74	ac	bb	dd	bc
75	cc	bb	cd	bb
76	cc	bb	cc	bc
77	ac	bb	cd	bb
78	cc	ab	dd	bb
79	cc	ab	cd	cc
80	ac	bb	dd	bb
81	ac	bb	cd	bb
82	cc	bb	cc	bc
83	cc	bb	cd	bb
84	ac	bb	cc	cc
85	cc	bb	cc	cc
86	aa	ab	cd	bb
87	ac	bb	cd	bb

Site 5. Pecos River at Texas Farm Road 1776, 21 km SE of Pyote, Reeves-Ward County line, Texas. 12 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
88	cc	bb	cd	bc
89	cc	ab	cd	bb
90	ac	bb	dd	bb
91	cc	bb	cd	bc
92	cc	bb	cd	bb
93	cc	aa	dd	bc
94	ac	bb	cc	bb
95	ac	ab	cd	bc
96	ac	bb	cc	bb
97	cc	bb	cd	bb
98	cc	ab	cd	bc
99	ac	bb	cd	bb
100	cc	ab	dd	bc
101	cc	bb	cd	bb
102	cc	ab	cd	bb

Site 6. Pecos River at Texas State Highway 18, 4 km SW of Grandfalls , Pecos-Ward County line, Texas. 13 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	cc	ab	cd	bb
2	ac	ab	cd	cc
3	cc	bb	cd	bb
4	cc	ab	cd	bc
5	cc	bb	cd	bb
6	cc	aa	cd	bc
7	cc	ab	dd	bb
8	ac	bb	cd	bc
9	cc	bb	cc	bc
10	cc	aa	dd	cc
11	cc	aa	dd	bc
12	cc	ab	cd	bb
13	ac	aa	cd	bc
14	aa	ab	dd	bc
15	cc	aa	dd	cc
16	cc	bb	cc	bb
17	cc	ab	cd	bc
18	aa	bb	cc	bb
19	ac	ab	cd	bb
20	aa	bb	cd	bc
21	ac	bb	cd	bb
22	cc	bb	cd	bc
23	ac	bb	cd	bc
24	aa	ab	dd	bc
25	ac	bb	cc	bc
26	cc	bb	cc	bb
27	ac	bb	cc	bb
28	ac	bb	cd	bb
29	ac	bb	cd	bc
30	ac	bb	cd	cc
31		bb	cd	bb
32	cc	ab	dd	bb
33	cc	ab	cd	bc
34	ac	ab	dd	cc
35	cc	bb	cc	bb
36	ac	bb	cc	bc
37	cc	ab	cd	bc
38	ac	ab	dd	bb
39	ac	bb	cd	bb
40	ac	ab	cd	bc
41		bb	cc	bb
42	aa	ab	cd	bb
43	ac	bb	cd	bc
44	cc	ab	cd	bc

Site 6. Pecos River at Texas State Highway 18, 4 km SW of Grandfalls , Pecos-Ward County line, Texas. 13 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	ac	aa	dd	bb
46	cc	ab	cd	bc
47		bb	cd	cc
48		bb	cd	cc
49		ab	cd	bc
50		bb	cc	bb
51		ab	cd	bb
52		bb	cd	bc
53		bb	cd	cc
54		ab	cd	cc
55	ac	ab	cd	bb
56	ac	ab	cd	bc
57	ac	ab	cd	cc
58	ac	ab	dd	bc
59	cc	bb	dd	bc
60	aa	ab	cc	bb
61		bb	cc	bb
62	aa	bb	cc	bb
63	ac	bb	dd	cc
64	ac	ab	cd	bc
65	ac	ab	dd	bc
66	aa	aa	cd	bc
67	ac	ab	cc	cc
68	ac	aa	cd	bc
69	aa	bb	cd	bb
70	aa	ab	cd	bb
71	ac		cd	bc
72	ac			bc
73	cc			bb
74	cc			bc
75	aa	bb	cc	bb
76	cc	ab	cd	bb

Site 7. Pecos River at Texas Farm Road 11, 5 km NW of Imperial, Crane-Pecos County line, Texas. 13 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	cc	ab	dd	bc
2	cc	aa	cd	cc
3	aa	aa	dd	cc
4	ac	ab	cc	bc
5	cc	aa	cd	cc
6	cc	ab	dd	bc
7	aa	aa	dd	bb
8	ac	aa	cd	cc
9	aa	bb	cc	cc
10	aa	ab	dd	cc
11	aa	ab	cd	cc
12	ac	ab	cd	cc
13	aa	aa	dd	cc
14	cc	bb	cd	cc
15	ac	ab	cd	bb
16	cc	ab	cd	bc
17	cc	ab	cd	bb
18	ac	aa	dd	cc
19	cc	bb	dd	cc
20	aa	aa	cd	bc
21	aa	aa	cd	bc
22	cc	bb	cd	bc
23	aa	aa	dd	bb
24	cc	ab	cd	bb
25	cc	bb	cd	bb
26	cc	ab	dd	cd
27	cc	ab	cd	cc
28	aa	bb	cd	bc
29	cc	ab	cd	bc
30	aa	bb	cc	cc
31	aa	ab	cd	cc
32	cc	bb	dd	bb
33	ac	ab	cc	bc
34	ac	ab	dd	bc
35	ac	bb	cc	bb
36	aa	ab	cd	bc
37	aa	ab	cd	bc
38	aa	bb	cd	bb
39	ac	bb	cd	bc
40	cc	ab	dd	cc
41	ac	aa	dd	cc
42	ac	bb	cc	bc
43	ac	aa	cd	cc
44	cc	bb	dd	cc

Site 7. Pecos River at Texas Farm Road 11, 5 km NW of Imperial, Crane-Pecos County line, Texas. 13 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	aa	aa	dd	bc
46	aa	ab	cc	bc
47	cc	bb	cc	cc
48	ac	aa	dd	cc
49	aa	aa	dd	bb
50	aa	bb	cd	bc
51	ac	aa	cd	cc
52	ac	aa	dd	bc
53	cc	ab	dd	cc
54	ac	ab	cd	bb
55	ac	bb	cd	bb
56	ac	ab	cd	bc
57	cc	ab	cd	bc
58	cc	ab	cd	bb
59	ac	ab	cd	bb
60	cc	ab	cc	bc
61	ac	aa	dd	cc
62	cc	bb	dd	cc
63	ac	ab	cd	bc

Site 8. Horsehead Crossing 6.4 km off Texas Farm Road 11, 23 km NW of Girvin, Crane-Pecos County line, Texas. 13 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	ac	aa	cd	bb
2	ac	aa	dd	cc
3	aa	ab	cd	cc
4	ac	bb	dd	cc
5	ac	aa	dd	bb
6	aa	aa	cd	cc
7	cc	ab	dd	bc
8	aa	aa	dd	bb
9	ac	aa	cd	bb
10	ac	aa	dd	cc
11	ac	aa	cd	cc
12	aa	aa	dd	cc
13	aa	ab	dd	bc
14	aa	bb	cd	cc
15	aa	ab	dd	bc
16	ac	ab	dd	bc
17	ac	ab	cd	bc
18	ac	aa	cd	bc
19	aa	ab	dd	bb
20	ac	bb	cd	bb
21	ac	ab	dd	bc
22	cc	ab	dd	bb
23	cc	aa	dd	bc
24	cc	bb	dd	bc
25	aa	ab	cc	bc
26	cc	ab	cd	bc
27	cc	ab	dd	bb
28	ac	ab	cd	cc
29	ac	bb	cd	cc
30	cc	aa	dd	bc
31	aa	aa	dd	bc
32	ac	bb	cc	cc
33	ac	aa	dd	cc
34	ac	ab	cd	cc
35	aa	aa	dd	bc
36	cc	ab	cd	bc
37	aa	bb	cd	bc
38	cc	ab	dd	bc
39	cc	ab	cd	bc
40	ac	ab	cc	bc
41	cc	ab	dd	cc
42	ac	ab	cd	bc
43	aa	bb	cc	cc

Site 8. Horsehead Crossing 6.4 km off Texas Farm Road 11, 23 km NW of Girvin, Crane-Pecos County line, Texas. 13 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
44	ac	aa	dd	cc
45	ac	bb	dd	bb
46	ac	bb	cd	cc
47	aa	aa	dd	
48	aa	aa	dd	bb
49	ac	bb	dd	cc
50	cc		cc	cc
51	cc	aa	dd	cc
52	ac	ab	dd	bb
53	cc	ab	dd	bc
54	ac	aa	dd	bc
55	aa	ab	dd	cc
56	ac	ab	cd	cc
57	aa	ab	cd	bb
58	ac	ab	dd	cc
59	cc	ab	dd	cc
60	aa	ab	dd	cc
61	ac	ab	dd	cc
62	aa	aa	cd	bc
63	ac	bb	cc	cc
64	aa	ab	cd	cc
65	aa	ab	cd	cc
66	aa	aa	dd	cc
67	ac	bb	cc	cc
68	ac	aa	cd	cc
69	ac	ab	cd	bc
70	ac	aa	dd	bc
71	aa	bb	cd	cc
72	aa	ab	cd	cc
73	cc	aa	dd	bc
74	aa	ab	cd	bc
75	ac	aa	dd	cc
76	ac	bb	cc	bc
77	cc	ab	dd	cc
78	ac	bb	cc	cc
79	ac	ab	dd	cc
80	ac	aa	dd	cc
81	ac	ab	cd	bb
82	ac	bb	dd	cc
83	ac	ab	dd	bb
84	cc	ab	cd	bc
85	cc	ab	cd	bb
86	cc	bb	cd	bc

Site 8. Horsehead Crossing 6.4 km off Texas Farm Road 11, 23 km NW of Girvin, Crane-Pecos County line, Texas. 13 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
87	aa	ab	dd	cc
88	aa	ab	cc	bb
89	cc	ab	dd	bb
90	ac	bb	dd	
91	cc	aa	cd	cc
92	ac	ab	cd	bb
93	aa	ab	dd	bc
94	cc	ab	dd	cc
95	aa	ab	dd	bc
96	ac	ab	dd	bc
97	cc	bb	cd	bb
98	ac	ab	dd	
99	ac	ab	cd	cc
100	ac	aa	cd	cc
101	cc	ab	cd	cc
102	ac	ab	dd	bc
103	aa	ab	dd	bb
104	aa	ab	dd	cc
105	ac	ab	cd	
106	ac	ab	cd	bc
107	ac	aa	dd	cc
108	aa	bb	dd	cc

Site 9. Pecos River at Texas Farm Road 1901, 12 km SW of McCamey, Crockett-Pecos County line, Texas. 13 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	aa	aa	dd	bb
2	ac	ab	dd	bb
3	aa	aa	cd	cc
4	aa	ab	dd	bc
5	ac	ab	cd	bc
6	ac	bb	cd	cc
7	aa	aa	dd	cc
8	ac	bb	cc	bc
9	ac	bb	cd	bc
10	ac	ab	dd	bc
11	ac	ab	dd	bc
12	ac	ab	cd	bc
13	aa	aa	dd	cc
14	cc	aa	dd	bc
15	ac	aa	cd	bc
16	ac	ab	dd	bc
17	cc	bb	cc	bc
18	ac	aa	dd	bc
19	ac	aa	dd	bc
20	aa	aa	dd	cc
21	ac	ab	cd	cc
22	aa	aa	dd	cc
23	aa	ab	dd	cc
24	ac	ab	dd	bc
25	cc	bb	cc	cc
26	ac	ab	cd	bc
27	cc	ab	cd	cc
28	ac	aa	dd	bb
29	ac	ab	cd	bb
30	aa	ab	cd	bc
31	cc	bb	cc	bb
32	ac	bb	cc	bb
33	aa	bb	cc	bc
34	cc	aa	dd	bc
35	cc	bb	dd	bb
36	ac	ab	dd	cc
37	ac	ab	dd	cc
38	aa	aa	dd	cc
39	ac	ab	cd	bb
40	aa	bb	cc	bc
41	aa	bb	cd	bb
42	aa	aa	dd	bc
43	cc	aa	dd	bc

Site 9. Pecos River at Texas Farm Road 1901, 12 km SW of McCamey, Crockett-Pecos County line, Texas. 13 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
44	aa	bb	cd	cc
45	aa	aa	dd	cc
46	ac	aa	dd	bc
47	cc	aa	dd	bc
48	ac	bb	cd	cc
49	ac	ab	cd	cc
50	aa	aa	dd	cc
51	cc	ab	cd	bc
52	aa	bb	cd	bc
53	ac	ab	dd	cc
54	cc	aa	cd	bc
55	aa	aa	dd	bc
56	aa	bb	dd	bb
57	ac	aa	dd	bb
58	cc	bb	dd	cc
59	cc	bb	cd	bc
60	aa	ab	dd	bc
61	aa	bb	cc	bb
62	cc	ab	cd	bc
63	ac	bb	cc	cc
64	cc	bb	cc	bb
65	ac	ab	dd	bc
66	aa	ab	cd	cc
67	ac	ab	dd	cc
68	ac	aa	dd	cc
69	aa	aa	dd	bc
70	cc	aa	dd	bc
71	aa	ab	cd	bb
72	aa	aa	dd	cc
73	aa	ab	cd	bc
74	ac	ab	dd	bc
75	ac	aa	dd	cc
76	aa	aa	dd	bb
77	aa	bb	cc	cc
78	aa	ab	cd	bc
79	aa	aa	dd	bc
80	cc	ab	dd	bb
81	ac	ab	cd	bc
82	aa	ab	cd	bb

Site 10. Pecos River at Texas Farm Road 305, 17.6 km S of McCamey, Crockett-Pecos County line, Texas. 13 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	aa	bb	cc	cc
2	aa	aa	dd	bb
3	ac	aa	cd	bc
4	cc	bb	cd	bc
5	aa	ab	cd	bc
6	aa	aa	dd	cc
7	ac	ab	cd	bc
8	cc	bb	cd	cc
9	ac	aa	dd	bc
10	ac	ab	dd	bc
11	aa	ab	dd	cc
12	ac	bb	dd	bc
13	ac	ab	cd	bc
14	ac	bb	cd	bb
15	ac	aa	cd	cc
16	cc	ab	dd	bc
17	ac	aa	cd	bc
18	ac	aa	dd	bc
19	ac	ab	cd	bc
20	ac	ab	dd	bb
21	ac	ab	dd	bc
22	cc	ab	cd	bc
23	aa	aa	dd	bc
24	cc	bb	cc	bb
25	cc	aa	dd	cc
26	ac	ab	cd	cc
27	ac	ab	dd	bc
28	cc	ab	dd	bc
29	cc	ab	cd	bc
30	ac	ab	cd	cc
31	ac	ab	cd	cc
32	ac	aa	dd	bc
33	ac	aa	dd	bc
34	ac	aa	cd	bb
35	ac	ab	cd	cc
36	ac	bb	cc	bc
37	aa	ab	dd	cc
38	ac	aa	cd	bc
39	cc	aa	dd	cc
40	aa	aa	dd	cc
41	cc	ab	cd	cc
42	ac	aa	dd	bb
43	ac	aa	dd	bc
44	ac	ab	cd	cc

Site 10. Pecos River at Texas Farm Road 305, 17.6 km S of McCamey, Crockett-Pecos County line, Texas. 13 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	aa	ab	cd	bc
46	aa	bb	cc	bb
47	ac	bb	cd	bb
48	ac	aa	dd	cc
49	ac	ab	cd	cc
50	ac	bb	cd	bb
51	ac	ab	cd	bc
52	ac	ab	dd	bc
53	ac	ab	cd	cc
54	ac	ab	dd	cc
55	aa	aa	dd	cc
56	cc	ab	dd	bb
57	ac	ab	cd	bc
58	aa	bb	cd	cc
59	ac	aa	dd	bc

Site 11. Pecos River at U. S. Highway 190, 1.6 km E of Iraan, Crockett-Pecos County line, Texas. 13 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	aa	bb	dd	cc
2	cc	bb	cd	bc
3	aa	ab	cc	bc
4	ac	ab	dd	bc
5	ac	aa	dd	cc
6	aa	bb	cd	bb
7	ac	ab	dd	bc
8	aa	ab	cd	bc
9	ac	bb	cd	bb
10	cc	aa	cd	cc
11	ac	bb	cd	bb
12	ac	ab	cd	bb
13	aa	ab	cd	bc
14	aa	ab	cd	bc
15	ac	bb	cd	bb
16	ac	aa	dd	bc
17	ac	ab	cd	bc
18	aa	aa	dd	cc
19	aa	aa	dd	cc
20	aa	aa	dd	cc
21	ac	aa	dd	bc
22	cc	ab	cd	bc
23	ac	aa	dd	cc
24	aa	aa	dd	cc
25	aa	ab	dd	bc
26	aa	bb	cd	bc
27	ac	ab	dd	bc
28	ac	ab	cd	bb
29	aa	bb	dd	bb
30	ac	ab	dd	cc
31	ac	ab	cd	bc
32	cc	ab	dd	bc
33	cc	aa	dd	cc
34	ac	aa	dd	bc
35	ac	bb	cd	cc
36	ac	bb	cd	bc
37	ac	aa	dd	cc
38	ac	ab	cd	cc
39	ac	ab	dd	bc
40	ac	ab	cd	cc
41	ac		dd	bc
42	ac	bb	cd	bb
43	aa	aa	dd	bc
44	ac	ab	cd	bb

Site 11. Pecos River at U. S. Highway 190, 1.6 km E of Iraan, Crockett-Pecos County line, Texas. 13 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	aa	ab	dd	cc
46	ac	aa	cd	bb
47	cc	ab	cd	bc
48	ac	bb	cc	cc
49	aa	ab	dd	bc
50	ac	bb	cd	bb
51	aa	aa	cd	bc
52	aa	bb	cd	cc
53	ac	ab	cd	cc
54	ac	ab	cd	bc
55	ac	bb	cd	bc
56	ac	bb	cc	cc
57	ac	ab	dd	cc
58	aa	bb	cc	cc
59	aa	aa	dd	bb
60	ac	ab	cd	cc
61	ac	ab	cd	bb
62	ac	ab	dd	bc
63	aa	bb	cd	bc
64	cc	ab	cd	cc
65	ac	aa	dd	bc
66	aa	ab	cd	bb
67	ac	aa	dd	bc
68	ac	ab	cd	bb
69	cc	ab	cd	cc
70	ac	ab	dd	bc
71	ac	ab	cd	cc
72	ac	ab	dd	bc
73	ac	bb	cc	bc
74	cc	bb	dd	cc

Site 12. Pecos River at Texas State Highway 290, 6.4 km E of Sheffield, Crockett-Terrell County line, Texas. 13 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	aa	ab	dd	bc
2	aa	ab	cd	bc
3	ac	aa	dd	bc
4	cc	bb	cd	bb
5	aa	ab	cd	bc
6	ac	bb	cd	bc
7	ac	ab	cd	bc
8	ac	bb	cc	bb
9	aa	aa	cd	cc
10	ac	bb	dd	bc
11	ac	ab	cd	bb
12	cc	ab	dd	bb
13	ac	ab	cd	cc
14	ac	aa	dd	cc
15	cc	ab	cd	bb
16	ac	bb	dd	bc
17	cc	bb	dd	bc
18	aa	ab	cd	bb
19	ac	bb	cd	bc
20	ac	bb	cc	bc
21	aa	aa	dd	cc
22	cc	ab	cd	cc
23	cc	ab	cd	cc
24	ac	aa	dd	bc
25	aa	aa	dd	bc
26	ac	aa	dd	bc
27	cc	bb	dd	bc
28	ac	ab	cd	bc
29	ac	ab	cd	bb
30	ac	aa	cd	cc
31	aa	ab	dd	cc
32	aa	aa	cc	bc
33	ac	ab	cd	bb
34	cc	bb	dd	bb
35	cc	bb	dd	bb
36	aa	bb	cd	bc
37	ac	ab	cd	bc
38	cc	ab	dd	cc
39	aa	aa	cc	bc
40	cc	bb	cd	cc
41	ac	aa	dd	bc
42	ac	aa	dd	bc
43	aa	bb	dd	bc

Site 12. Pecos River at Texas State Highway 290, 6.4 km E of Sheffield, Crockett-Terrell County line, Texas. 13 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
44	aa	aa	cd	cc
45	aa	bb	dd	cc
46	cc	ab	dd	cc
47	ac	bb	cd	cc
48	cc	aa	dd	cc
49	ac	bb	cd	bc
50	aa	ab	cd	cc
51	ac	ab	cd	cc
52	ac	bb	cd	bc
53	ac	ab	cd	bc
54	cc	bb	cd	bc
55	ac	ab	cd	bc
56	aa	aa	dd	cc
57	aa	bb	cd	bb
58	cc	ab	dd	cc
59	cc	ab	dd	cc
60	aa	aa	cd	bb
61	ac	ab	dd	bc
62	aa	bb	dd	cc
63	aa	aa	dd	bc
64	cc	ab	cd	cc
65	aa	ab	cd	bc
66	cc	aa	dd	bc
67	cc	bb	dd	bc
68	aa	bb	cd	bb
69	ac	bb	dd	bc
70	ac	ab	cd	cc
71	ac	aa	dd	bc
72	cc	ab	cd	bc
73	ac	ab	dd	bc
74	cc	bb	dd	cc
75	cc	bb	cc	bb
76	ac	aa	dd	bc
77	ac	ab	cd	bc
78	ac	ab	dd	bc
79	ac	ab	cd	bc
80	cc	ab	dd	bb
81	cc	bb	dd	cc
82	aa	bb	cd	cc

Site 13. Pecos River above the mouth of Independence Creek, Crockett-Terrell County line, Texas. 14 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	ac	bb	cc	bc
2	cc	bb	cc	bb
3	ac	aa	dd	cc
4	cc	ab	cd	cc
5	aa	ab	cd	bc
6	ac	aa	dd	bc
7	aa	bb	cd	bc
8	cc	aa	cc	cc
9	aa	bb	cd	bb
10	cc	aa	dd	bc
11	cc	bb	cd	bc
12	ac	bb	cc	bc
13	cc	ab	cd	bb
14	ac	ab	dd	bc
15	ac	ab	dd	cc
16	ac	ab	cd	cc
17	ac	bb	dd	bc
18	cc	ab	cd	cc
19	aa	ab	cd	cc
20	ac	ab	cc	bb
21	ac	aa	cd	cc
22	cc	ab	dd	cc
23	cc	ab	dd	bb
24	ac	ab	dd	bb
25	ac	ab	cd	cc
26	aa	bb	cd	bc
27	ac	bb	cd	bc
28	cc	aa	dd	bc
29	ac	ab	cd	bc
30	aa	ab	dd	cc
31	cc	ab	cd	cc
32	cc	ab	cd	cc
33	ac	ab	cd	bc
34	aa	ab	cd	cc
35	ac	ab	cd	bc
36	aa	aa	dd	bc
37	cc	ab	dd	cc
38	aa	ab	dd	cc
39	cc	ab	cd	bc
40	cc	ab	cd	bc

Site 13. Pecos River below the mouth of Independence Creek, Crockett-Terrell County line, Texas. 14 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	cc	bb	dd	cc
2	cc	bb	cc	bc
3	cc	bb	cd	bc
4	ac	ab	dd	bc
5	cc	ab	cd	cc
6	aa	ab	dd	cc
7	aa	ab	cd	bb
8	cc	bb	cc	cc
9	cc	aa	dd	bc
10	ac	bb	cd	bc
11	cc	bb	cd	cc
12	aa	ab	cd	bc
13	cc	ab	dd	bb

Site 14. Pecos River at Farm Road 2083, 10 km SW of Pandale, Val Verde County, Texas. 14 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	cc	bb	cd	bb
2	cc	bb	cd	bb
3	cc	aa	cc	bb
4	cc	ab	cd	cc
5	cc	bb	dd	bb
6	ac	aa	cd	cc
7	cc	bb	dd	cc
8	cc	ab	dd	bc
9	cc	ab	cd	bb
10	ac	bb	cd	bb
11	ac	bb	dd	bb
12	ac	ab	dd	bc
13	cc	ab	dd	cc
14	cc	bb	dd	cc
15	cc	ab	cd	bc
16	ac	ab	cd	bb
17	aa	bb	cc	bc
18	ac	bb	cc	bb
19	cc	bb	dd	bb
20	cc	bb	cd	cc
21	cc	bb	dd	bb
22	cc	aa	dd	bb
23	cc	bb	cd	bb
24	ac	bb	cd	bc
25	cc	bb	dd	bc
26	cc	ab	dd	bc
27	cc	bb	dd	bb
28	cc	ab	dd	bb
29	ac	bb	cd	bc
30	ac	bb	dd	bc
31	cc	ab	cd	bb
32	ac	ab	dd	bb
33	ac	ab	dd	cc
34	cc	ab	cd	bc
35	ac	ab	dd	bb
36	cc	bb	cd	bb
37	cc	ab	dd	bc
38	cc	aa	dd	bb
39	cc	ab	dd	bc
40	cc	bb	cd	bb
41	cc	bb	dd	bb
42	cc	ab	cd	bc
43	cc	ab	dd	bb
44	cc	bb	dd	bc

Site 14. Pecos River at Farm Road 2083, 10 km SW of Pandale, Val Verde County, Texas. 14 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	ac	ab	dd	bc
46	cc	ab	dd	bc
47	ac	bb	dd	bb
48	cc	bb	dd	bb
49	cc	bb	cd	bb
50	aa	bb	cd	bb

Site 2. Pecos River below Reeves County W.I.D. NO. 2 diversion dam (Brush Dam), 10 km SW of Mentone, Reeves-Ward County line, Texas. 20 August 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	cc	ab	cd	bb
2	cc	bb	cd	bb
3	ac	bb	cd	bb
4	ac	bb	cd	cc
5	ac	bb	cd	bb
6	cc	bb	cd	bb
7	cc	ab	cd	bc
8	cc	bb	cd	bb
9	ac	bb	cd	bc
10	cc	bb	cd	bb
11	cc	ab	dd	bb
12	cc	bb	cc	bb
13	ac	ab	dd	bb
14	cc	bb	cd	bb
15	cc	bb	dd	bb
16	ac	ab	cc	bb
17	cc	bb	cc	bb
18	cc	ab	cd	bb
19	ac	bb	cd	bc
20	cc	bb	cc	bb
21	ac	ab	cd	cc
22	ac	ab	dd	bc
23	cc	bb	dd	bb
24	aa	bb	cd	bb
25	cc	bb	cc	bb
26	ac	bb	cd	bb
27	cc	bb	cd	bb
28	ac	bb	cd	bb
29	cc	ab	cc	bc
30	ac	ab	cd	bc
31	ac	bb	cc	bb
32	cc	bb	cc	bb
33	ac	bb	cd	bb
34	cc	ab	cd	bc
35	cc	bb	cc	bb
36	ac	bb	dd	bb
37	cc	bb	cd	bc
38	cc	bb	cc	cc
39	cc	bb	cd	bb
40	cc	bb	cc	bc
41	cc	bb	cc	bb
42	ac	ab	cd	bb
43	cc	bb	cd	bb

Site 2. Pecos River below Reeves County W.I.D. NO. 2 diversion dam (Brush Dam), 10 km SW of Mentone, Reeves-Ward County line, Texas. 20 August 1988. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
44	cc	bb	cd	bb
45	ac	ab	dd	bc
46	ac	bb	cd	bc
47	cc	bb	cc	bb
48	ac	ab	dd	bc
49	ac	aa	dd	cc
50	ac	ab	dd	cc
51	cc	bb	cc	bb
52	cc	bb	cd	
53	ac	bb	cc	bb
54	ac	bb	cd	bb
55	ac	ab	dd	bb
56	aa	bb	cc	
57	cc	bb	cc	bb
58	cc	bb	cd	bc
59	cc	bb	cc	bb
60	cc	bb	cc	bc
61	cc	ab	cd	cc
62	cc	bb	cd	bc
63	cc	aa	cd	bb
64	cc	bb	cd	bc
65	cc	bb	cc	bc
66	cc	bb	cc	bb
67	cc	ab	dd	bb
68	ac	bb	cc	bb
69	cc	bb	cd	bb
70	ac	bb	dd	bc
71	cc	bb	cd	bb
72	cc	bb	cd	bb
73	cc	bb	cd	cc
74	cc	bb	cd	bb
75	cc	bb	cc	bb
76	cc	bb	cd	bb
77	cc	bb	dd	bc
78	cc	bb	cd	bb
79	cc	bb	cd	bb
80	cc	ab	cd	bb
81	cc	ab	dd	bc
82	cc	bb	cd	bb
83	cc	ab	cd	bb
84	cc	bb	cc	bb
85	ac	bb	cd	bc
86	cc	bb	cd	bb

Site 2. Pecos River below Reeves County W.I.D. NO. 2 diversion dam (Brush Dam), 10 km SW of Mentone, Reeves-Ward County line, Texas. 20 August 1988. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
87	cc	bb	cd	bb
88	cc	bb	cc	bb
89	cc	bb	dd	bb
90	aa	bb	cd	bb
91	cc	bb	cd	bb
92	cc	bb	cc	bb
93	cc	bb	cd	bb
94	cc	bb	cc	bb
95	cc	bb	cd	bc
96	ac	bb	dd	bb
97	cc	bb	cd	bb
98	cc	bb	cc	bb
99	cc	bb	dd	bb
100	cc	ab	cd	bb
101	cc	bb	cd	bb
102	cc	bb	cd	bb

Site 3. Pecos River at U. S. Highway 80, 1.5 km E of Pecos, Reeves-Ward County line, Texas. 20 August 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	cc	bb	dd	bb
2	cc	bb	cc	bc
3	ac	bb	cd	bb
4	cc	ab	dd	bb
5	cc	bb	dd	bc
6	cc	bb	cd	bb
7	cc	bb	cc	bb
8	cc	bb	cc	bc
9	ac	bb	cc	bb
10	cc	bb	cc	bb
11	ac	bb	cd	bb
12	cc	bb	cc	bb
13	cc	bb	cc	bb
14	ac	bb	cd	bc
15	cc	ab	dd	bc
16	cc	bb	cd	bb
17	cc	bb	cc	bc
18	cc	bb	cd	bb
19	cc	bb	cd	bb
20	cc	bb	cc	bb
21	cc	bb	dd	cc
22	cc	bb	cd	cc
23	cc	ab	cd	bb
24	cc	bb	cc	bb
25	cc	bb	cc	bb
26	cc	bb	cc	bb
27	ac	bb	cd	bc
28	ac	ab	dd	bb
29	cc	bb	cd	bb
30	cc	bb	cd	bc
31	cc	bb	dd	bb
32	cc	bb	cd	bb
33	ac	ab	cc	bc
34	cc	bb	cc	bb
35	cc	bb	cd	bc
36	cc	ab	cd	bc
37	cc	ab	cd	bb
38	ac	ab	cd	bc
39	cc	ab	cd	bb
40	cc	bb	cd	bb
41	cc	bb	dd	bb
42	cc	bb	cd	bc
43	ac	bb	dd	cc
44	cc	bb	cc	bb

Site 3. Pecos River at U. S. Highway 80, 1.5 km E of Pecos, Reeves-Ward County line, Texas. 20 August 1988. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	ac	bb	dd	bb
46	cc	bb	cd	bb
47	cc	bb	cd	bb
48	cc	bb	cc	bb
49	ac	bb	cc	bb
50	cc	bb	cd	bb
51	cc	ab	cd	bb
52	cc	bb	cd	bb
53	ac	bb	cc	bb
54	cc	bb	cc	bb
55	cc	bb	cd	bc
56	cc	bb	cc	bb
57	cc	ab	cd	bb
58	cc	bb	cd	bb
59	ac	bb	dd	bb
60	cc	bb	dd	bb
61	aa	bb	cd	bb
62	aa	bb	cd	bb
63	aa	bb	cc	bb
64	ac	ab	cd	bb
65	aa	bb	cc	bb

Site 7. Pecos River at Texas Farm Road 11, 5 km NW of Imperial, Crane-Pecos County line, Texas. 20 August 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	aa	bb	cd	cc
2	cc	ab	dd	cc
3	cc	ab	dd	cc
4	ac	ab	cd	cc
5	cc	bb	cd	cc
6	aa	bb	cd	cc
7	cc	ab	cd	cc
8	cc	bb	cd	bb
9	cc	ab	cc	bb
10	ac	bb	cd	bc
11	cc	bb	cd	cc
12	aa	aa	cd	cc
13	ac	aa	dd	bc
14	cc	bb	cd	cc
15	aa	bb	cc	bb
16	cc	ab	cc	bc
17	ac	bb	cc	cc
18	cc	bb	dd	bc
19	aa	bb	ce	bc
20	aa	bb	dd	bc
21	ac	bb	cd	bc
22	ac	ab	cd	bb
23	ac		dd	bb
24	aa	bb	cc	bb
25	cc	ab	cc	bc
26	aa	ab	cd	cc
27		bb	dd	bc
28	ac	ab	cc	cc
29	ac	ab	cc	cc
30	cc	bb	cd	bb
31	cc	ab	cd	bc
32	ac	bb	cd	cc
33	aa	bb	cc	cc
34	aa	ab	cd	bc
35	cc	bb	dd	bc
36	cc	bb	cd	bb
37	cc	ab	cd	bc
38	ac	aa	cd	bc
39	ac	ab	dd	
40	cc	ab	cc	

Site 8. Horsehead Crossing 6.4 km off Texas Farm Road 11, 23 km NW of Girvin, Crane-Pecos County line, Texas. 20 August 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	ac	bb	cd	bb
2	ac	ab	dd	bc
3	ac	ab	cd	bb
4	ac	ab	cd	bc
5	cc	ab	cd	bc
6	ac	bb	cc	bc
7	ac	ab	dd	bc
8	aa	bb	dd	bb
9	aa	bb	cd	cc
10	ac	ab	dd	bc
11	cc	ab	cd	bc
12	aa	ab	cd	cc
13	aa	aa	dd	cc
14	ac	aa	dd	bc
15	cc	ab	cd	bb
16	aa	aa	dd	bc
17	ac	bb	cc	bb
18	ac	ab	cd	cc
19	ac	ab	dd	cc
20	aa	bb	cc	bb
21	cc	bb	cc	cc
22	aa	ab	dd	cc
23	ac	bb	cc	bb
24	ac	aa	dd	cc
25	cc	ab	dd	bc
26	aa	ab	dd	cc
27	cc	ab	cd	bc
28	ac	ab	dd	bb
29	aa	bb	cd	bb
30	ac	bb	cd	cc
31	cc	bb	cd	bb
32	ac	ab	cd	bb
33	aa	ab	cd	bc
34	ac	bb	cc	bb
35	ac	ab	cd	bc
36	aa	aa	dd	bc
37	aa	bb	cd	bb
38		bb	cc	cc
39		ab	cd	bb
40	aa	bb	cd	bb
41	aa	ab	cd	bb
42	ac	bb	cc	bb
43	aa	bb	cd	bb

Site 8. Horsehead Crossing 6.4 km off Texas Farm Road 11, 23 km NW of Girvin, Crane-Pecos County line, Texas. 20 August 1988. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
44	cc	ab	cd	bb
45	ac	bb	cc	cc
46	ac	aa	dd	cc
47	ac	ab	cd	bc
48	aa	ab	cd	bc
49	ac	ab	cd	cc
50	ac	bb	cd	bc
51	cc	ab	cd	bb
52	ac	ab	dd	bc
53	ac	ab	cd	cc
54	cc	bb	cd	bc
55	aa	ab	dd	bc
56	cc	ab	cd	bc
57	aa	bb	cc	bc
58	ac	bb	cd	cc
59	cc	bb	cd	bc
60	ac	bb	cc	bb
61	aa	bb	dd	cc
62	ac	ab	cd	bc
63	cc	bb	dd	bc
64	ac	bb	cc	cc
65	ac	bb	cd	bc
66	cc	bb	dd	bc
67	aa	bb	cd	bc
68	aa	bb	cd	bc
69	ac	bb	cc	bc
70	ac	ab	cd	bc
71	ac	bb	dd	bc
72	aa	ab	cd	cc
73	cc	ab	dd	bc
74	cc	ab	dd	bc
75	cc	ab	dd	bc
76	ac	bb	cc	cc
77	cc	ab	dd	bb
78	aa	bb	cc	cc
79	cc	bb	cd	cc
80	cc	ab	dd	cc
81	cc	bb	cc	cc
82	ac	ab	cd	bc
83	cc	ab	dd	cc
84	aa	ab	dd	cc
85	aa	ab	dd	cc
86	aa	ab	cd	cc

Site 8. Horsehead Crossing 6.4 km off Texas Farm Road 11, 23 km NW of Girvin, Crane-Pecos County line, Texas. 20 August 1988. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
87	cc	ab	cd	cc
88	aa	bb	cc	bc
89	ac	ab	cc	bc
90	aa	ab	cd	cc
91	ac	ab	cc	cc
92	ac	bb	cc	bb
93	cc	ab	cd	cc
94	cc	bb	cd	bc
95	cc	bb	cd	bb
96	ac	aa	dd	cc
97	ac	ab	cd	bc
98		bb	cc	bb
99	cc	aa	dd	bc
100	ac	ab	cd	cc

Site 9. Pecos River at Texas Farm Road 1901, 12 km SW of McCamey, Crockett-Pecos County line, Texas. 20 August 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	ac	bb	cd	bc
2	ac	bb	cd	cc
3	cc	bb	cd	bc
4	aa	bb	cc	bc
5	ac	ab	dd	cc
6	ac	ab	cd	bb
7	ac	aa	dd	bc
8	ac	bb	cd	bc
9	ac	ab	dd	bb
10	ac	bb	cc	cc
11	cc	ab	dd	bc
12	ac	bb	cc	bb
13	ac	bb	cc	bc
14	aa	ab	cc	bc
15	cc	aa	dd	bb
16	ac	ab	cd	cc
17	ac	bb	de	cc
18	ac	ab	cd	bb
19	cc	ab	dd	bb
20	ac	bb	cc	cc
21		aa	dd	bb
22	ac	ab	dd	bb
23	ac	aa	dd	bb
24	ac	ab	cd	bb
25	aa	ab	dd	bc
26	aa	aa	cd	cc
27	ac	ab	dd	bb
28	cc	ab	dd	bb
29	cc	ab	dd	cc
30	cc	bb	cc	cc
31	ac	ab	cd	bb
32	aa	bb	dd	cc
33	ac	ab	cd	bc
34	aa	ab	cd	bb
35	ac	bb	cc	bb
36	ac	aa	dd	bc
37	ac	ab	cd	bc
38	ac	aa	dd	bc
39	ac	aa	dd	bc
40	cc	bb	cd	bb
41	aa	bb	cd	bc
42	ac	bb	cc	bc
43	cc	bb	cd	bb
44	aa	ab	cc	bc

Site 9. Pecos River at Texas Farm Road 1901, 12 km SW of McCamey, Crockett-Pecos County line, Texas. 20 August 1988. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	cc	ab	dd	bb
46	aa	ab	dd	bc
47	cc	bb	cd	cc
48	aa	bb	dd	
49	ac	bb	cc	bc
50	ac	ab	cd	cc
51	cc	bb	cc	bc
52	ac	ab	cc	bc

Site 11. Pecos River at Texas State Highway 349, 6 km NW of Iraan, Pecos-Crockett County line, Texas. 20 August 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	ac	bb	dd	
2	ac	ab	dd	
3	ac	ab	cd	bb
4	aa	ab	cd	bc
5	aa	bb	cc	cc
6	cc	bb	cd	cc
7	ac	aa	dd	cc
8	ac	bb	cd	bc
9	aa	bb	cc	cc
10	ac	ab	cd	bc
11	aa	ab	dd	cc
12	aa	ab	cd	bb
13	ac	ab	dd	bc
14	cc	bb	dd	bb
15	ac	bb	dd	
16	ac	ab	cd	
17	ac	aa	dd	bc
18	ac	bb	cd	bc
19	ac	ab	cc	bb
20	cc	ab	dd	bc
21	ac	bb	cd	bc
22	ac	bb	cc	cc
23	ac	aa	cc	bb
24	ac	ab	cd	cc
25	ac	ab	dd	cc
26	aa	ab	cd	bc
27	aa	ab	cd	bb
28	ac	bb	cd	bc
29	cc	ab	cd	bc
30	cc	bb	cd	bc
31	ac	ab	dd	bb
32	aa	bb	cd	cc
33	cc	bb	dd	bc
34	cc	bb	cd	bb
35	aa	bb	cd	cc
36	ac	bb	cc	bc
37	cc	aa	cd	cc
38	aa	ab	dd	cc
39	ac	bb	cd	bb
40	ac	aa	dd	bc
41	ac	aa	cd	cc
42	aa	ab	cd	bc
43	aa	bb	cd	bc
44	cc	ab	cd	cc

Site 11. Pecos River at Texas State Highway 349, 6 km NW of Iraan, Pecos-Crockett County line, Texas. 20 August 1988. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	cc	bb	dd	bb
46	cc	ab	cd	bb
47	ac	ab	dd	cc
48	aa	bb	cd	cc
49	aa	ab	cd	cc
50	cc	bb	dd	bc
51	aa	ab	cd	bb
52	cc	ab	cd	bc
53	cc	ab	dd	cc
54	aa	bb	dd	cc
55	cc	aa	dd	bc
56	aa	ab	dd	bb
57	ac	ab	cd	cc
58	cc	bb	cc	bc
59	ac	ab	dd	bb
60	aa	ab	dd	bc
61	ac	ab	dd	bb
62	cc	aa	cd	bc
63	aa	ab	cd	bc
64	ac	bb	cc	cc
65	aa	ab	cc	cc
66	cc	bb	cd	bb
67	aa	ab	cd	bc
68	cc	bb	cd	bc
69	ac	aa	dd	bb
70	ac	bb	cc	cc
71	cc	bb	dd	bb
72	ac	ab	cd	bb
73	ac	aa	dd	bc
74	aa	ab	cd	bc
75	cc	bb	cd	bc
76	aa	ab	cd	bc
77	cc	ab		cc
78	ac	aa	dd	bc
79	ac	bb	cd	cc
80	cc	aa	cc	bc
81	aa	aa	cc	cc
82	ac	ab	cd	bb
83	ac	aa	dd	bc
84	ac	ab	dd	bb
85	ac	ab	cd	bb
86	cc	bb	cc	bb
87	ac	ab	dd	cc

Site 11. Pecos River at Texas State Highway 349, 6 km NW of Iraan, Pecos-Crockett County line, Texas. 20 August 1988. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
88	cc	ab	cd	bc
89	aa	aa	cc	bc
90	aa	ab	dd	cc
91	aa	ab	cd	bc
92	ac	bb	cc	bc
93	cc	bb	dd	bb
94	ac	bb	cc	bc
95	cc	ab	dd	cc
96	cc	bb	cc	bc
97	ac	aa	cd	bb
98	cc	ab	cd	bb
99	cc	ab	cd	bc
100	aa	aa	dd	bb
101	aa	ab	cd	bc
102	cc	aa	dd	bb

Site P1. Pecos River 8 km E, 4 km S of Malaga, Eddy County, New Mexico. 1987.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	aa	aa	dd	cc
2	aa	aa	dd	cc
3	aa	aa	de	cc
4	aa	aa	de	cc
5	aa	aa	dd	cc
6	aa	aa	dd	cc
7	aa	aa	dd	cc
8	aa	aa	dd	cc
9	aa	aa	dd	cc
10	aa	aa	dd	cc
11	aa	aa	dd	cc
12	aa	aa	de	cc
13	aa	aa	dd	cc
14	aa	aa	dd	cc
15	aa	aa	dd	cc
16	aa	aa	dd	cc
17	aa	aa	dd	cc
18	aa	aa	dd	cc
19	aa	aa	dd	cc
20	aa	aa	dd	cc
21	aa	aa	dd	cc
22	aa	aa	dd	cc
23	aa	aa	dd	cc
24	aa	aa	dd	cc
25	aa	aa	dd	cc
26	aa	aa	de	cc
27	aa	aa	dd	cc
28	aa	aa	de	cc
29	aa	aa	dd	cc
30	aa	aa	dd	cc
31	aa	aa	dd	cc
32	aa	aa	dd	cc
33	aa	aa	dd	cc
34	aa	aa	dd	cc
35	aa	aa	dd	cc
36	aa	aa	de	cc

Site P2. Red Bluff Reservoir on east shore, 2 km N of stateline, Eddy County, New Mexico. 9 September 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	cc	aa	dd	bc
2	aa	aa	dd	bc
3	aa	ab	cd	bb
4	ac	bb	cd	bc
5	aa	bb	cd	cc
6	ac	ab	de	bc
7	aa	aa	dd	bc
8	cc	ab	cd	cc
9	cc	ab	dd	cc
10	ac	ab	cd	cc
11	aa	ab	cc	cc
12	aa	aa	dd	cc
13	ac	ab	cd	bb
14	cc	ab	cd	cc
15	aa	ab	cd	bc
16	aa	aa	dd	bc
17	ac	ab	dd	bc
18	cc	ab	dd	bb
19	aa	ab	cd	cc
20	ac	aa	dd	bc
21	ac	aa	dd	bc
22	aa	aa	cd	bc
23	aa	ab	cc	bb
24	cc	ab	cd	bc
25	aa	ab	dd	bc
26	ac	ab	dd	bb
27	cc	ab	cd	bc
28	aa	ab	cd	bc
29	ac	aa	dd	bc
30	ac	ab	ce	bb
31	ac	bb	cc	cc
32	ac	ab	dd	bb
33	ac	aa	dd	bc

Site P3. Red Bluff Reservoir on east shore near boat ramp, Loving County line, Texas. 11 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	ac	ab	dd	bc
2	ac	ab	cd	cc
3	cc	ab	dd	cc
4	aa	ab	dd	cc
5	ac	ab	dd	bc
6	ac	ab	dd	bc
7	ac	ab	dd	cc
8	aa	aa	dd	cc
9	aa	ab	cd	bc
10	ac	aa	cd	cc
11	aa	aa	dd	cc
12	aa	aa	cd	cc
13	ac	bb	de	cc
14	aa	ab	dd	cc
15	aa	ab	dd	bc
16	aa	ab	cd	bc
17	aa	ab	dd	cc
18	ac	ab	dd	bc
19	aa	aa	dd	cc
20	ac	aa	dd	cc
21	aa	ab	cd	bc
22	ac	bb	dd	cc
23	ac	ab	cd	cc
24	ac	aa	dd	bc
25	ac	ab	cd	bc
26	aa	ab	cc	bc
27	ac	aa	dd	cc
28	aa	ab	cc	cc
29	aa	ab	dd	cc
30	ac	ab	dd	bc
31	aa	aa	df	cc
32	aa	ab	cd	bc
33	aa	ab	dd	bc
34	aa	aa	dd	cc
35	ac	aa	dd	bc
36	aa	aa	dd	cc
37	aa	aa	dd	bb
38	ac	ab	cd	bb
39	ac	ab	dd	bc
40	ac	aa	cd	cc
41	cc	ab	cd	cc
42	aa	ab	cd	cc
43	aa	ab	cd	bc
44	aa	aa	dd	cc

Site P3. Red Bluff Reservoir on east shore near boat ramp, Loving County line, Texas. 11 August 1986. (Continued.)

ID	Adh-1	Est-1	Gpi-a	Pdp-a
45	aa	aa	dd	cc
46	ac	aa	dd	cc
47	aa	ab	cd	cc
48	aa	ab	dd	bc
49	ac	ab	dd	bc
50	aa	ab	de	cc
51	aa	aa	dd	cc
52	aa	ab	dd	bb
53	ac	aa	dd	cc
54	aa	aa	dd	cc
55	aa	aa	dd	cc
56	aa	ab	dd	cc
57	cc	ab	cd	cc
58	ac	ab	cd	cc
59	aa	ab	ce	cc
60	ac	ab	de	bc
61	aa	aa	dd	cc
62	ac	ab	dd	bc
63	ac	ab	cd	cc
64	aa	aa	dd	cc
65	aa	aa	dd	cc
66	cc	ab	cd	bc
67	aa	aa	de	cc
68	ac	ab	cd	bc
69	ac	ab	dd	cc

Site P4. Salt Creek below waterfalls, 2.4 km upstream from the Pecos River, Reeves County, Texas. 9 June 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	aa	ab	cd	cc
2	aa	ab	dd	cc
3	aa	aa	dd	bc
4	aa	aa	dd	cc
5	aa	aa	dd	bc
6	aa	ab	cd	bb
7	cc	aa	dd	cc
8	aa	aa	dd	cc
9	ac	aa	dd	cc
10	ac	aa	dd	cc
11	ac	ab	dd	bc
12	aa	aa	dd	cc
13	ac	aa	dd	cc
14	aa	aa	dd	cc
15	aa	aa	dd	cc
16	aa	aa	dd	cc
17	aa	aa	dd	cc
18	aa	aa	dd	cc
19	aa	aa	dd	cc
20	aa	aa	dd	cc
21	aa	aa	dd	cc
22	aa	aa	dd	bc
23	aa	ab	cd	cc

Site P4. Salt Creek below waterfalls, 2.4 km upstream from the Pecos River, Reeves County, Texas. 20 August 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	aa	aa	dd	cc
2	aa	aa	dd	cc
3	aa	aa	dd	cc
4	aa	aa	dd	cc
5	aa	aa	dd	cc
6	aa	aa	dd	cc
7	aa	aa	dd	cc
8	ac	ab	dd	cc
9	aa	ab	cd	bc
10	aa	ab	dd	bc
11	aa	aa	de	cc
12	ac	aa	dd	bc
13	aa	aa	dd	cc
14	aa	aa	de	cc
15	aa	ab	cd	bc
16	aa	aa	dd	cc
17	aa	ab	cd	bc
18	aa	aa	dd	cc
19	aa	aa	dd	cc
20	aa	aa	dd	cc
21	aa	aa	dd	cc
22	aa	aa	dd	cc
23	aa	aa	dd	cc
24	ac	aa	dd	cc
25	aa	aa	dd	cc
26	aa	ab	cd	bc
27	aa	aa	dd	cc
28	aa	aa	dd	cc
29	aa	aa	dd	cc
30	ac	aa	dd	cc

Site P5. Salt Creek at low water bridge on U. S. Highway 285, Reeves County, Texas. 9 June 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	aa	aa	dd	cc
2	aa	aa	de	cc
3	aa	aa	dd	cc
4	aa	aa	dd	cc
5	aa	aa	dd	cc
6	aa	aa	dd	cc
7	aa	aa	dd	cc
8	aa	aa	dd	cc
9	ac	ab	dd	cc
10	aa	aa	dd	cc
11	aa	aa	dd	cc
12	aa	aa	dd	cc
13	aa	aa	dd	cc
14	aa	aa	dd	cc
15	aa	aa	dd	cc
16	aa	aa	dd	cc
17	aa	aa	dd	cc
18	aa	aa	dd	cc
19	aa	aa	dd	cc
20	aa	aa	dd	cc
21	aa	aa	dd	cc
22	aa	aa	dd	cc
23	aa	aa	dd	cc
24	aa	aa	de	cc

Site P6. Salt Creek 0.5 km below the Red Bluff Reservoir spillway, Reeves County, Texas. 20 August 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	aa	aa	dd	cc
2	aa	aa	dd	cc
3	aa	aa	dd	cc
4	aa	aa	dd	cc
5	aa	aa	dd	cc
6	aa	aa	dd	cc
7	aa	aa	dd	cc
8	aa	aa	dd	cc
9	aa	aa	dd	cc
10	aa	ab	dd	bc
11	aa	aa	dd	cc
12	aa	aa	dd	cc
13	aa	aa	dd	cc
14	aa	aa	dd	cc
15	aa	aa	dd	cc
16	aa	aa	dd	cc
17	aa	aa	dd	cc
18	aa	aa	dd	cc
19	aa	aa	dd	cc
20	aa	aa	dd	cc
21	aa	aa	dd	cc
22	aa	aa	dd	cc
23	aa	aa	dd	cc
24	aa	aa	dd	cc
25	aa	aa	cd	cc
26	aa	aa	dd	cc
27	aa	aa	dd	cc
28	aa	aa	dd	cc
29	aa	aa	dd	cc
30	aa	aa	dd	cc

Site P7. Salt Creek at Texas Farm Road 652, 9 km W of Orla, Reeves County, Texas. 8 September 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	aa	aa	dd	cc
2	aa	aa	dd	cc
3	aa	aa	dd	cc
4	aa	aa	dd	cc
5	aa	aa	dd	cc
6	aa	aa	dd	cc
7	aa	aa	dd	cc
8	aa	aa	dd	cc
9	aa	aa	dd	cc
10	aa	aa	dd	cc
11	aa	aa	dd	cc
12	aa	aa	dd	cc
13	aa	aa	dd	cc
14	aa	aa	dd	cc
15	aa	aa	dd	cc
16	aa	aa	dd	cc
17	aa	aa	dd	cc
18	aa	aa	dd	cc
19	aa	aa	dd	cc
20	aa	aa	dd	cc
21	aa	aa	dd	cc
22	aa	aa	dd	cc
23	aa	aa	dd	cc
24	aa	aa	dd	cc
25	aa	aa	dd	cc
26	aa	aa	dd	cc
27	aa	aa	dd	cc
28	aa	aa	ee	cc
29	aa	aa	dd	cc
30	aa	aa	dd	cc

Site P8. Irrigation canal below Reeves County W.I.D. NO. 2 diversion dam (Brush Dam), 10 km SW of Mentone, Reeves County, Texas. 20 August 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	ac	ab	cd	bb
2	ac	ab	cc	bc
3	ac	ab	dd	cc
4	ac	ab	cd	bc
5	cc	ab	dd	bc
6	cc	ab	cd	cc
7	aa	bb	dd	cc
8	aa	bb	dd	cc
9	aa	bb	cd	cc
10	ac	ab	dd	cc
11	cc	ab	dd	bc
12	ac	bb	cc	bb
13	cc	ab	cd	bc
14	cc	ab	cd	cc
15	cc	ab	dd	bb
16	ac	aa	dd	cc
17	cc	ab	dd	bc
18	aa	ab	dd	bc
19	ac	ab	dd	bb
20	ac	ab	cd	bb
21	ac	bb	cd	cc
22	cc	ab	dd	cc
23	cc	aa	dd	cc
24	ac	bb	cd	bc
25	cc	ab	dd	cc
26	aa	ab	dd	bb
27	ac	aa	dd	bc
28	aa	ab	cd	bb
29	ac	ab	cd	bc
30	ac	bb	cd	cc

Site P9. Porter's Gravel Company pit 6 km W of Grandfalls, Ward County, Texas. 28 July 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	cc	bb	cd	cc
2	cc	bb	cd	bc
3	ac	bb	cc	bb
4	cc	bb	cd	bb
5	ac	bb	cc	bc
6	cc	bb	cc	cc
7	cc	bb	cd	bb
8	cc	bb	cd	bc
9	cc	bb	cd	bc
10	cc	bb	cc	bc
11	cc	bb	cc	bc
12	cc	bb	cc	bb
13	cc	bb	cd	bb
14	cc	bb	cd	bc
15	cc	bb	cc	bc
16	cc	bb	cc	bb
17	cc	bb	cc	bc
18	cc	bb	cd	bc
19	cc	bb	cc	bc
20	cc	bb	cd	bc
21	cc	bb	cc	bc
22	aa	bb	dd	bc
23	cc	bb	cd	bc
24	cc	bb	cd	bc
25	cc	bb	cd	bc
26	cc	bb	cc	bc
27	cc	bb	cd	bc
28	cc	bb	dd	bc
29	cc	bb	cc	bc
30	ac	bb	cc	bc

Site P10. Phipp's Gravel Company pits, 6 km SW of Grandfalls, Ward County, Texas. 10 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	aa	aa	dd	bc
2	aa	aa	dd	cc
3	aa	ab	dd	bc
4	aa	aa	dd	cc
5	aa	aa	dd	cc
6	aa	ab	dd	bc
7	aa	ab	dd	bc
8	aa	ab	dd	cc
9	aa	aa	dd	cc
10	aa	aa	dd	cc
11	aa	aa	dd	bc
12	aa	aa	dd	cc
13	aa	aa	dd	cc
14	aa	ab	dd	bc
15	aa	aa	dd	cc
16	aa	aa	dd	cc
17	aa	aa	dd	cc
18	aa	aa	dd	cc
19	aa	aa	dd	cc
20	aa	aa	dd	cc
21	aa	aa	dd	cc
22	aa	aa	dd	cc
23	aa	aa	dd	cc
24	aa	aa	dd	cc
25	aa	ab	dd	cc
26	aa	aa	dd	cc
27	aa	aa	dd	cc
28	aa	aa	dd	cc
29	aa	aa	dd	cc
30	aa	aa	dd	cc

Site P10. Phipp's Gravel Company pits, 6 km SW of Grandfalls, Ward County, Texas. 20 August 1988.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	aa	aa	dd	cc
2	aa	aa	dd	cc
3	aa	aa	dd	cc
4	aa	aa	dd	bc
5	aa	aa	dd	cc
6	aa	aa	dd	cc
7	aa	aa	dd	cc
8	aa	aa	dd	cc
9	aa	aa	dd	cc
10	aa	aa	dd	cc
11	aa	aa	dd	cc
12	aa	aa	dd	cc
13	aa	aa	dd	cc
14	aa	aa	dd	cc
15	aa	aa	dd	cc
16	aa	aa	dd	cc
17	aa	aa	dd	cc
18	aa	aa	dd	cc
19	aa	aa	dd	bc
20	aa	aa	dd	cc
21	aa	aa	dd	cc
22	aa	aa	dd	cc
23	aa	aa	dd	cc
24	aa	aa	dd	cc
25	aa	aa	dd	cc
26	aa	aa	dd	cc
27	aa	aa	dd	cc
28	aa	aa	dd	cc
29	aa	aa	dd	cc
30	aa	aa	dd	cc

Site P11. West shore of Imperial Reservoir, 13.4 km W of Imperial, Pecos County, Texas. 13 August 1986.

ID	Adh-1	Est-1	Gpi-a	Pdp-a
1	ac	bb	dd	bb
2	ac	bb	cd	bb
3	ac	bb	cd	bb
4	cc	bb	cc	bb
5	ac	bb	cc	bc
6	cc	bb	dd	bc
7	cc	aa	cd	bb
8	cc	bb	dd	bc
9	cc	aa	cc	bb
10	ac	bb	cd	bb
11	ac	bb	cd	bb
12	cc	bb	dd	bc
13	ac	bb	dd	bb
14	cc	bb	cd	bb
15	cc	ab	dd	bb
16	aa	bb	cd	bc
17	cc	bb	cc	cc
18	cc	ab	cd	bb
19	cc	bb	cd	bb
20	ac	ab	cd	bc
21	ac	bb	cc	bb
22	cc	bb	cd	bb
23	cc	bb	cd	bb
24	cc	bb	cd	bb
25	ac	bb	cd	bb
26	cc	ab	cc	bc
27	cc	bb	cd	bb
28	ac	bb	cc	cc
29	cc	bb	cd	bb
30	cc	ab	dd	bc
31	cc	aa	cd	bb
32	cc	bb	cd	bb
33	cc	bb	cd	bc
34	ac	bb	cc	bc
35	cc	bb	cd	bb
36	ac	bb	cc	bb

VITA 2

Gene R. Wilde

Candidate for the Degree of

Doctor of Philosophy

Dissertation: SPATIAL AND TEMPORAL PATTERNS IN THE COVARIANCE OF GENETIC AND MORPHOLOGIC CHARACTERS IN A PUPFISH HYBRID SWARM

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Minor Field: Statistics

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Professional Experience: Undergraduate Research Assistant, Department of Biological Sciences, University of Nevada, Las Vegas, September, 1976, to May, 1978; Research Assistant, Department of Zoology, University of Oklahoma, July, 1978, to December, 1979; Research Assistant, Department of Biological Sciences, University of Nevada, Las Vegas, January, 1980, to May, 1983; Field Technician, Strobeck and Associates, Inc., Las Vegas, Nevada, September, 1983, to January, 1985; Scientist, Lockheed Engineering Management Services, Company, Las Vegas, Nevada, from February, 1985, to July, 1985; Teaching Assistant, Department of Zoology, Oklahoma State University, from August, 1985, to August, 1988; Research Associate, Lake Mead Limnological Research Center, University of Nevada, Las Vegas, from April, 1989,to May, 1990; Fishery Analyst, Texas Parks and Wildlife Department, Austin, Texas, from May 1990 to May 1994.

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