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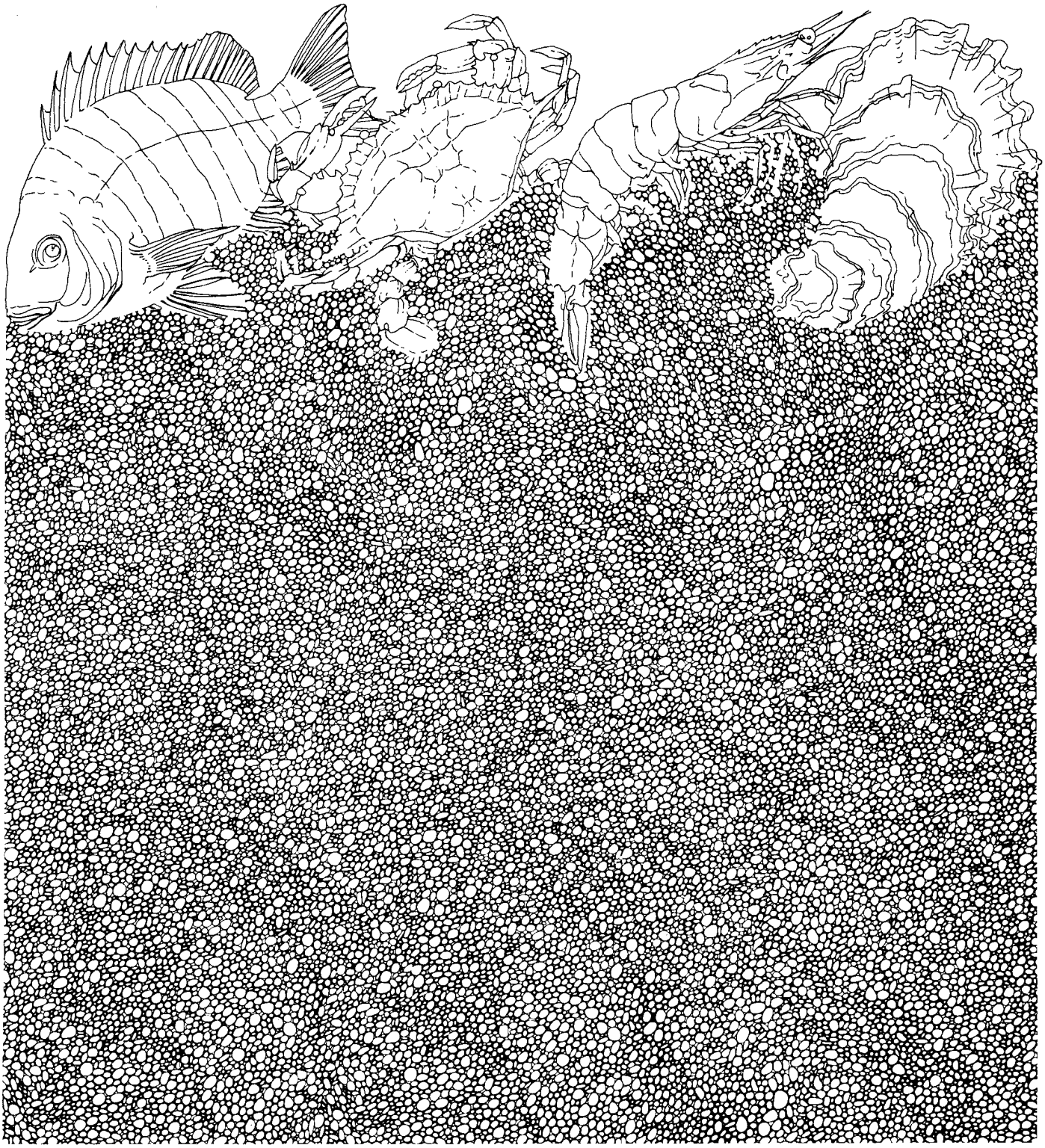

A PRELIMINARY ELECTROPHORETIC ASSESSMENT OF THE POPULATION STRUCTURE OF SPOTTED SEATROUT INHABITING THE TEXAS GULF COAST

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ABSTRACT

An examination of the electrophoretically detectable allelic variation of 24 enzymes and 8 structural proteins in spotted seatrout (Cynoscion nebulosus) from four localities on the Texas Gulf coast resulted in scorable phenotypes for 44 putative gene loci. Levels of genetic variability found were less than that reported for other marine teleosts. Polymorphic loci per population ranged from 9.0 to 13.6% and average individual heterozygosity for all loci ranged from 0.7 to 1.9%. F-statistics suggested a low degree of differentiation into subpopulations with a mean F_{ST} of 0.009. Although genetic similarities between the four locations were relatively high, averaging 0.973, some differentiation of the genome was demonstrated via cluster analysis of Rogers's genetic similarity estimates. A geographic cline in the frequency of the Aat-1^{80} allele and in average individual heterozygosity as a function of degrees west longitude was observed. Spotted seatrout inhabiting the Texas Gulf coast can be described as possessing low levels of genetic variation and little differentiation into subpopulations.

INTRODUCTION

The Texas Gulf coast and its embayments form an environmentally diverse ecosystem that supports an abundance of marine organisms. The spotted seatrout (Cynoscion nebulosus) once sustained a valuable commercial and recreational fishery in this region of the Gulf of Mexico (Meador and Green 1986). However, increased fishing pressure, catastrophic meteorological events, and blooms of red tide (Ptychodiscus brevis) prompted a reassessment of management practices by the Texas Parks and Wildlife Department, culminating in a suspended spotted seatrout commercial fishery and a restricted sport fishery (Anonymous 1983, Meador and Green 1986).

Effective management of fisheries resources requires an extensive knowledge of population structure, particularly the identification of stocks and estimates of gene exchange between stocks (Weinstein and Yerger 1976). Present literature on movement of spotted seatrout is contradictory (Baker et al. 1986). Various studies have found that few long range migrations occur from bay to bay (Moffet 1961, Iverson and Tabb 1962, Weinstein and Yerger 1976, Ramsey and Wakeman 1987) and there is growing evidence that large bays may accommodate genetically distinct subpopulations or stocks as a result of isolation (Baker et al. 1986). However, fish tagged in a Texas bayou apparently moved to the Gulf of Mexico in summer and returned to the same bayou in the fall (McEachron and Matlock 1980).

Genetic subdivision has been inferred by previous investigators of life history and protein variation in spotted seatrout (Ramsey and Wakeman 1987). Iversen and Tabb (1962) suggested that Florida fishes were broken into geographic units based on data showing differential growth rates, low dispersal, and the disjunct occurrence of bay habitat. Weinstein and Yerger (1976) inferred that independent, genetically distinct populations of spotted seatrout occurred in seven of the major bays from Texas to eastern Florida. Ramsey and Wakeman (1987) found evidence for regional differentiation in the gene pool of spotted seatrout from the Gulf of Mexico but found no indication of subpopulations among Florida bay systems.

The purpose of the present study was twofold. First, to provide a preliminary evaluation of the amount of genetic variation present in spotted seatrout populations inhabiting the Texas Gulf coast as determined from examination of electrophoretically detectable allelic variation. Secondly, to attempt to document the extent of differentiation of spotted seatrout into subpopulations. Two localities in Galveston Bay were surveyed to determine if subpopulations exist as tagging studies suggest (Baker et al. 1986). Galveston Bay spotted seatrout were then compared with mid-coastal Matagorda Bay and lower Laguna Madre fish.

MATERIALS AND METHODS

From September 1987 through May 1988 spotted seatrout were collected from four general localities within three Texas bay systems: 1. Trinity Bay in the Galveston Bay complex; 2. West Bay in the Galveston Bay complex at Bastrop Bayou; 3. Matagorda Bay near Green's Bayou on Matagorda Peninsula; and 4. the

lower Laguna Madre near the Brownsville ship channel (Figure 1). Sampling was conducted by angling or shoreline sets with gill nets. Live fish were transported in fish hauling trailers to the Perry R. Bass Marine Fisheries Research Station in Palacios, Texas for processing. Moribund or dead fish were processed on site with tissues frozen in liquid nitrogen for transport. Standard length (mm) and sex were determined for each specimen prior to removal of tissue samples. Neural (brain and eye), liver, muscle, and cardiac tissues were homogenized separately in an equivalent amount of tissue buffer (0.01 M tris-HCl, 0.001 M ß-mercaptoethanol, 0.001 M EDTA, pH 7.5; Selander et al. 1971), centrifuged for 15 minutes at 5,000 rpm, and stored in either liquid nitrogen or in an ultra-cold freezer until electrophoretic examination. Blood was obtained by cardiac puncture, diluted with an equal volume of a 0.85% saline solution containing 150 units/ml of heparin, and centrifuged at 5,000 rpm for 10 minutes. Diluted plasma was removed with a pipette and divided into two equal aliquots. One was frozen immediately for serum analysis. The remaining aliquot was used to isolate transferrin in the serum bands. This was performed by mixing 5 parts Rivanol (6,9-Diamino-2-ethoxyacridine lactate; 1.6% in LiOH A), 2 parts ferric ammonium citrate (0.6% in LiOH A), and 2 parts plasma in a centrifuge tube, steeped at 4 C for 15 minutes, centrifuged at 5,000 rpm, and the supernatant frozen for analysis (Selander et al. 1971). The red blood cells and other formed elements were resuspended and washed in an equal volume of saline and lysed by shaking for 1 minute with an equal volume of deionized water. This solution was centrifuged at 5,000 rpm for 20 minutes, and the clear hemolysate extracted and frozen until analysis.

Protein variation was assayed by horizontal starch-gel electrophoresis (Selander et al. 1971, Ayala et al. 1974). All gels were prepared as 12% suspensions of hydrolyzed starch (Electrostarch Co., Madison, WS). Gel and electrode buffers utilized were: tris borate EDTA, pH 8.0; tris citrate, pH 6.7; tris citrate, pH 8.0; lithium hydroxide, pH 8.2; tris HCl, pH 8.5 (Selander et al. 1971); tris borate EDTA, pH 9.0; tris citrate, pH 7.0 (Ayala et al. 1972); amine citrate, pH 6.1 (Clayton and Tretiak 1972); a nd tris citrate, pH 8.0 (Ridgeway et al. 1970). Supernatants from centrifuged tissues were absorbed onto filter papers, the papers blotted, and placed along the insertion line approximately 3 cm from the center of the each gel. Dilute red dye number 2 was placed on one filter paper to provide an estimate of the distance of protein migration.

Histochemical staining followed the methods of Shaw and Prasad (1970), Selander et al. (1971), Ayala et al. (1974), Siciliano and Shaw (1976) and Harris and Hopkinson (1976). Enzymes and proteins were stained in solutions containing specific substrates. Gels were incubated at 37 C in the dark until enzyme patterns became scorable; some gene products were viewed under a longwave UV light. Genotypes from protein patterns were coded by assigning alphabetic characters to electromorphs in order of decreasing anodal migration.

Initially all tissues were surveyed utilizing each buffer system to determine the most appropriate buffer for consistent resolution of a given protein system. Once all scorable loci were identified, individuals were surveyed to identify polymorphic loci (gene loci in which the most common allele exhibited a frequency < 0.99 were considered polymorphic).

Levels of genetic variability within and between bay populations compared by analysis of the frequencies of allelic variants. Biosys-1, a FORTRAN-based software package (Swofford and Selander 1981) was employed to ascertain the proportion of loci heterozygous in the average individual (H), the proportion of the loci polymorphic (P) for each bay population, genetic distance (modified Rogers's distance, D_T; Wright 1978) and genetic similarity (S; Rogers 1972) of paired combinations of bay populations. Cluster analysis, using the unweighted pair-group method with arithmetic averaging (UPGMA) (Sneath and Sokal 1973, Swofford and Selander 1981), was employed to provide a graphical representation of the genetic similarity of bay populations.

Tests of heterogeneity among localities were determined by chi-square test on contingency tables of allele counts (Hartl 1981). A modification of significance levels to account for the increase in type I error when several tests are performed simultaneously (Cooper 1968, Grant et al. 1980) was applied by dividing the desired alpha by the number of tests at each locus and the corresponding critical value was used as the rejection criterion for the null hypothesis of no heterogeneity.

Genetic divergence among populations was quantified utilizing the F-statistics of Wright (1965, 1978) and evaluated by methods presented in Workman and Niswander (1970). F_{IT} estimates the associated influence of nonrandom mating and random genetic drift. Therefore, F_{IT} is negative if there is little systematic subdivision and low inbreeding. F_{IS} is the measurement of the agreement of observed and expected heterozygote frequencies based on Hardy-Weinberg proportions of genotypes among subpopulations and was computed for each population according to Nei and Chesser (1983). The null hypothesis (random mating within subpopulations), $F_{IS} = 0$, was evaluated by a chi-square test (Li and Horvitz 1953). F_{ST} is an indicator of differentiation among subpopulations and a measure of the effects of random genetic drift among subpopulations. The unbiased estimates of gene diversities described by Nei and Chesser (1983) were utilized to estimate the F_{ST}. A chi-square test (Workman and Niswander 1970) was also used to evaluate the null hypothesis for single-locus F_{ST} values.

Regression analysis (SAS Institute Inc. 1985) was used in examination of clinal trends in average heterozygosity and variation in allelic frequencies over the range of this study. F-statistics were employed to determine the significance of such variation.

RESULTS

Survey of 24 enzymes and 8 structural proteins in spotted seatrout produced scorable phenotypes for 44 putative gene loci (Table 1). Five loci, aspartate aminotransferase-1 (Aat-1), alcohol dehydrogenase-A (Adh-A), glucose-6-phosphate isomerase-B (Gpi-B), isocitrate dehydrogenase-2 (Icdh-2) and iditol dehydrogenase-A (Iddh-A), were found to be polymorphic at all localities with the exception that Gpi-B was not variable in the samples from Trinity Bay. Glucose-6-phosphate isomerase-A was polymorphic in West Galveston Bay samples only. Aconitate hydratase-1, which possesses at least three allelomorphs, could not be surveyed consistently in all populations and

therefore was excluded from analyses. Lactate dehydrogenase-C, phosphoglucomutase-B, s-superoxide dismutase-A, m-aspartate aminotransferase-2, and esterase-2 exhibited rare variants in one or more samples and the remaining 32 loci displayed no genetic variation.

Allelic variation in spotted seatrout from four localities on the Texas coast is presented in Table 2. The percentage of polymorphic loci ranged from 9.1% in Trinity Bay fish to 13.6% in West Galveston Bay fish, while the percentage of heterozygous loci per individual for all loci ranged from 0.7% in Trinity Bay to 1.9% in the lower Laguna Madre.

Significant deviation from Hardy-Weinberg expected frequencies of genotypes was detected at the Adh-A locus in Trinity Bay ($\underline{X}^2$=19.16, d.f.=3, p<001) and the lower Laguna Madre ($\underline{X}^2$=31.88, d.f.=3, p<.001). No other deviations were observed.

Tests of heterogeneity of allele frequencies among localities indicated that allele counts of the five polymorphic loci were distributed homogeneously among the four localities (Table 3). $\underline{F}$-statistics revealed little deviation from panmixia within and between each locality (Table 4). The mean fixation index, F_{IS}, was 0.083 and displayed a highly significant divergence from random mating in individual frequencies for Adh-A. Mean standardized variance in allele frequency, F_{ST}, was 0.009, with no significant divergence among localities. The mean F_{IT}, the measure of overall differentiation, was 0.091, being elevated by contributions of Adh-A and Aat-1 genotypes.

Estimates of genetic similarity of spotted seatrout ranged between 0.980 between West Galveston Bay and Matagorda Bay to 0.961 between Trinity Bay and lower Laguna Madre (Table 5). Genetic distance ranged from 0.027 between West Galveston and Matagorda Bay to 0.047 between Trinity Bay and lower Laguna Madre. A graphical representation of the genetic similarity of the four localities is presented in Figure 2. Spotted seatrout from Trinity Bay were most divergent with a clustering level of 0.968 and a mean similarity with the three remaining localities of 0.968. West Galveston Bay and Matagorda Bay spotted seatrout shared the highest level of similarity (0.980) and clustered together.

Examination of allelic frequencies revealed a statistically significant clinal pattern of genetic variation. A cline was exhibited in the frequency of the Aat-1^{80} allele with respect to degrees west longitude ($\underline{F}_{(1,2)}$=77.12, p<0.013, adjusted R^2=0.962). The frequency of the Aat-1^{80} allele increased from 0.026 in Trinity Bay to 0.112 in lower Laguna Madre (Figure 1). A cline also existed in average individual heterozygosity with respect to degrees west longitude (Figure 3; $\underline{F}_{(1,2)}$=28.92, p<0.033) suggesting a longitudinal increase in heterozygosity from east to west in this portion of the Gulf of Mexico.

DISCUSSION

Spotted seatrout from four localities on the Texas Gulf coast demonstrated fewer polymorphic loci (9-14%) and less individual heterozygosity (2%) than previously reported for other marine teleosts including sciaenids. Smith and Fujio (1982) reported that marine teleosts were found to be

polymorphic at 20-25% of their loci with individual heterozygosity of 5%, while sciaenids demonstrated slightly fewer polymorphic loci at 15-20% of their loci and individual heterozygosity of 3% (Ramsey and Wakeman 1987). This finding is likely due to the low number of collecting localities and low sample sizes compared in the present study.

Spotted seatrout from West Galveston Bay exhibited several polymorphisms (variants) at low levels of variability. This may have been a result of a larger sample of fish surveyed (95) from this locality. Ramsey and Wakeman (1987) observed similar polymorphisms in spotted seatrout surveyed from other localities in the Gulf of Mexico and the Atlantic Ocean. Perhaps the effective population size of this prolific marine teleost is sufficiently large and the level of electrophoretically detectable variation so small as to warrant the survey of sample sizes in excess of one hundred individuals before tenable frequency inferences can be made for some gene loci.

The deviation from Hardy-Weinberg equilibrium observed at the Adh-A locus in spotted seatrout surveyed from Trinity Bay and the lower Laguna Madre is possibly attributed to low sample sizes, however, selection for homozygous genotypes should not be ruled out. Additional collections are needed to ascertain the true distribution of Adh-A genotypes from these localities.

A low degree of differentiation into subpopulations was observed from spotted seatrout inhabiting the Texas Gulf coast. Allele frequencies within Galveston Bay (Trinity and West Galveston) and between all bays were homogeneously distributed as determined by the chi-square contingency test of heterogeneity. Ramsey and Wakeman (1987), surveying a larger area of the spotted seatrout range, reported spatial heterogeneity in allele frequencies for Adh-A, Aat-1, and Gpi-B and indicated the presence of regional differentiation between the eastern and western Gulf of Mexico.

F-statistics further illustrated the lack of population subdivision in spotted seatrout surveyed. The mean F_{ST} (0.009) was relatively low, compared to other marine teleosts whose values have ranged from 0.014 for pink salmon to 0.354 for silversides (Ramsey and Wakeman 1987), suggesting little population subdivision. Ramsey and Wakeman (1987) reported somewhat more differentiation with a mean F_{ST} of 0.034 for spotted seatrout collected at 15 localities from Port Aransas, Texas to St. Augustine, Florida. Our preliminary results do not provide genetic evidence supporting independent subpopulations in individual Texas bays as has been suggested for Florida bays by Iverson and Tabb (1962).

There is an indication, however, of some differentiation in the genome of spotted seatrout on the Texas Gulf coast. Cluster analysis (Figure 2) of Rogers's genetic similarity estimates indicated that spotted seatrout from Trinity Bay were the most divergent geographic population of fish in the study. This result is attributable to the absence of the Gpi-B^{22} allele, the low frequency of the Aat-1^{80} allele (0.026) and the overall low levels of individual heterozygosity (0.7%) observed for this locality. Similarly, the spotted seatrout from the lower Laguna Madre were divergent from those of the remaining bay systems due to elevated levels of the Aat-1^{80} allele (0.112) and individual heterozygosity (1.9%).

Aspartate aminotransferase is a key metabolic enzyme of cellular respiration. Therefore, the statistically significant geographic cline in the Aat-1^{80} allele frequency (Figure 1) may indicate that the gene products of this allele are more efficient in warmer temperatures and higher salinities characteristic of the south Texas coast. Evidence for single-locus selection has appeared in the form of geographical clines in gene frequency in areas characterized by spatial changes of allele frequency with concomitant geographical variation (Koehn et al. 1980). Buroker (1983) reported a macrogeographic cline in the western Gulf of Mexico in leucine aminopeptidase-2^{94} (Lap-2^{94}) allele frequencies in American oysters Crassostrea virginica. Buroker concluded that the Lap-2^{94} allele is selected 'against' in an environment with excessive freshwater discharge, while the Lap-2^{92} allele is selected 'for' in such environments.

The increase in average individual heterozygosity as a function of west longitude (Figure 3) in spotted seatrout may be the result of selection for heterozygous genotypes better able to adapt to spatio-temporal variation in temperature and salinity characteristic of this portion of the Gulf of Mexico. Buroker (1983) reported that the American oyster exhibited clinal variation in average individual heterozygosity along the western Gulf of Mexico including the Texas Gulf coast. Buroker (1983) suggested that due to the westward dispersion of planktonic oyster larvae, a selection-migration model would best explain the increase in heterozygosity where some form of heterozygote advantage and the migration of alleles westward along the Texas coast produced such a cline. An insufficient number of localities have been surveyed in the present study to conclude that a true, evolutionarily significant cline exists in spotted seatrout inhabiting the Texas coast or to suggest a causal mechanism.

In summary, it is clear from this cursory survey that spotted seatrout inhabiting the Texas Gulf coast can be described as possessing low levels of genetic variation and little population subdivision. However, sufficient selective forces are apparently in place to produce a geographic cline in genetic variation. An insufficient number of collecting sites and polymorphic gene loci precluded tenable estimation of the amount and direction of gene flow along the Texas Gulf coast. It is premature to conclude that differentiation into subpopulations is nonexistent in spotted seatrout inhabiting the Texas Gulf coast.

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Table 1. Enzyme and structural protein systems surveyed in spotted seatrout from the Texas Gulf coast.

Protein system[a]	E.C.[a]	Loci
Acid phosphatase	3.1.3.2	1
Aconitate hydratase	4.2.1.3	2
Adenylate kinase	2.7.4.3	1
Alcohol dehydrogenase[b]	1.1.1.1	1
Aspartate aminotransferase[b]	2.6.1.1	2
Calcium-binding protein	(nonspecific)	4
Catalase	1.11.1.6	1
Creatin kinase	2.7.3.2	2
Dipeptidase	3.4.13.11	2
Dihydrolipoamide dehydrogenase	1.6.4.3	1
Esterase	(nonspecific)	3
Fructose-biphosphate aldolase	4.1.2.13	1
Fumarate hydratase	4.2.1.2	1
Glucose-6-phosphate isomerase[b]	5.3.1.9	2
Glutamate dehydrogenase	1.4.1.2	1
Glyceraldehyde-3-phospate dehydrogenase	1.2.1.12	2
L-Iditol dehydrogenase[b]	1.1.1.14	1
Isocitrate dehydrogenase[b]	1.1.1.42	2
L-Lactate dehydrogenase	1.1.1.27	3
Malate dehydrogenase	1.1.1.37	2
Malic enzyme	1.1.1.40	1
Mannose-6-phosphate isomerase	5.3.1.8	1
Phosphoglucomutase	2.7.5.1	1
Phosphogluconate dehydrogenase	1.1.1.44	1
Superoxide dismutase	1.15.1.1	1
Albumin		1
Transferrin		1
Hemoglobin		2
		44

[a] Names and numbers recommended by the Enzyme Nomenclature Committee (Harris and Hopkinson 1976).

[b] denotes polymorphic systems used in statistical analyses.

Table 2. Allele frequencies for polymorphic loci, percentage of polymorphic loci per population, and percentage of heterozygous loci per individual at 44 loci in spotted seatrout from four localities along the Texas Gulf coast.

		Locality			
		Trinity Bay	W.Galveston Bay	Matagorda Bay	L.Laguna Madre
Locus	Allele	N = 39	95	50	49
Aat-1	100	0.974	0.942	0.920	0.888
	80	0.026	0.058	0.080	0.112
Iddh-A	100	0.077	0.068	0.020	0.051
	25	0.923	0.932	0.980	0.949
Icdh-2	100	0.013	0.011	0.010	0.010
	80	0.962	0.963	0.970	0.918
	50	0.025	0.026	0.020	0.071
Adh-A	-20	0.910	0.947	0.910	0.908
	-66	0.013	0.005	0.030	0.031
	-100	0.077	0.047	0.060	0.061
Gpi-B	22	0.000	0.021	0.020	0.020
	-44	1.000	0.979	0.980	0.980
Polymorphic loci per population		0.091	0.136	0.125	0.125
Overall heterozygous loci per individual		0.007 ± 0.023	0.012 ± 0.034	0.012 ± 0.037	0.019 ± 0.046

Table 3. Results of contingency chi-square analysis of heterogeneity for spotted seatrout from the Texas Gulf coast.

Locus	Alleles	X^2	D.F.	Probability
Aat-1	2	4.685	3	0.196
Iddh-A	2	3.710	3	0.295
Icdh-2	3	5.271	6	0.510
Adh-A	3	4.698	6	0.583
Gpi-B	2	1.641	3	0.650
Totals		20.005	21	0.521

Table 4. F-statistics for spotted seatrout from four localities along the Texas Gulf coast.

Locus	F_{IS}	F_{IT}	F_{ST}
Aat-1	0.084	0.097	0.014
Iddh-A	0.059	0.068	0.009
Icdh-2	-0.050	-0.040	0.009
Adh-A	0.198[a]	0.201	0.003
Gpi-B	-0.021	-0.016	0.005
Mean	0.083	0.091	0.009

[a] $p<0.001$ for $F_{IS}=0$

Table 5. Matrix of genetic similarity (above diagonal) and genetic distance (below diagonal) of spotted seatrout from four localities on the Texas Gulf coast.

	Trinity Bay	W.Galveston Bay	Matagorda Bay	L.Laguna Madre
Trinity Bay	*****	0.976	0.967	0.961
W.Galveston Bay	0.030	*****	0.980	0.974
Matagorda Bay	0.040	0.027	*****	0.979
L.Laguna Madre	0.047	0.030	0.029	*****

Figure 1. Map of general collection localities and pie charts illustrating Aspartate aminotransferase allele frequencies of geographic populations of spotted seatrout collected from selected Texas bays. 1. Trinity Bay in the Galveston Bay complex; 2. West Bay in the Galveston Bay complex near Bastrop Bayou; 3. Matagorda Bay near Green's Bayou at Matagorda Peninsula; and 4. lower Laguna Madre near the Brownsville ship channel. Linear regression of AAT-1^{80} allele frequency as a function of west longitude resulted in the following equation and statistics: AAT-1^{80}= -2.91 + 0.03(longitude); adjusted R-square=0.962, F=77.12, P<0.013.

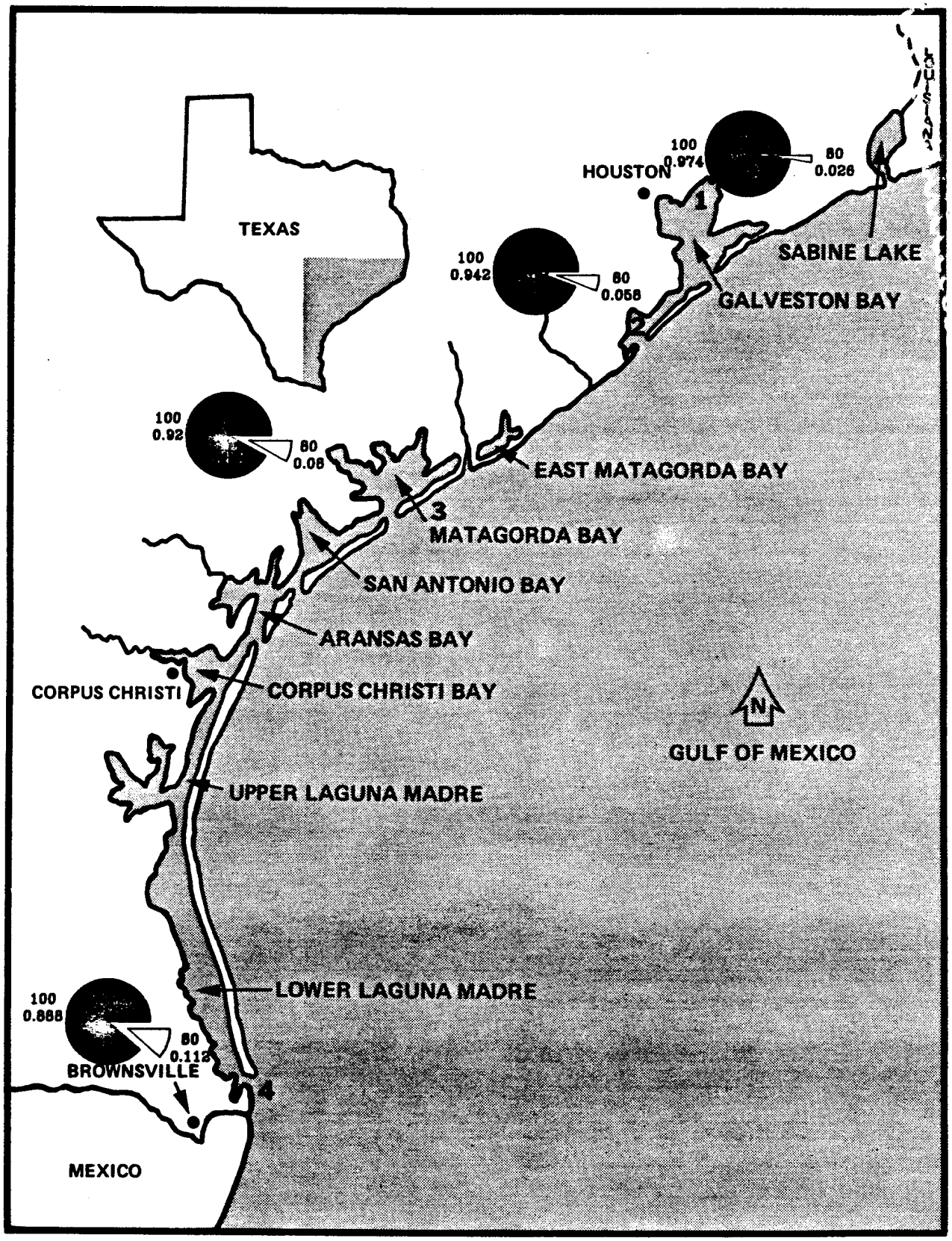

TEXAS
LOUISIANA
HOUSTON
100
0.974
80
0.026
1
SABINE LAKE
100
0.942
80
0.058
GALVESTON BAY
2
100
0.92
80
0.08
EAST MATAGORDA BAY
3
MATAGORDA BAY
SAN ANTONIO BAY
ARANSAS BAY
CORPUS CHRISTI
CORPUS CHRISTI BAY
N
GULF OF MEXICO
UPPER LAGUNA MADRE
LOWER LAGUNA MADRE
100
0.888
80
0.112
BROWNSVILLE
4
MEXICO

Figure 2. Phenogram of unweighted pair-group method cluster analysis of Roger's genetic similarity estimates for spotted seatrout from Texas bays. Cluster levels are presented.

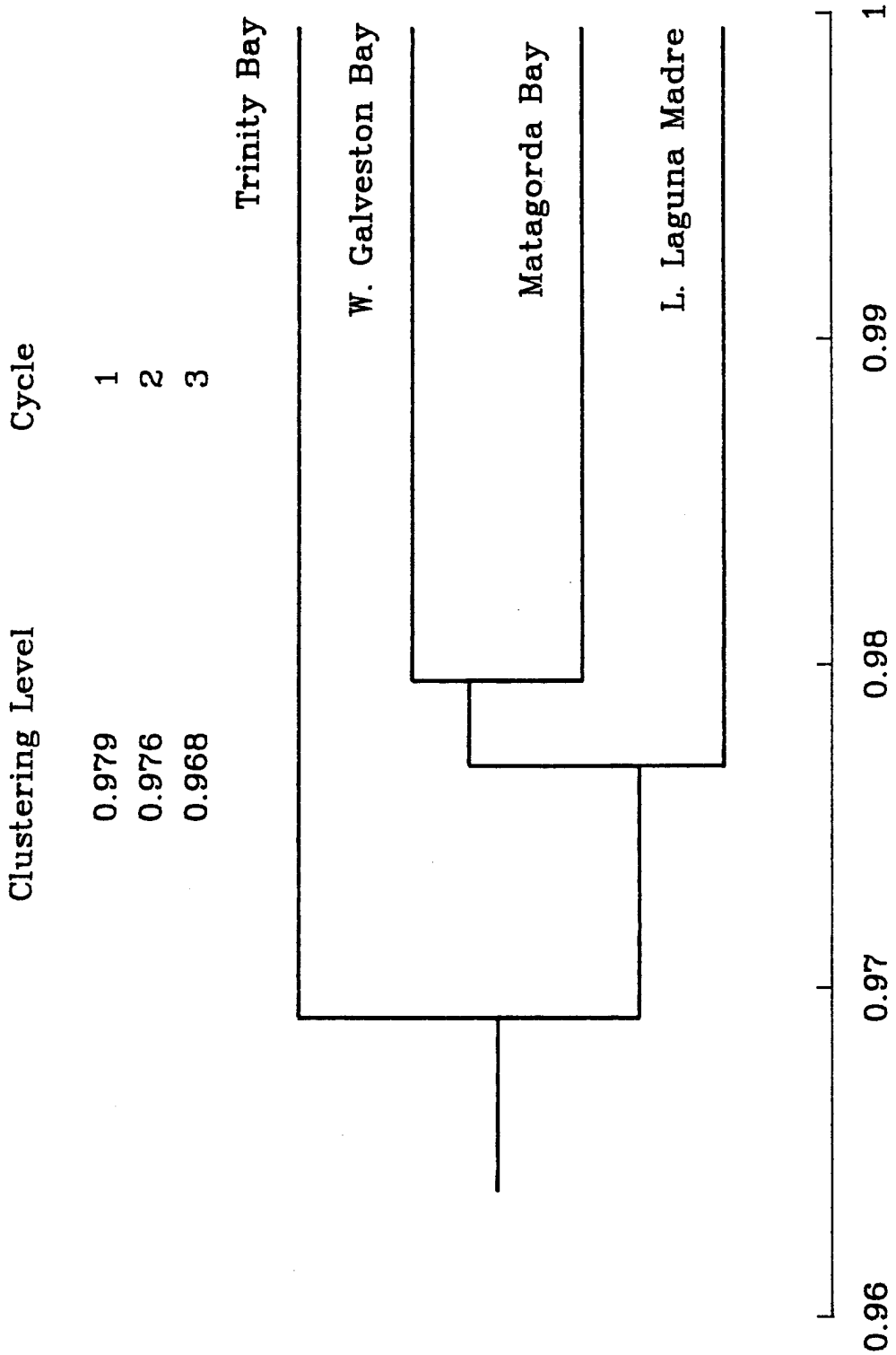
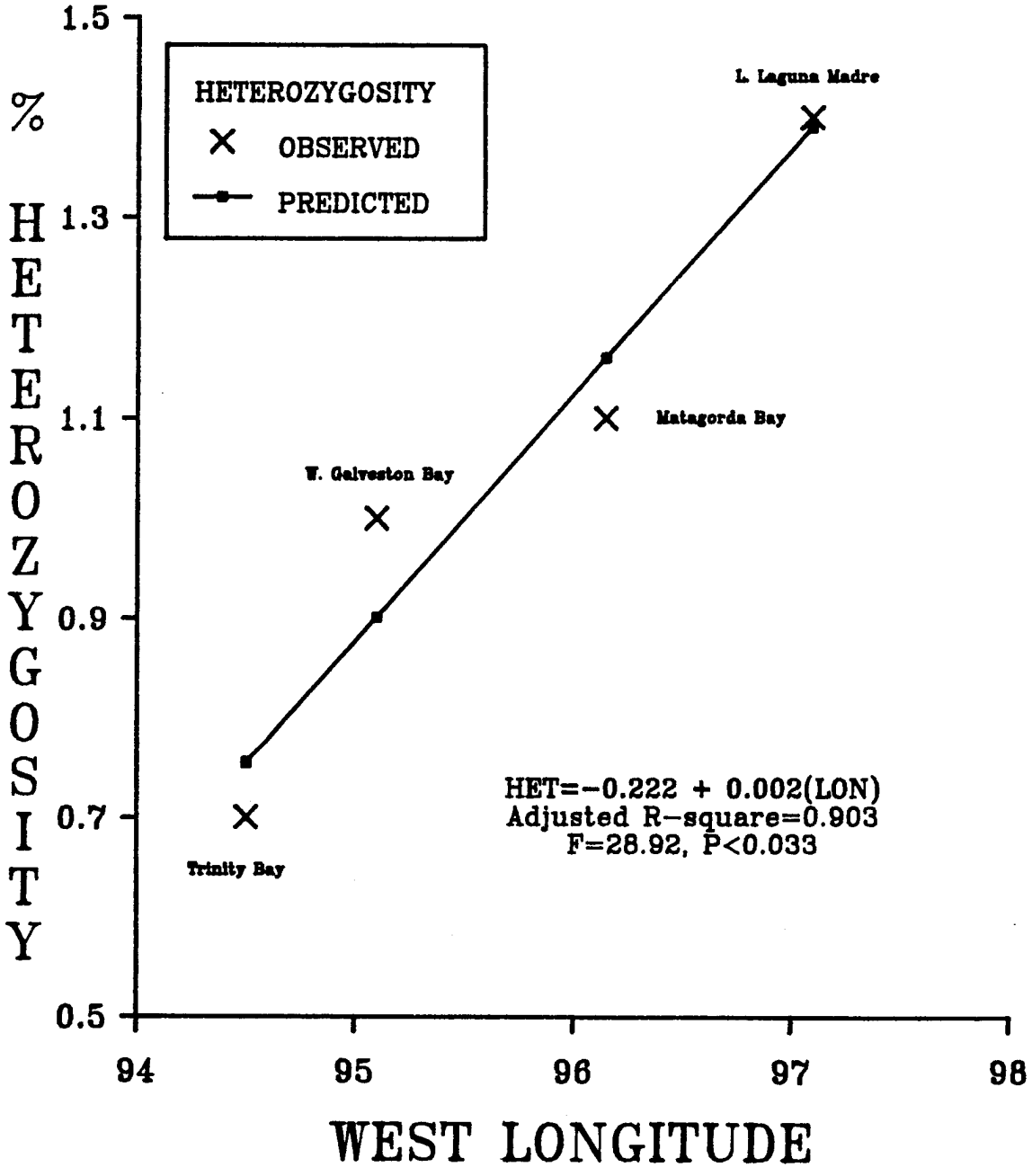

Clustering Level
Cycle
0.979
1
0.976
2
0.968
3
Trinity Bay
W. Galveston Bay
Matagorda Bay
L. Laguna Madre
0.96
0.97
0.98
0.99
1

Figure 3. Observations and least-squares regression for average individual heterozygosity in spotted seatrout as a function of degrees west longitude.


HETEROZYGOSITY
OBSERVED
PREDICTED
% HETEROZYGOSITY
1.5
1.3
1.1
0.9
0.7
0.5
L. Laguna Madre
Matagorda Bay
W. Galveston Bay
Trinity Bay
HET=-0.222 + 0.002(LON)
Adjusted R-square=0.903
F=28.92, P<0.033
94
95
96
97
98
WEST LONGITUDE

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