TEXAS FRESHWATER FISH ASSEMBLAGES FOLLOWING THREE DECADES OF ENVIRONMENTAL CHANGE

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ABSTRACT—In 1953, C. Hubbs and colleagues surveyed fishes from a large number and variety of freshwater habitats throughout the state of Texas. Thirty-three years later, he replicated sampling at 129 of these sites within the Red, Sabine, Neches, Trinity, Brazos, Colorado, Guadalupe, San Antonio, Nueces, and Rio Grande drainages. Care was taken to match original sampling effort, times, and dates at each location. Relative proportional abundances of families showed numerous changes from 1953 to 1986 within the ten basins. Mantel tests comparing family abundances in 1953 and 1986 datasets showed little overall change statewide. Sites in the eastern half of the state that did not contain marine species showed less significant positive covariation between early and recent datasets than those in western Texas. Rank plots of species diversity (H') for the two regions of the state showed a consistent trend of decreased diversity over time in eastern Texas. A similar plot for west Texas showed decreased diversity on a local scale, but also reveal relative stability in statewide and regional ichthyofaunas. Despite the encouraging large-scale trends, several Texas fishes went extinct and others are threatened as a result of local habitat disturbances, including alteration of instream flow, eutrophication, and exotic species introductions.

Long-term ecological studies enhance our understanding of large-scale processes and anthropogenic changes. Much can be gained by examining different spatial scales, and similarly, a temporal context is requisite to understanding transient ecological phenomena (Tilman, 1989; Magnuson, 1990; Levin, 1992). Comparative studies that encompass long time intervals are few, and data for such studies usually must be reconstructed from historic records. Historic ecological data are available, but collectors' notes can be missing or cryptic, and sampling efforts may be impossible to duplicate. Previous studies have compared old collections to recent ones, but these were relatively limited in geographic or temporal scale (Moyle and Vondracek, 1985; Rutherford et al., 1987; Matthews et al., 1988; Grossman et al., 1990; Weaver and Garman, 1994).

Clark Hubbs, with colleagues and graduate students, collected in numerous freshwater habitats in Texas during 1953. Thirty-three years later, Hubbs repeated his collecting efforts at most of those sites. Hubbs observed numerous habitat changes, and this study utilizes his early (1953) and recent (1986) datasets to explore the extent that these changes have coincided with changes in fish populations and faunas. The major strength of this study is that the same individual conducted the sampling efforts in both the early and recent collections, so that site revisitation and catch per unit effort were relatively uniform between early and recent surveys. Similar studies that have examined sites over long periods of time have generally not had the same individual performing the field sampling.

Texas has a diverse freshwater fish fauna, with 247 nominal species in 45 families. Five species have become extinct and three have been extirpated; these comprise over 5% of the non-estuarine native ichthyofauna (Hubbs et al., 1991). Approximately 20% of the native fishes are in need of conservation efforts, mostly due to human activities (Hubbs et al., 1991). Based on the fact that several native fish species have either become



FIG. 1—Map of Texas indicating approximate locations of collection sites (one dot may represent more than one site).

extinct or extirpated, we hypothesized a priori that the 1986 Texas data set would show large faunal changes.

MATERIALS AND METHODS-Hubbs and colleagues collected in 129 sites throughout (and bordering) Texas in 1953 (Fig. 1). These sites covered a diverse array of freshwater stream habitats in different river drainages across the southeastern two-thirds of the state. Fish were collected by 1.8 m and 3 m seines, 7.6 m bag seine, and push nets; repeated seine hauls were made at a site until no new species were captured. Seining time averaged about one hour per site and ranged from 0.5 to 2 hours. Larger fishes were identified and counted in the field, and smaller fishes were preserved and identified in the laboratory. In 1986, the sites were revisited, and care was taken to duplicate Julian date, time of day, and total collecting effort (number of collectors and sampling gear). All sampling was done with the goal of surveying the local ichthyofauna and not of collecting one particular species. A total of 69,844 individual specimens representing 153 species and at least 21 families was captured in the combined early and recent collections.

Collection samples were used to compute relative abundances of species and families per site. Sampling effort (number of collectors and gear) did not change between 1953 and 1986, but the amount of time collecting per site may have varied because the end time was determined by the absence of new species in the seine haul. We thus chose to use relative proportions for our analyses. For analyses of family proportions, marine species were combined as one group. Sites were classified, by drainage, as being in either the eastern or western half of the state based on a watershed map of Texas (Wurbs, 1985). The Red, Sabine, Neches, Trinity, and Brazos drainages were classified as east, and the Colorado, Guadalupe, Nueces, San Antonio, and Rio Grande drainages as west. Histograms of relative proportions for families were plotted, and Chisquare tests for homogeneity of proportions were made for the entire state, regions (east and west), and individual river drainages.

We performed Mantel tests (Mantel, 1967; Sokal, 1979; Douglas and Endler, 1982) comparing similarity matrices of between-site family proportions, and computed individual site changes between early (1953) and recent (1986) collections, using NTSYS-pc (Rohlf, 1993). Horn's (1966) modification of the Morisita in-

Family	Texas		Ea	ast	West		
	1953	1986	1953	1986	1953	1986	
Amiidae							
Anguillidae					< 0.001		
Aphredoderidae		0.003		0.005			
Atherinidae		0.125		0.203	0.004	0.032	
Catostomidae		0.003		0.002	0.006	0.003	
Centrarchidae		0.119		0.125	0.131	0.111	
Characidae		0.003			0.019	0.007	
Cichlidae		0.007			0.012	0.014	
Clupeidae		0.039	0.034	0.070	0.014	0.001	
Cyprinidae		0.364	0.454	0.302	0.473	0.439	
Cyprinodontidae		0.002	0.009	< 0.001	0.033	0.003	
Elassomatidae		0.004	0.008	0.007			
Esocidae		0.001	0.010	0.001			
Fundulidae		0.018	0.040	0.030	0.009	0.002	
Ictaluridae		0.014	0.062	0.019	0.020	0.009	
Lepisosteidae		0.002	0.003	0.003	0.001	< 0.001	
Marine families		0.059	0.013	0.050	0.003	0.069	
Moronidae		0.001	0.001	0.002		< 0.001	
Percidae		0.047	0.110	0.038	0.144	0.058	
Petromyzontidae		0.001	0.001	0.001			
Poeciliidae		0.190	0.061	0.140	0.132	0.250	
Sciaenidae		0.001	0.004	0.002			

TABLE 1—Proportional abundances of families for the entire state, eastern, and western regions (blanks indicate zero). Ameiuridae was included with Ictaluridae.

dex (C_{λ}), which has an upper limit of unity, was used as a similarity index. To examine changes in the nonestuarine fauna, we repeated the Mantel tests for sites that did not include marine species in either the early or recent collections.

Spearman's rank correlation coefficient (r_*) was computed (as Pearson's correlation coefficient of ranks) for species ranks within drainages, regions (east and west), and the entire state between 1953 and 1986. Shannon's index of species diversity (H') was computed for each site, and rank plots of this index were done separately for the east and west. The shift in rank plots was tested using Kruskal-Wallis' Chi-square approximation.

RESULTS—Chi-square tests for homogeneity revealed that temporal changes in family proportions were significant (P < 0.001) for all subsets of the data (including the entire state, and east and west separately). When compared to statewide trends, relative proportions of families for east and west regions showed similar patterns of change (Table 1). Cyprinidae accounted for the greatest proportion of the species richness, and the relative proportion of cyprinids decreased in 1986 for all data subsets. Poeciliidae (mosquitofish), Atherinidae (silversides), and Clupeidae (shad) increased in virtually all recent collections, but Ictaluridae (catfishes), Percidae (darters), Catostomidae (suckers), and Cyprinodontidae (pupfishes) decreased. These changes included a nine-fold increase in atherinids (largely due to introductions of *Menidia beryllina* to new habitats), and a doubling of poeciliids and eastern clupeids. Ictalurids decreased by twothirds; there was an eight-fold decrease in catostomids, and a decrease of more than half for the percids. A notable difference between eastern and western collections was a small decrease in Centrarchidae for the west.

Within each region, family proportions varied among drainages. Temporal patterns within drainages did not necessarily follow the regional or statewide trend (Fig. 2). For example, the relative abundance of cyprinids decreased markedly over time in all eastern drainages except the Sabine, where they increased slightly. In the west, cyprinid relative abundance increased markedly in the San Antonio and Nueces systems, increased slightly in the Guadalupe, remained the same in the Colorado, and declined markedly in the Rio Grande. Centrarchid relative abundance declined

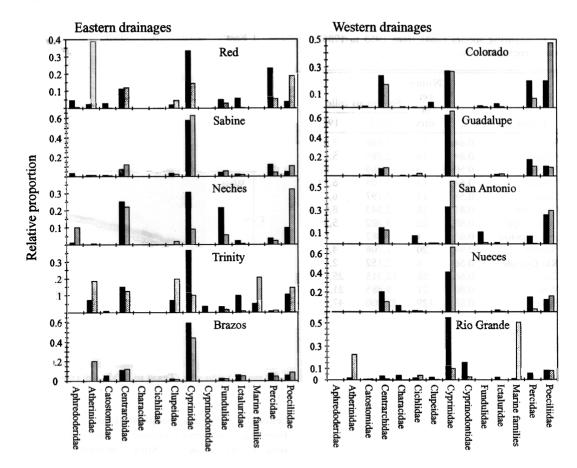


FIG. 2—Relative proportions of families for all drainages. Dark bars are 1953, lighter bars are 1986. Families that comprised less than 0.5% of all specimens collected were omitted from the graphs.

in the Neches and Trinity drainages, but showed small increases in the other eastern river systems.

Mantel tests comparing early (1953) and recent (1986) matrices indicate very strong statewide similarity (t = 6.72, P < 0.001) for withinsite family proportions. Mantel results for the dataset partitioned by region also revealed a strong general pattern of concordance of local fish assemblage structure over time (east, t = 4.05, P < 0.001; west, t = 5.35, P < 0.001). For those sites that did not contain marine species, the pattern of positive covariation was less significant for eastern sites (t = 1.94, P = 0.03) than for western sites (t = 5.02, P < 0.001), indicating that temporal similarity was slightly less but still concordant for eastern freshwater assemblages.

Rank correlations (Table 2) between early and recent surveys show that fish assemblage structure was conserved to a very large degree for some river drainages (i.e., Nueces, Guadalupe, Sabine, and Colorado; $r_s = 0.81$ to 0.95), whereas it changed considerably more for others (i.e., Neches, Rio Grande, and Brazos; $r_s = 0.50$ to 0.59). Greater change in regional assemblage structure was observed for the east ($r_s = 0.66$) than the west ($r_s = 0.80$), and the statewide correlation coefficient was lower than that of the eastern region.

Plots of H' (Fig. 3) showed a marked decrease in species diversity in the east (P = 0.001). Species diversity also decreased in the west, but this trend was not statistically significant (P = 0.08). Greatest temporal reduction in species diversity occurred among sites with low and intermediate diversity ranks, indicating that sites containing the most species showed the smallest changes in H'. In addition to changes in species richness, the distribution of species probably influenced changes

TABLE 2—Spearman's rank correlation coefficient (r_s) comparing species ranks from 1953 to 1986, for each geographic unit.

		Num- ber of	Specimens collected				
Region	r,	sites	1953	1986			
Red	0.64	12					
Sabine	0.84	18					
Neches	0.50	3					
Trinity	0.64	13					
Brazos	0.58	12					
Colorado	0.81	16					
Guadalupe	0.89	25					
San Antonio	0.67	4					
Nueces	0.94	20					
Rio Grande	0.56	6					
East	0.66	58					
West	0.80	71					
State	0.59	129					

in H'. More than twice as many individual specimens were collected in 1986 relative to 1953, and this was generally true for data from separate river systems (Table 2). Given the criterion used for collecting effort, this result indicates that, in general, greater effort was required during 1986 to obtain uncommon species. Therefore, species abundance ranks were more skewed in the 1986 samples which contributed to lower H' values.

Most localities had substantial changes in relative abundances of individual species (Fig. 4). Eighty percent of the similarity values were under 0.6, and the majority were under 0.45 ($\bar{X} = 0.41$, SD = 0.25; Fig. 4). Habitat changes are categorized by type of alteration in Table 3. The field data sheets (or memory of CH) recorded habitat changes between the sampling times. One overriding change was the amount of rainfall during the two years. Texas had a severe drought in 1953, and 1986 had an average rainfall. As a result, five stations without surface water flowing between pools in 1953 had consistent flow in 1986, and two with abundant vegetation in 1953 had very little in 1986, presumably because of high flows. The natural alterations showed impact; the five that were flowing in 1986 but not in 1953 had Morisita indices between 0.3 and 0.4. Those with a dramatic decrease in vegetation had lower Morisita indices. Sample stations impounded between sampling intervals were also altered. Six of the 16 impounded sites had Morisita indices

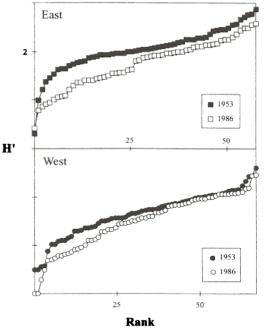


FIG. 3—Rank plots of Shannon's diversity index (H') for east and west Texas in 1953 and 1986.

below 0.1. Similarly, sample stations downstream from impoundments had four of seven with Morisita indices below 0.1. Sites that were dredged also had low Morisita indices. Three of the 10 had signs of extensive dredging, and for seven the dredged area was only about 100 m at the sampling station. The three with extensive dredging had Morisita indices below 0.1. Pollution showed detrimental effects, but the reduction of the Morisita indices was less extensive than construction activities. Two sites in the Rio Grande had saline intrusions (Edwards and Contreras-Balderas, 1991) and relatively low Morisita indices.

DISCUSSION—The results of our coarse-scale analyses of long-term changes in the Texas freshwater ichthyofauna generally indicate a conservation of species richness, species diversity, and local assemblage structure. Nonetheless, exceptions were uncovered, and at smaller geographic and taxonomic scales of resolution some major changes are apparent. Several fishes formerly endemic to Texas spring habitats are now extinct (e.g., *Gambusia amistadensis*, *G. georgei*; Miller et al., 1989) and a host of others are now endangered (e.g., *Cyprinodon elegans*, *G. nobilis*; Hubbs et al.,

1991) or are of special concern (e.g., C. pecosensis, Dionda diaboli; Hubbs et al., 1991). Relative abundances of darters (Etheostoma spp., Percina spp.; Percidae) have declined within virtually all major river drainages within the state. Minnows (Cyprinidae) show a clear pattern of declining relative abundances within all but one of the state's eastern river systems. Catfishes (Ictaluridae) also show a pattern of reduced relative abundances in most Texas rivers. When family relative abundances were aggregated on regional and statewide levels, several taxa showed marked declines over time (e.g., catostomids, cyprinids, ictalurids, and percids), and others showed marked increases (e.g., atherinids and poeciliids). The poeciliid increase reflects increased abundance of Gambusia affinis despite the extinction of two congeners. Decreasing proportions of families that have historically dominated the Texas freshwater ichthyofauna (catostomids, cyprinids, cyprinodontids, and percids) indicates a shift toward greater evenness in the statewide diversity.

Causes for these changes can only be surmised based on the findings of this study. However, several environmental changes are well documented over the past three decades. Construction and operation of numerous dams has increased the relative availability of lentic habitats within stream systems, altered natural regimes of instream discharge, and modified limnological conditions (Marsh, 1980). Proliferation of exotic species may have altered assemblage structure in some areas, particularly the Rio Grande (Edwards and Contreras-Balderas, 1991; Contreras-B and Lozano-V., 1994) and spring outflows where endemic species are affected by exotics (Hubbs, 1971). In addition, the ever-increasing demand for water by municipalities and agriculture has

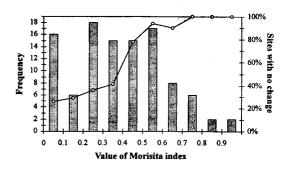


FIG. 4—Frequency histogram of values of the Morisita index for all sites (bars) and the proportion of sites for each category that experienced no habitat change (line).

led to changes in stream conditions, undoubtedly to the detriment of some species and to the benefit of others (Hubbs et al., 1991; Garrett et al., 1992). The statewide, regional, and local increases in Gambusia affinis and Menidia beryllina likely reflect an increase in the frequency and intensity of habitat disturbances of various kinds. These species were characterized as relatively extreme forms of the opportunistic life-history strategy in fishes by Winemiller and Rose (1992). According to their model, small opportunistic species have reproductive and demographic attributes that permit rapid colonization of disturbed habitats. Interestingly, pupfishes (Cyprinodontidae) have similar life-history attributes (e.g., rapid maturation, high reproductive effort, and frequent repeat spawning), yet pupfishes ranked lower in the more recent collections. This decline in pupfish relative abundances can probably be explained by a chronic reduction of shallow water habitats, especially spring outflows, resulting from instream flow reductions, and the introduction of

TABLE 3—Number of sites for intervals of the Mo	sita index, categorized by change in habitat between 1953
and 1986.	- , ,

Habitat change	Morisita index									
	<0.1	<0.2	<0.3	<0.4	<0.5	<0.6	<0.7	<0.8	<0.9	≤1.0
No change	5	2	8	7	14	16	9	10	4	4
Reservoir	6	2	5	1	2					
Below reservoir	4		2	1						
Dredging	3	1	2	1	1	1	1			
Pollution		1	3	2		1				
Exotic introduction	1									
Natural change		1	1	5						
Salination			1		1					

exotic species, including predators and sibling species that out-compete and/or interbreed with western endemics.

Large changes in fish assemblage structure of the Rio Grande system were expected given the major environmental changes that have transpired (reservoirs, water removal, exotic species, and pollution). Edwards and Contreras-Balderas (1991) also detailed major faunal changes in the lower Rio Grande. Most of the Brazos sites were located in the upper-middle reaches near the Edwards escarpment, where impoundments have been created during the past three decades. In addition, the Brazos watershed contains some of the state's best soils for row cropping, and many tons of agricultural chemicals are applied each year in the regions surrounding the middle and lower reaches.

From Hubbs' habitat descriptions, many individual site changes are easy to interpret, whereas some are not. Of the 15 sites that showed the most change at the species level, six have been affected by water impoundment that occurred since the early collections and four were immediately downstream from an existing impoundment; faunal changes are known to occur within and below reservoirs as water qualities change through time (Baxter, 1977; Brooker, 1981). Two sites, located near Trinity Bay southeast of Houston, have been subjected to dredging, pollution, and increased wetland destruction (White et al., 1993). Two sites located not far from Brownsville are also in an area of industrialization and increased salinity due to irrigation demands along the lower Rio Grande (Contreras-B. and Lozano-V., 1994). Five sites have experienced changes due to increased water volume because of higher rainfall in 1986 than in 1953. One site (Lake Texoma) had no noted physical alteration; however, the dominant species in 1953, Labidesthes sicculus, had been replaced by the introduced Menidia beryllina (Mense, 1967), and consequently the site had a Morisita index below 0.1. Reasons for other faunal changes were not as apparent because habitat alteration may not have been observable at the time of collection.

In conclusion, the state's ichthyofauna as a whole appears to remain intact in roughly similar relative proportions when viewed at a very broad scale of resolution. However, as the scale of spatial resolution is reduced, regional and local changes in species and family relative abundances are revealed. Most notable is the general statewide trend in a reduction of lotic adapted taxa with narrow habitat requirements (darters, minnows, suckers, and catfishes) and increase in opportunistic species (mosquitofish and silversides) tolerant of variable habitat conditions and able to respond quickly to habitat disturbances. Overall, east Texas has shown greater change in 33 years compared to the west, in part, due to its greater overall diversity, with a downward shift in local species diversity combined with alterations in assemblage composition.

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