Geobiologic Study of the South Texas Outer Continental Shelf

GEOLOGICAL SURVEY PROFESSIONAL PAPER 1238

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A description of the biofacies and ichnofacies of the South Texas Outer Continental Shelf

UNITED STATES DEPARTMENT OF THE INTERIOR

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GEOLOGICAL SURVEY

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CONTENTS

ILLUSTRATIONS

CONTENTS

TABLES

GEOBIOLOGIC STUDY OF THE
SOUTH TEXAS OUTER CONTINENTAL SHELF

By GARY W. HILL,[1] KENNETH A. ROBERTS,[2] JACK L. KINDINGER,[2]
and GEORGE D. WILEY[2]

ABSTRACT

The zonation of macrobenthic infauna on the South Texas Outer Continental Shelf is related to water depth and sediment facies. The zonation is based on species distribution and density, diversity, equitability, and biogenic sedimentary structures.

The numbers of species and individuals per unit area correlate locally with substrate characteristics (particularly sand-to-mud ratios). Sandier substrates have more species and individuals than muddier ones. In the study area, sand-to-mud ratios generally decrease as water depth increases. Consequently, the numbers of species and individuals decrease away from land.

Diversity (H'') is higher in sandier substrates than in muddier substrates. Overall diversity decreases in a seaward direction. Equitability increases as sand-to-mud ratios decrease and thus tends to increase as water depth increases.

Biogenic sedimentary structures on the South Texas Outer Continental Shelf result from the interaction of biologic and geologic processes. The zonation of the structures is useful in overall environmental interpretations of Holocene events and processes. The zonation can be defined in terms of diversity, density, and distribution.

Zonation of biogenic sedimentary structures parallels macrobenthic infaunal zonation. Substrates with diverse and dense biogenic sedimentary structures are associated with diverse, dense macrobenthic infaunal assemblages. The distribution of biogenic sedimentary structures is similar to the distribution of sediment types. Diversity and density of biogenic sedimentary structures decrease away from land. Locally, individual biogenic sedimentary structures become more obvious and distinct in finer sediments and deeper water.

INTRODUCTION

Recent investigation of various Holocene and ancient sedimentary environments have shown that in many instances biogenic processes affecting the substrate fabric subsequent to deposition are as important as the physical processes involved during deposition (for example, Howard and others, 1972). Because bioturbation modifies grain-size characteristics and depositional structures markedly in some depositional environments, an understanding of benthic biological processes is useful to sedimentological, paleoecological, and overall environmental interpretations. In this report we identify, classify, and interpret the distribution of large bottom-dwelling animals (macrobenthic infauna) as it relates to the sedimentological processes active on the South Texas Outer Continental Shelf.

The interaction of physical and biological processes on the continental shelves has been little studied. In the United States, investigations of animal-sediment relations have been largely restricted to the east coast, particularly off Georgia (for example, Howard and Reineck, 1972). Animal-sediment relations off the south Texas coast received only meager study (Hunter and others, 1972; Hill, 1974) until the U.S. Bureau of Land Management began environmental studies in the area in 1974.

STUDY AREA

Geographic Extent.—The study area (fig. 1) is that part of the Continental Shelf in the western Gulf of Mexico designated by the Bureau of Land Management for lease sale purposes as the South Texas Outer Continental Shelf (OCS). This area extends from Matagorda Peninsula in the north to the Rio Grande in the south and seaward to about the 200-m isobath. The 20-m isobath is the general inshore boundary. The study area encompasses 24,000 km².

Geomorphology.—The South Texas OCS can be characterized topographically as relatively smooth and gently sloping (fig. 2). The shelf averages about 100 km

[1]U.S. Geological Survey, Menlo Park, CA 94025.
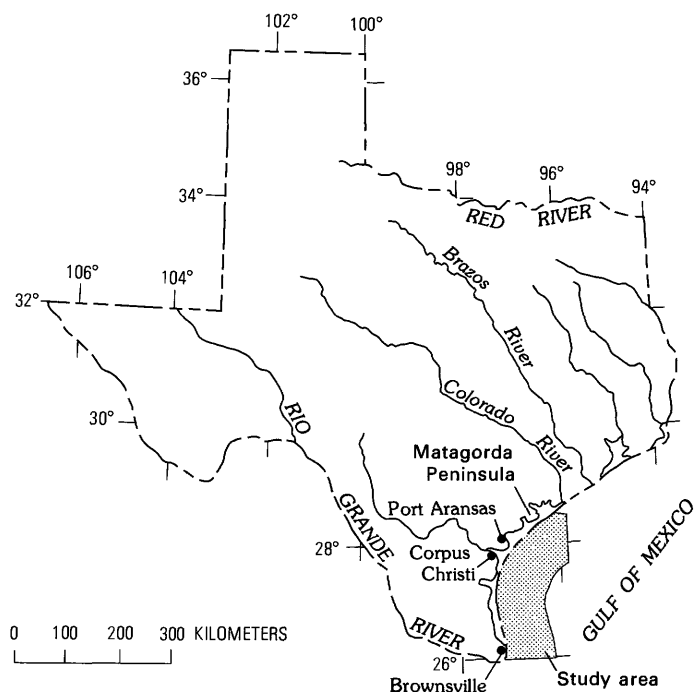[2]U.S. Geological Survey, Corpus Christi, TX 78411.

FIGURE 1.—Index map of Texas showing study area on Continental Shelf in western Gulf of Mexico.

in width and has an average gradient of 1.9 m/km. Irregular topographic features include relict carbonate banks, most of which occur within the 25- to 50-fathom (45- to 90-m) interval. Two prominent seaward-facing topographic salients at the north and south ends of the study area mark the locations of the ancestral Brazos-Colorado and Rio Grande deltas.

Substrate.—The substrate of the study area has been classified as a clayey silt province (Shideler, 1976). Sand-dominated areas occur within the ancestral Brazos-Colorado and Rio Grande deltas of the northern and southern sections of the study area, respectively. Gravel is found locally around isolated carbonate banks and within the ancestral Rio Grande delta. The gravel fraction is bioclastic, consisting mainly of molluscan shells and some coral and algal reef debris (Berryhill and others, 1976).

Modern, palimpsest, and relict deposits occur in the study area (Berryhill and others, 1976). The southern ancestral Rio Grande delta is largely relict Pleistocene and early Holocene deposits. The central part of the study area is a depocenter of modern fine sediment. The northern delta is characterized by partially reworked sediments that are being influenced by the modern hydrologic regime (palimpsest deposits).

Textural parameters show regional trends (Shideler, 1976); sediments become finer in a seaward direction and from the north and south toward the central area.

Climate.—The study area is in a subhumid to semiarid warm-temperature climate. Mean annual rainfall at Corpus Christi is 72.5 cm; mean monthly temperature ranges from 14.0°C in January to 29.0°C in August, and the mean annual temperature is 22.1°C (NOAA, 1974a). In Brownsville, mean annual rainfall is 63.7 cm; the mean monthly temperature ranges from 15.7°C in January to 29.1°C in August, and a mean annual temperature is 23.2°C (NOAA, 1974b). Mean annual wind speed at Corpus Christi is 5.3 m/s, and the resultant wind direction is 121°. At Brownsville, the mean annual wind speed is 2.7 m/s, and the resultant wind direction is 127°. The wind direction is predominantly southeasterly during the summer, easterly during the fall and spring, and northerly in winter.

Tides, water properties, and wave climate.—The South Texas shelf is microtidal, the tides having a mean diurnal range of 51.8 cm at Port Aransas (NOAA, 1975). Curray (1960) used Fleming's (1938) tidal current velocity formula to predict that maximum velocities near the central OCS region would be found approximately 40 km offshore (45- to 55-m isobaths) rather than at the edge of the Continental Shelf.

Very few temperature-salinity data exist for the study area. Mean monthly water temperature at Port Aransas ranges from 13.6°C in January to 30.0°C in August, and mean annual water temperature is 22.7°C (NOAA, 1973). The mean monthly salinity, calculated from the water density at Port Aransas, ranges from 29.5 ppt (parts per thousand) in May to 36.6 ppt in August, and the mean annual salinity is 32.0 ppt (NOAA, 1973).

Temperature and salinity stratification is known to be intermittently well defined off the southern Texas coast (Jones and others, 1965), but the distribution pattern has never been determined over a large area. Winter water temperatures in the northern Gulf of Mexico are similar to those found off North Carolina to Long Island; in the summer, temperatures rise higher than in the Caribbean. Parker (1960), in comparing summer and winter average bottom-water temperatures in the northern Gulf of Mexico, noted convergence of summer and winter temperature values in the depth range of 40 to 60 fathoms (80–120 m).

Few data exist regarding wave climate. The heights of breakers along the shore are normally 0.3 to 1.0 m. Breakers higher than 2 m occur several days per year, largely during storms in the fall, winter, and spring. Waves approach the coast from the southeast during the summer and are dominatly from the northeast during the winter.
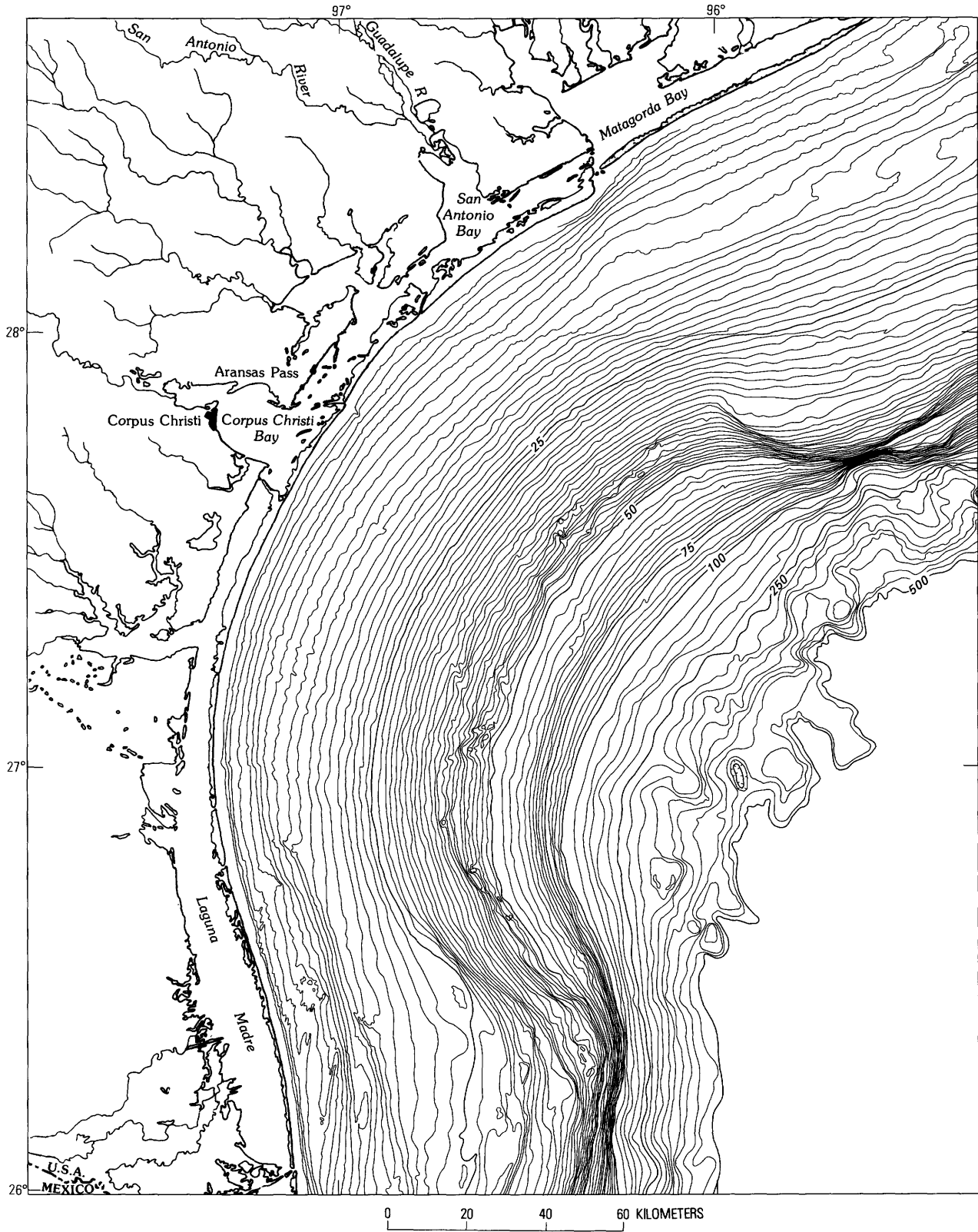
FIGURE 2.—Study area showing isobaths in fathoms (from Berryhill and others, 1976).

Currents.—Circulation patterns of littoral and semi-permanent shelf currents are complex on the South Texas OCS. A comparison of a number of investigations, made in the study area to determine drift rates and patterns (Lohse, 1955; Curray, 1960; Kimsey and Temple, 1963, 1964; Watson and Behrens, 1970; Hunter and others, 1974; Hill and others, 1975), suggests that a yearly cycle of coastwide water movement is controlled primarily by seasonal winds. Seasonally, southward drift is best developed during the summer.

Geographically, southward drift is strongest in the north part of the study area, and northward drift is strongest in the south due to the orientation of the shore relative to the predominantly southeasterly winds. Uniform southward winter drift and uniform northward summer drift define the extremes of seasonal variation along the south Texas coast, but these extreme conditions may not occur every year. Kimsey and Temple (1964) noted that the characteristic pattern of a given season can be delayed, curtailed, or modified by winds atypical of the season.

During some seasons, a drift convergence may occur in the study area. Its position tends to shift northward during the spring and southward during the fall, but its average position is centered along the south-central Texas coast. The convergence is complex in structure both in the horizontal plane and in vertical section.

METHODS

Bottom samples from 264 stations (pl. 1) were analyzed for biological content. Subsamples were removed from each sample for sedimentological and geochemical studies. The investigative steps used in this study are outlined in table 1. The handling, preservation and identification of the sample material followed procedures that are in general use.

Macrobenthic infaunal assemblages were classified using numerical analysis. The computer program was supplied by Joseph L. Simon, Department of Biology, University of South Florida. Correlation coefficients were determined using the modified USGS RAS-STATPAC program for correlation analysis (DO101) and general regression analysis (DO095).

The Shannon diversity index, $H' = \Sigma\, P_i \ln P_i$ (P_i is the proportion of the ith species in the collection), utilized to calculate diversity, is influenced by two components: the total number of species present (species richness component) and the evenness of distribution of the individuals among the different species (equitability component) (Shannon and Weaver, 1963; Lloyd and

TABLE 1.—*General outline of investigative steps*

Step 1. Sample collection	1.1 Samples collected.
	1.2 Samples washed through 0.5-mm sieve.
	1.3 Samples stored in labeled glass jars.
	1.4 Pertinent sample data entered in master log.
	1.5 Sample inventoried on ship and storage location noted.
Step 2. Sample preservation	2.1 Samples fixed in 5-percent formalin solution.
	2.2 Samples converted to 45-percent isopropyl alcohol solution for preservation.
	2.3 Samples inventoried in lab and storage.
Step 3. Differentiation phase, initial sorting.	3.1 Organic versus inorganic separation.
	3.2 Identifiable organic material versus unidentifiable organic material separation.
	3.3 Separation of identifiable organic material to phylum level.
Step 4. Differentiation phase, final sorting.	4.1 Separation of identifiable organic material to species level.
	4.2 Cursory description of unidentifiable organic material.
	4.3 Cursory description of inorganic material.
Step 5. Identification phase	5.1 Taxonomic identification of species.
	5.2 Biomass calculation.
Step 6. Classification (community level phase).	6.1 Numerical analysis.
	6.2 Diversity-equitability analysis.
	6.3 Biofacies analysis.
Step 7. Interpretation phase	7.1 Interfacing analytical results.
	7.2 Data processing for computer.
	7.3 Parameter tabulation.
	7.4 Interpretation of results.

Ghelardi, 1964). To apply Shannon's formula to a sample from a population, H' must be estimated by the equation,

$$H'' = \frac{N_i}{N}\, \ln\, \frac{N_i}{N} \quad \text{natural bels/individuals}$$

where N_i is the number of individuals in the ith species and N is the total number of individuals collected.

The species richness component was measured by Margalef's index, $d = (s-1)/\log N$, where s is the number of species and N is the number of individuals in the sample (Margalef, 1958). Relative species abundance was measuredy Lloyd and Ghelardi's (1964) equitability index, $E = s'/s$, where s' is the number of species predicted for the calculated H'' by the "broken-stick" model of MacArthur and Wilson (1967) and s is the number of species.

Two important points need emphasis. First, the entire study area was sampled from October 25 to December 22, 1974. This study, therefore, represents a synoptic picture of the benthic biological conditions. Second, only one grab sample (approximately 12.5 liters) was taken at each station because of time and logistic constraints. Holland (1976) pointed out that one grab sample will obtain approximately 30 percent of the species that might be expected to exist at a specific inshore station. He also expressed the opinion that 50 or more samples at an individual site might be needed to sample the total infaunal population completely. Therefore, large random variations in the values of biologic parameters may be expected between adjacent stations. This variability reduces the accuracy of the contouring of maps. Consequently, map contours in this report must be considered approximations.

As a first step toward the interpretation of benthic biological processes, macrobenthic infaunal zonation must be described and the factors controlling it defined. To determine the significance of variations in the spatial distribution of benthic organisms, the characteristics of macrobenthic infauna are described, first for the entire study area in general and then by specific assemblages.

GENERAL CHARACTERISTICS OF THE MACROBENTHIC INFAUNA

NUMBER OF SPECIES AND INDIVIDUALS

The 264 samples examined yielded 14,313 individuals representing several taxonomic groups (table 2) and 205 species (table 3). The taxonomic groups having the greatest numbers of species were Polychaeta (48 percent), Crustacea (24 percent), and Mollusca (22 percent). The same groups had the greatest number of individuals (Polychaeta, 62 percent; Crustacea, 16 percent; and Mollusca, 12 percent). Other taxonomic groups accounted for 10 percent or less of the total number of species and individuals.

TABLE 2.—*Number of species and individuals collected from 264 samples*

[Percent in parentheses]

Taxon	No. of species		No. of individuals	
Polychaeta..	98	(48)	8895	(62)
Crustacea...	49	(24)	2291	(16)
Mollusca ...	46	(22)	1629	(12)
Others	12	(6)	1498	(10)
Total.....	205	(100)	14313	(100)

The number of species per sample (0.0125 m³) ranged from zero to 39; the mean was 7.6 (table 4). The regional distribution by number of species (fig. 3) showed two general trends for the South Texas OCS. First, the number of species was smallest in the central sector, increasing to the north and south. Second, the number of species generally decreased seaward. The numbers of species were largest in the general area of the ancestral Brazos-Colorado and Rio Grande deltas, particularly in the nearshore parts.

The number of individuals per sample ranged from zero to 810; the mean was 54.2 (table 4). Two general trends were evident in the regional pattern of the number of individuals (fig. 4). First, numbers of individuals generally decreased across the shelf as water depth increased. Second, the central part of the area had fewer individuals than the northern and southern parts. As with the distribution of species, the number of individuals was largest in the shallower water over the ancestral Brazos-Colorado and Rio Grande deltas.

In the northern Gulf of Mexico, a number of investigators (Parker, 1956, 1960; Boyer, 1970; Stanton and Evans, 1971, 1972) have noted the close relation between the distribution of macro-invertebrates and variations in depth of water and type of sediment. Comparison of the regional distribution maps for numbers of species and individuals (figs. 3, 4) with a bathymetric map of the study area (fig. 2) suggests a general correlation with depth of water. A similarity in distribution also is evident when the biological maps are compared to any of several sedimentological maps, such as maps of sand-to-mud ratio (fig. 5), mean diameter (fig. 6), and standard deviation (fig. 7).

A good correlation exists between the number of species and of individuals. The largest numbers of species and individuals are in relatively shallow water and in parts of the shelf that have high sand-to-mud ratios.

Areas of low population density occur within both the ancestral Brazos-Colorado and Rio Grande deltas, which

TABLE 3.—*Benthic invertebrates collected*

PHYLUM
  Class
    Order
      Family
        Species

COELENTERATA
  Anthozoa
    Pennatulacea
      Renillidae
        Renilla mulleri
    Actiniaria
        unidentified anemone
PLATYHELMINTHES
  Turbellaria
    Polycladida
        unidentified flatworm
NEMERTINEA
        unidentified nemerteans
ANNELIDA
  Polychaeta
    Phyllodocida
      Phyllodocidae
        Phyllodocid
      Polynoidae
        Phyllohartmania taylori
      Sigalionidae
        Leanira sp.
        Sthenelais sp.
      Chrysopetalidae
        Paleonotus heteroseta
      Glyceridae
        Glycera tesselata
        Glycera sp
      Gonididae
        Glycinde sp.
        Goniada sp.
      Nephtyidae
        Aglaophamus verrilli
        Nephtys picta
        Nephtys sp. A
        Nephtys sp. B
      Syllidae
        Exogone dispar
        Exogone sp.
        syllid A
        syllid B
        syllid C
      Hesionidae
        Nereimyra punctata
        hesionid
      Pilargidae
        Ancistrosyllis papillosa
        Ancistrosyllis cf. *rigida*
        Sigambra tentaculata
        pilargid A
        pilargid B
        pilargid C
      Nereidae
        Nereis sp. A
        Nereis sp. B
        nereid A
        nereid B

TABLE 3.—*Benthic invertebrates collected*—Continued

PHYLUM
  Class
    Order
      Family
        Species

ANNELIDA—Continued
  Polychaeta—Continued
    Capitellida
      Capitellidae
        Leiocapitella glabra
        Notomastus cf. *hemipodus*
        Notomastus latericeus
      Maldanidae
        Branchioasychis americana
        Clymenella torquata
        maldanid A
        maldanid B
        maldanid C
      Opheliidae
        Armandia agilis
        Armandia maculata
        Armandia sp.
        Polyophthalmus pictus
    Sternaspida
      Sternaspidae
        Sternaspis scutata
    Spionida
      Spionidae
        Laonice cirrata
        Malacoceros indicus
        Malacoceros sp.
        Paraprionospio pinnata
        Prionospio cirrifera
        Prionospio sp.
        Scolelepis sp.
        Spiophanes cf. *bombyx*
        Spiophanes sp.
        spionid A
        spionid B
      Heterospionidae
        heterospionid
      Trochochaetidae
        trochochaetid
      Paraonidae
        Aricidea sp. A
        Aricidea sp B.
        Cirrophorus branchiatus
        Paraonides sp.
        Paraonis sp.
        paraonid A
        paraonid B
        paraonid C
      Chaetopteridae
        chaetopterod
    Eunicida
      Onuphidae
        Diopatra cuprea
        Onuphis sp. A
        Onuphis sp. B
      Eunicidae
        Marphysa aransensis

TABLE 3.—*Benthic invertebrates collected*—Continued

PHYLUM
  Class
    Order
      Family
        Species

ANNELIDA—Continued
  Polychaeta—Continued
    Eunicida—Continued
      Lumbrineridae
        Lumbrineris sp. A
        Lumbrineris sp. B
        Lumbrineris sp. C
        Ninoe nigripes
      Arabellidae
        Arabella sp.
        Drilonereis magna
      Lysaretidae
        Lysarete brasiliensis
        lysaretid
    Amphinomida
      Amphinomidae
        Amphinome rostrata
        Chloeia viridis
        Pseudeurythoe sp.
    Magelonida
      Magelonidae
        Magelona pettiboneae
        Magelona sp.
    Ariciida
      Orbiniidae
        orbiniid
    Cirratulida
      Cirratulidae
        cirratulid A
        cirratulid B
      Cossuridae
        Cossura delta
    Oweniida
      Oweniidae
        Owenia fusiformis

    Terebellida
      Pectinariidae
        Pectinaria gouldii
    Ampharetida
        Melinna maculata
      Terebellidae
        Terebellides stroemi
    Flabelligerida
      Flabelligeridae
        Diplocirrus cf. *capensis*
        flabelligerid A
        flabelligerid B
        unidentified polychaete A
        unidentified polychaete B
        unidentified polychaete C
        unidentified polychaete D
MOLLUSCA
  Gastropoda
    Rissionida
        Zebina browniana
      Vitrinellidae
        Episcynia inornata

TABLE 3.—*Benthic invertebrates collected*—Continued

PHYLUM
  Class
    Order
      Family
        Species

MOLLUSCA—Continued
  Gastropoda—Continued
      Melanellidae
        Strombiformis sp.
      Naticidae
        Polinices duplicatus
        Natica pusilla
      Ringiculidae
        Ringicula semistriata
      Retusidae
        Volvulella texasiana
        Pyrunculus caelatus
        gastropod

  Scaphopoda
      Dentaliidae
        Dentalium eboreum
        Dentalium sp. A
        Dentalium sp. B

  Bivalvia
      Nuculidae
        Nucula proxima
      Nuculanidae
        Nuculana acuta
        Nuculana concentrica
        Yoldia solenoides
        Yoldia sp.
        nuculanid A
        nuculanid B
      Arcidae
        Anadara transversa
      Lucinidae
        Linga amiantus
        Linga multilineata
      Thyasiridae
        Thyasira sp.
      Diplodontidae
        Diplodonata sp.
      Carditidae
        Cycolcardia sp.
      Veneridae
        Cyclinella tenius
        Anomalocardia auberiana
        Chione clenchi
        Chione intapurpurea
      Crassatellidae
        Crassinella lunulata
      Tellinidae
        Tellina squamifera
        Tellina versicolor
        Macoma sp.
      Semelidae
        Abra aequalis
      Corbulidae
        Corbula sp.
      Periplomatidae
        Periploma sp.

TABLE 3.—*Benthic invertebrates collected*—Continued

| PHYLUM |
| Class |
| Order |
| Family |
| Species |

MOLLUSCA—Continued
   Bivalvia—Continued
      Verticordiidae
         Verticordia ornata
         Verticordia sp.
      Cuspidariidae
         Cardiomya perrostrata
         Cardiomya sp.
      Leptonidae
         Mysella sp.
      Lasaeidae
         Aligena sp.
         bivalve A
         bivalve B
ARTHROPODA
   Crustacea
      Nebaliacea
         Nebalia sp.
      Cumacea
         Leuconidae
            Eudorella monodon
            Eudorella sp.
            leuconid
            unidentified cumacea
      Tanaidacea
         Apseudidae
            Leptognatha gracilis
            apseudid
         Tanaidae
            Pseudotanais oculatus
            unidentified tanaid A
            unidentified tanaid B
      Isopoda
         Gnathiidae
            Gnathia cf. *prouctatrideus*
         Anthuridae
            Hyssura sp.
            anthurid
      Stomatopoda
         Squillidae
            Squilla empusa
            Squilla sp.
      Amphipoda
         Ampeliscidae
            Ampelisca cristoides
            Ampelisca cf. *cucullata*
            Ampelisca cf. *cristata*
            Ampelisca cf. *vera*
         Ampithoidae
            Ampithoe sp.
         Gammaridae
            Gammarus sp. A
            Gammarus sp. B
            Gammarus sp. C
         Lysianassidae
            Tmetonyx sp.
            Orchomonella pinguis
            lysiannassid

ARTHROPODA—Continued
   Crustacea—Continued
      Amphipoda—Continued
         Phoxocephalidae
            Heterophoxus sp.
            Proharpina antipoda
            Proharpina tropicana
            Pseudharpina cf. *dentata*
            unidentified amphipod A
            unidentified amphipod B
            unidentified amphipod C
      Decapoda
         Penaeidae
            Penaeus aztecus
            penaeus setiferus
         Alpheidae
            Alpheus sp.
         Callianassidae
            Callianassa sp.
         Leucosiidae
            Myropsis quinquespinosa
         Xanthidae
            Micropanope sp.
            xanthid
         Pinnotheridae
            Pinnixa retinens
            Pinnixa sayana
            Pinnixa sp.
         Goneplacidae
            Speocarcinus sp.
            Goneplax hirsuta
            Chasmocarcinus mississippiensis
            Euryplax nitida
         Raninidae
            Raninoides louisianensis
            unidentified crab A
            unidentified crab B
SIPUNCULIDA
         sipunculid A
         sipunculid B
ECHIURIDA
         echiurid A
         echiurid B
BRYOZOA
         unidentified bryozoan
ENCHINODERMATA
   Echinoidea
      Spatangoida
         Schizasteridae
            Moira atropos
   Asteroidea
      Paxillosida
         Astropectinidae
            Astropecten sp.
   Ophiuroidea
      Ophiurida
         unidentified brittle star
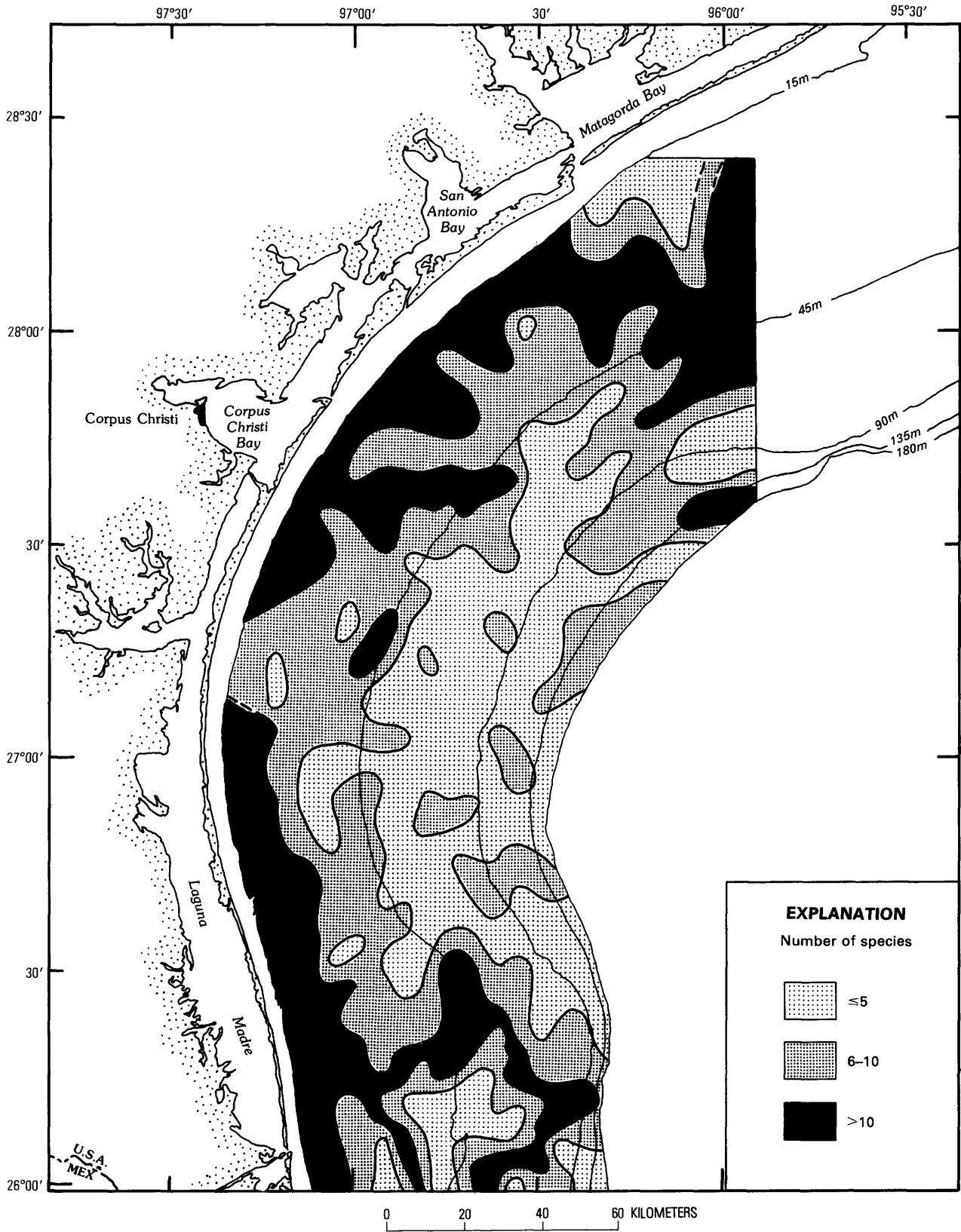
FIGURE 3.—Distribution of total number of species per sample (0.0125 m³).
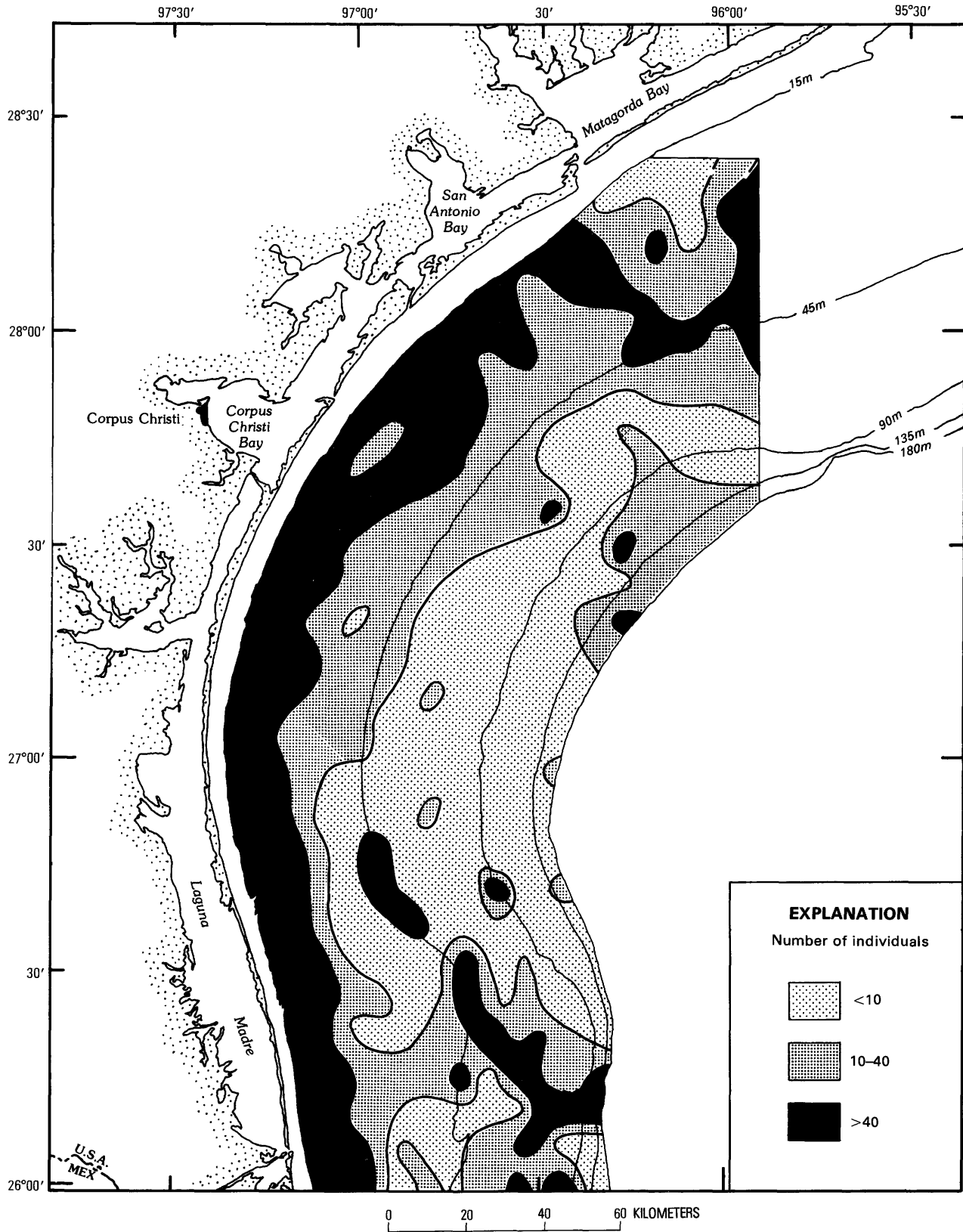
FIGURE 4.—Distribution of total number of individuals per sample (0.0125 m³).
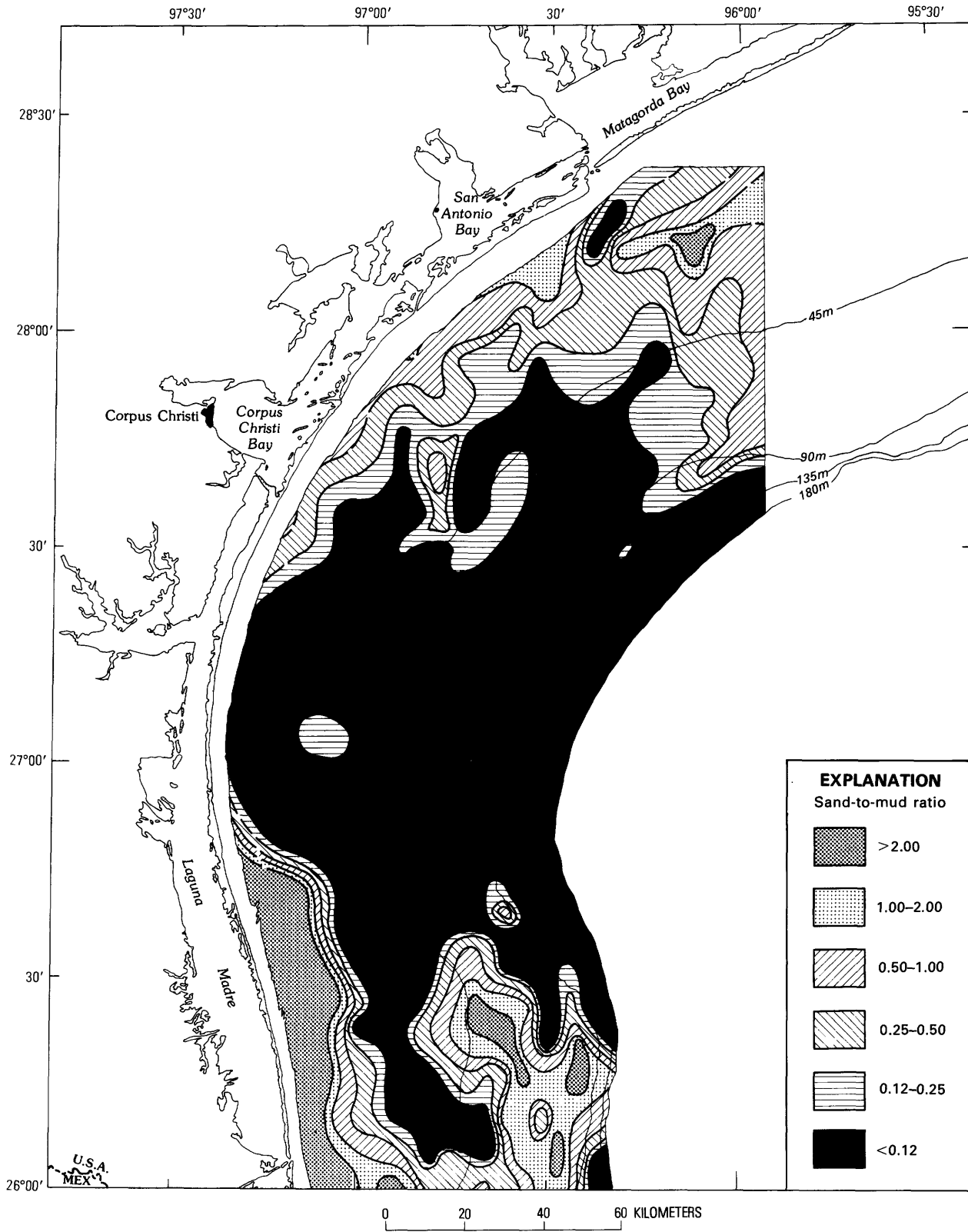
FIGURE 5.—Sand-to-mud ratios, of benthic sediments; from Berryhill and others (1976).
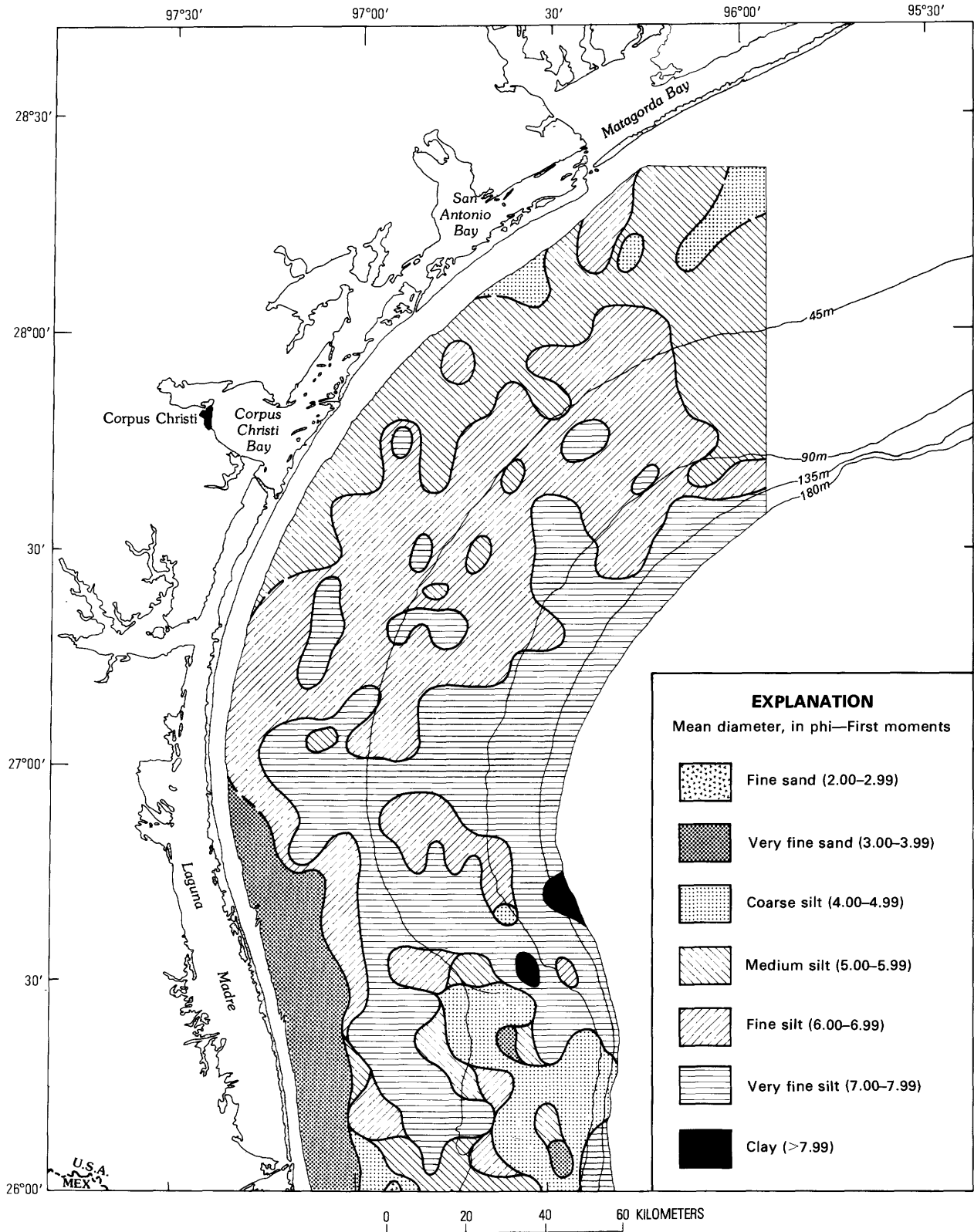
FIGURE 6.—Mean diameters of grain sizes, benthic sediments; from Berryhill and others (1976).
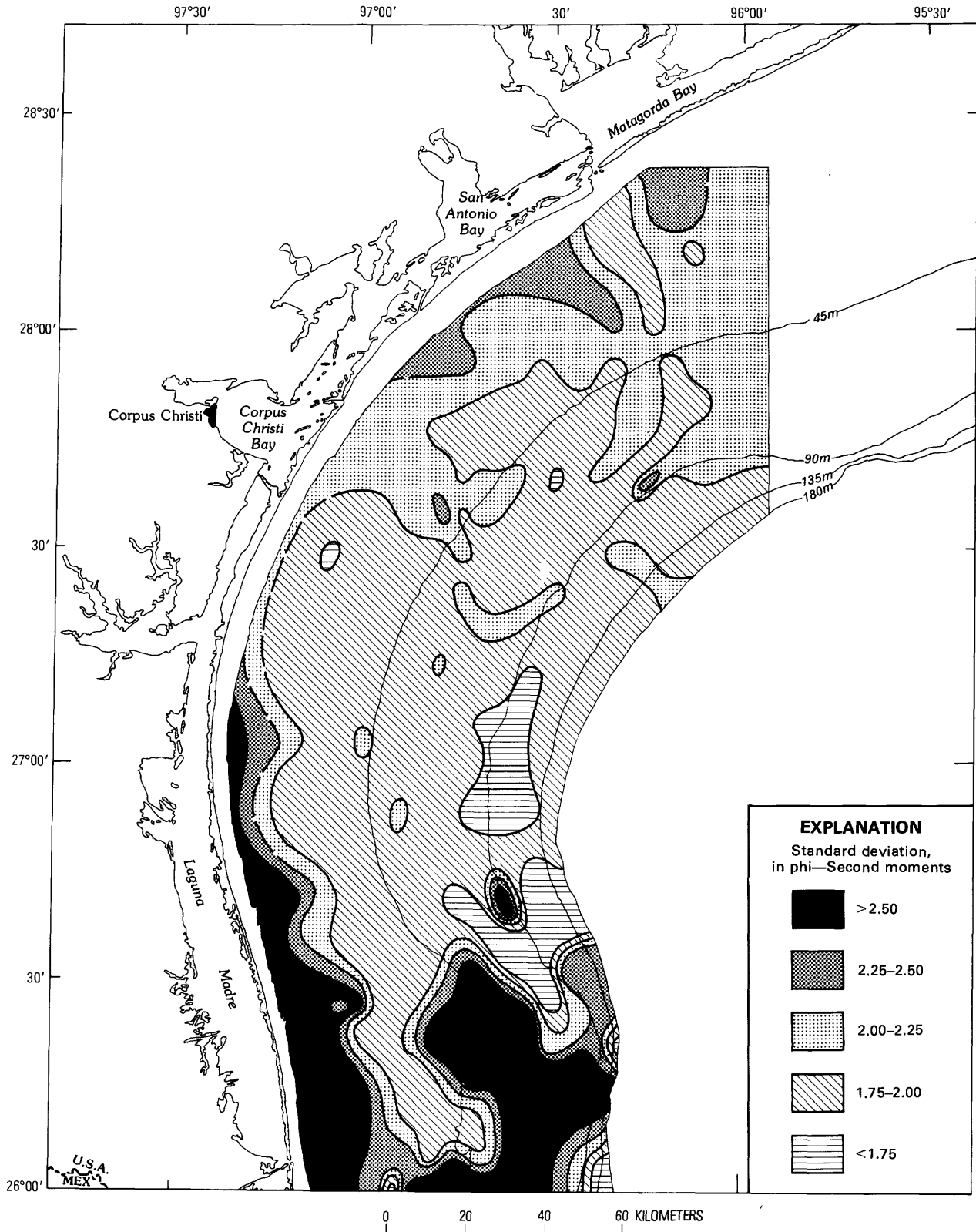
FIGURE 7.—Standard deviations of grain sizes, benthic sediments; from Berryhill and others (1976).

TABLE 4.—*Biological character-
istics by sample*

Parameter	Mean	Standard deviation
No. of species ..	7.62	4.98
No. of individuals	54.2	24.2
Biomass (g)	.44	.63
Diversity (H'')..	1.63	.68
Equitability....	.59	.21

on the whole had relatively high densities. Both anomalies probably reflect a biological response to local areas of sand defiency (fig. 5). An area of high population density occurs south of the ancestral Brazos-Colorado delta along the east edge of the study area. The higher density there probably reflects a response to a sedimentological characteristic not indicated by figures 5–7. The bottom sediments in the area contained many foraminiferal tests, among which *Orbulina* sp. is conspicuous. The numerous foraminifers in otherwise muddy sediments would effectively alter the textural characteristics of the sediment and thus affect the number and types of infauna.

Overall, the density of species and individuals over the South Texas OCS is low compared to that in the coastal waters adjacent to the OCS and in parts of the Continental Shelf farther north. For example, Holland and others (1974) reported 338 benthic taxa from Corpus Christi, Nueces, and Copano Bays and standing crops as large as 11,896 individuals/0.5 ft^3 (840,100/m^3). Manheim (1975) reported 190 species of polychaetous annelids alone from the shelf off Mississippi, Alabama, and the Florida Panhandle. The overall densities on the South Texas OCS probably are the result of the relatively homogenous fine-grained sediments characteristic of the region and the relatively high sedimentation rates of about 0.1 cm/yr (Berryhill and others, 1976).

BIOMASS

The biomass per sample ranged from zero to 29.9 g; the mean was 0.44 g (table 4). The gross biomass data in the study were subject to more sources of error than other aspects of the biological data for two reasons: First, the biomass per sample was generally very small and difficult to measure accurately; second, biomass per sample was influenced greatly by chance recovery of unusually large or heavy organisms. Mollusks are particularly troublesome because of their relatively heavy shells.

Areas of large biomass (>0.15 g) were in shallow water (generally <45 m) and in the extreme northern and southern parts of the region (fig. 8). A few isolated areas of small biomass (<0.05 g) were in deep water at the edge of the shelf. The ancestral Rio Grande and Brazos-Colorado deltas had relatively high biomass values (>0.15 g) compared to the central sector of the shelf.

The general decrease in biomass seaward agrees with results from a number of studies on the continental shelves of the United States (Sanders and Hessler, 1969). The areas of anomalously small biomass to the extreme north and anomalously large biomass south of the ancestral Brazos-Colorado delta on the shelf edge are similar in location, extent, and trend to the areas of anomalous density of species and individuals. The two areas of large biomass at midshelf in the central part of the study area reflect the chance recovery of large heart urchins (*Moira atropos*), which are known to occur in clusters.

Biomass is influenced by variations in rate of food supply related to such factors as proximity to source and transport processes. Patterns in the biomass distribution appear to match that of sediment distribution in the study area. It is, therefore, assumed that animal and sediment distribution reflect the influence of the same environment factors.

DIVERSITY AND EQUITABILITY

Calculated diversity (H'') values per sample ranged from zero to 3.10; the overall mean was 1.63 (table 4). The regional distribution pattern (fig. 9) is very irregular. The lowest values for diversity (<1.75) are in the central sector of the shelf between two ancestral deltas; the highest (>2.75) are concentrated mainly in the southern one-third of the study area and are associated with coarse-grained substrates. For the South Texas OCS in general, values for diversity are low.

The equitability per sample varied between zero and 1.0; the mean value was 0.59 (table 4). According to the regional distribution pattern for equitability (fig. 10), most of the study area is characterized by values between 0.4 and 0.7 the lowest values (<0.4) are prevalent in shallow water along the inner OCS, and the highest values are concentrated in the outer half of the OCS. Generally, values for equitability increase seaward.

The definition, significance, causes, and uses of various indices for diversity have been widely discussed in the literature (Hulbert, 1971; Hendrickson and Ehrlich, 1971; Margalef, 1958; MacArthur and Wilson, 1967; Sanders, 1968, 1969; Paine, 1966; Klopfer, 1959; Pianka, 1966; Woodwell and Smith, 1969; Johnson, 1970). The Shannon diversity index (H'') was chosen because it is based on both numbers of species and relative abundance, is relatively independent of sample size (Sanders, 1968), tends to be normally distributed
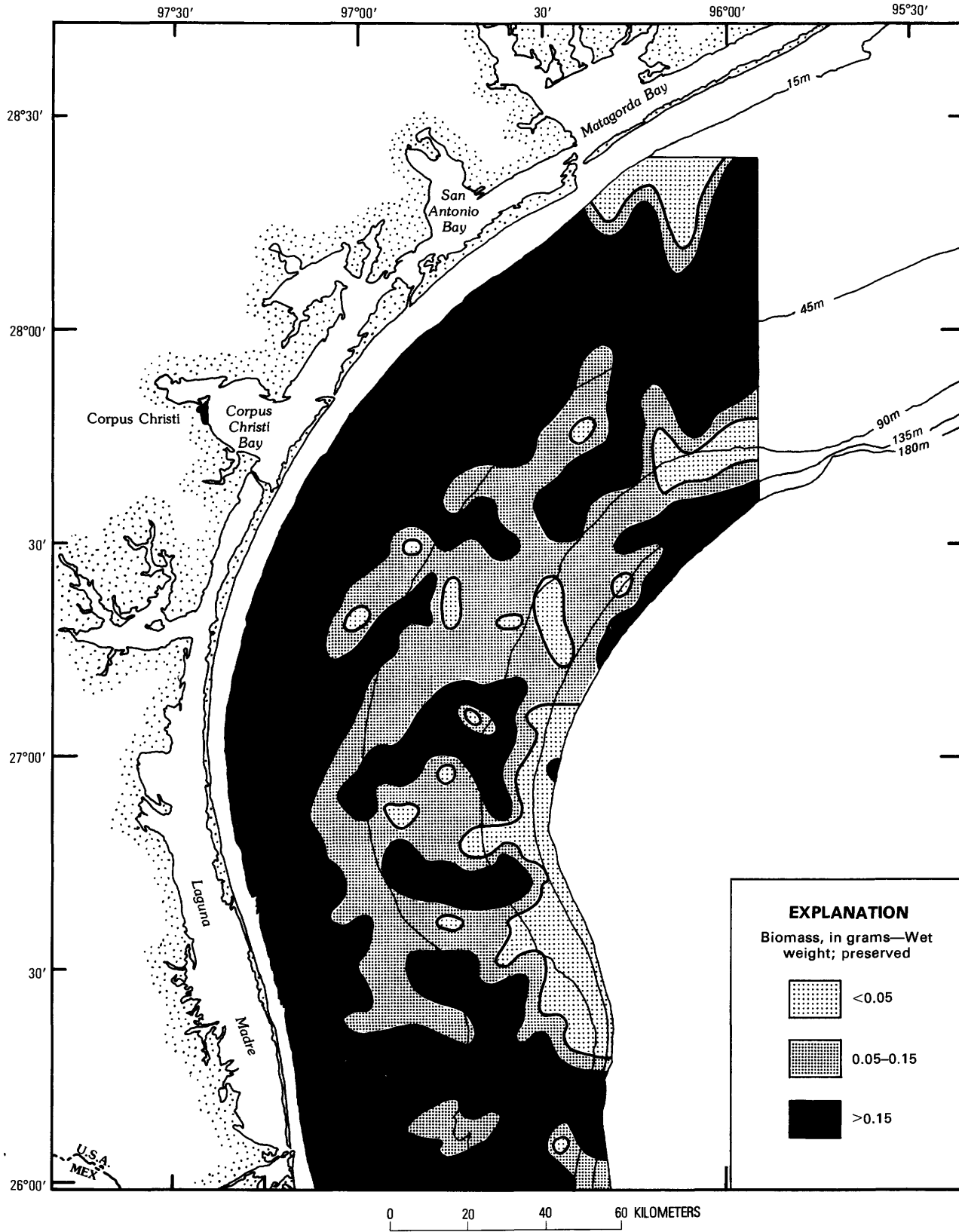
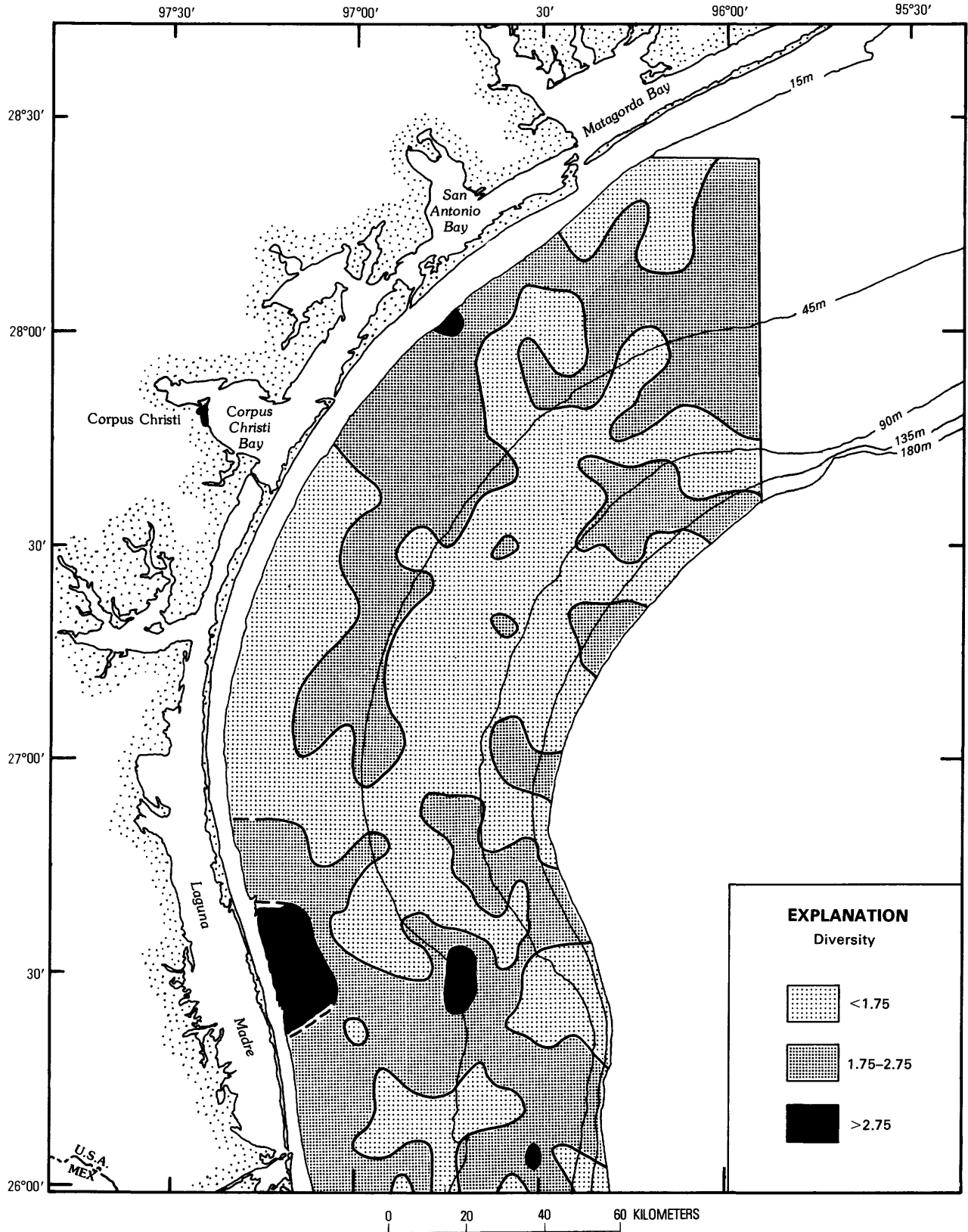FIGURE 8.—Distribution of biomass per sample (0.0125 m³).

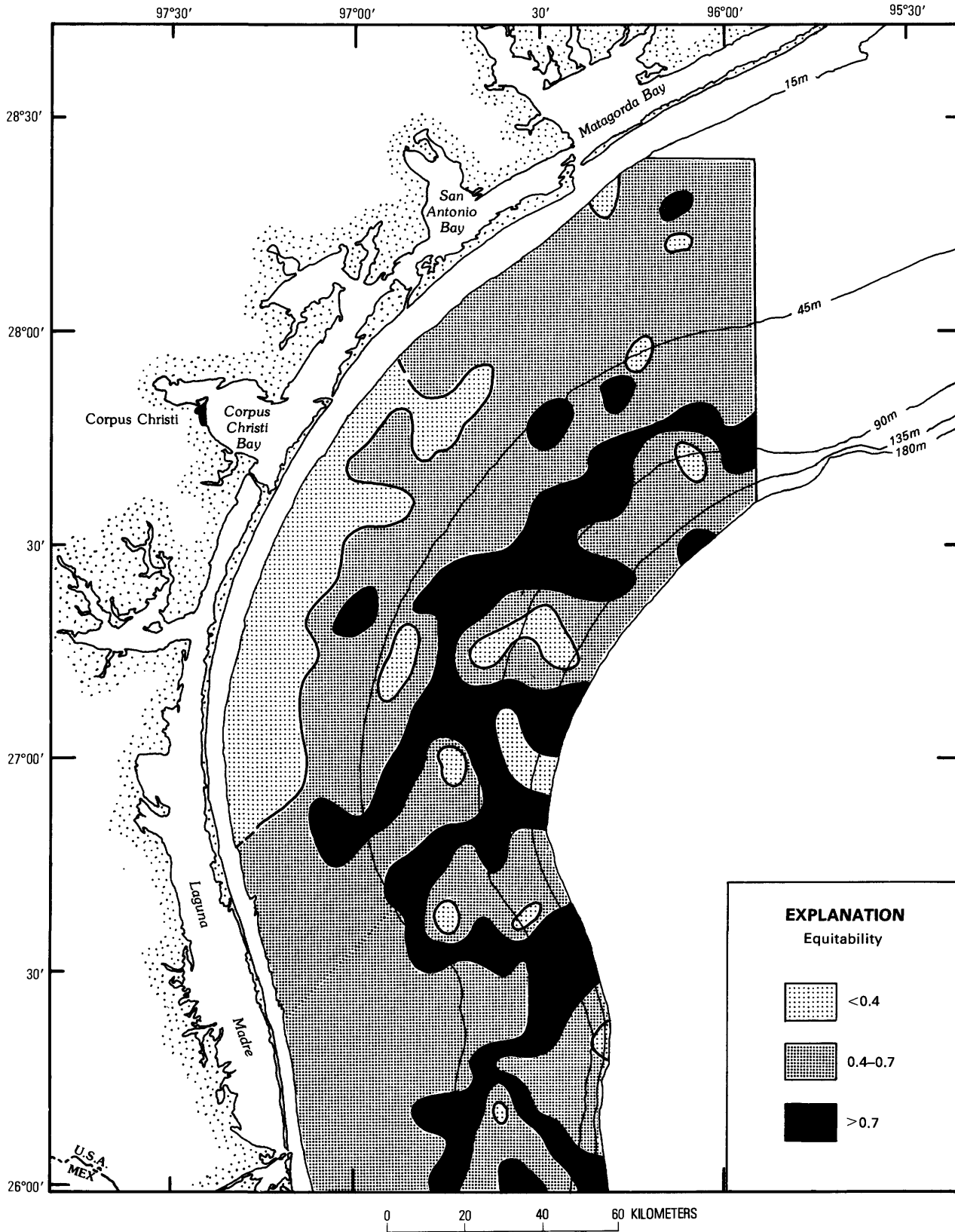FIGURE 9.—Infaunal diversity (H'') per sample (0.0125 m³).

FIGURE 10.—Infaunal equitability per sample (0.0125 m³).

(Hutchenson, 1970), and is easily calculated. The large volume of literature that attempts to explain observed patterns of diversity has been reviewed by Valentine (1971) and others. After reviewing the literature, R. J. Stanton (written commun., 1973) stated that "diversity is determined by the interplay of historical factors with the biological and physical factors in the ecosystem of time, stability, and resources." As a measurement of processes operating in an ecological system, diversity reflects external environmental stresses as well as internal stability and productivity (Beerbower and Jordan, 1969).

The regional patterns of diversity and equitability of the South Texas OCS do not agree completely with what has been found elsewhere. In studies of other shelves, both diversity and equitability increased in a seaward direction, away from the more variable and rigorous environments of the inner shelf and coastal waters (Stanton and Evans, 1971). Over the South Texas OCS, diversity generally decreases and equitability increases with increasing water depth.

At least two explanations are possible for these trends. First, as the number of species depends on the structural diversity of the habitat, in contrast to equitability, which is more sensitive to the stability of physical conditions (Beerbower and Jordan, 1969), the physical characteristics of the sediments flooring the South Texas OCS might explain the observed regional patterns of distribution for diversity and equitability. The shallow parts of the OCS and the ancestral deltas of the Brazos-Colorado Rivers and Rio Grande have the greatest variation in grain size of the sediment (habitat diversity) (fig. 7) and consequently support a more diverse fauna than the relatively homogeneous fine-grained sediments of the central, deeper sector. Second, because only one grab sample was taken at each station, moderate numbers of one or two very common species and a few individuals from a large group of uncommon or rare species theoretically could be recovered by each sample. If more grabs had been taken at each station, the numbers of individuals of the ubiquitous to very common species would probably increase at a higher rate than the numbers of common to rare species, as the number of grabs per station increased. Also, the domination of the total sample by the ubiquitous to very common group would be much greater, and so the equitability and diversity would be diminished. Consequently, the dominance by a few species would reflect less diversity for a given sample. Holland (1976) found through repetitive sampling at each of 12 stations on the South Texas OCS that inshore stations were dominated by a few species; thus, equitability and diversity of the total sample were low compared to offshore samples. Taking into consideration the results of previous studies, the regional distribution of equitability values over the study area, and the increasing dominance of a few

species relative to the number of individuals as water depth decreases (discussed later in this report), diversity (H'') probably increases in a seaward direction and decreases in the areas of the ancestral Brazos-Colorado and Rio Grande deltas.

General trends in the patterns for equitability are similar to those observed in other areas. As water depth decreases, the physical conditions (temperature, salinity, currents) are more variable, and the successional sequence leading to high equitability does not have time to develop fully before the ecosystem returns to a less mature state because of environmental change (Gibson, 1966).

SPECIES DISTRIBUTION

The macrobenthic infauna can be divided into three groups on the basis of distribution. The first consists of the common species, which were collected in 25 percent or more of the samples:

> polychaetes
> > *Paraprionospio pinnata*
> > *Nereis* sp.
> > *Magelona* sp.
> > *Nephtys picta*
> > *Cossura delta*
> amphipod
> > *Ampelisca* cf. *cucullata*
> nemerteans
> unidentified ophiurid

The second group consists of species that were not as widely distributed and occurred in 5–25 percent of the samples:

> polychaetes
> > *Ninoe nigripes*
> > unidentified paraonid
> > *Onuphis* sp.
> > *Lumbrineris* sp.
> > unidentified maldanid
> > *Sigambra tentaculata*
> > *Armandia agilis*
> > *Notomastus latericeus*
> > *Stehenelais* sp.
> > *Diopatra cuprea*
> > unidentified cirratulid
> > *Glycera* sp.
> > unidentified spionid
> > *Armandia maculata*
> mollusks
> > *Corbula* sp.
> > *Nuculana acuta*
> > *Diplodonta* sp.
> > *Nuculana concentrica*
> > unidentified gastropod

crustaceans
    Eudorella monodon
    Leptognatha gracilis
    Ampelisca cristoides
    Ampelisca cf. *cristata*
    Chasmocarcinus mississippiensis
    Speocarcinus sp.
    Pinnixa retinens
    unidentified sipunculid

The majority of the infaunal species were in the third group, the rare species that were found in less than 5 percent of the samples.

The spatial distribution of most common and uncommon species appears to be restricted (pl. 1). By dividing the study area latitudinally into thirds, four broad patterns of distribution were indicated:

1. Species that were most common in the north sector or south sector, or both, at all water depths, as well as in the inner half of the central sector. This was the most common distribution pattern.

    Ampelisca cf. *cucullata*
    Nereis sp.
    Paraprionospio pinnata
    unidentified nemertean
    Magelona sp.
    Chasmocarcinus mississippiensis
    Ninoe nigripes
    Onuphis sp.
    Speocarcinus sp.
    unidentified maldanid
    Ampelisca cristoides
    Nuculana concentrica
    Sigambra tentaculata
    Armandia agilis
    Ampelisca cf. *cristata*
    Notomastus latericeus
    Diopatra cuprea
    Nuculana acuta
    Armandia maculata
    undientified spionid
    Sthenelais sp.
    Eudorella monodon

2. Species collected from midshelf stations in all three sectors.

    Pinnixa retinens
    Leptognatha gracilis
    unidentified gastropod

3. Species mainly in the central sector and seaward of midshelf in the north or south sector or both.

    Cossura delta
    unidentified ophiurid
    Corbula sp.

4. Species primarily seaward of midshelf in the central sector, at all depths in the south sector to a lesser degree in deeper water in the north sector.

    Diplodonta sp.
    Glycera sp.
    unidentified echiurid
    unidentified cirratulid

The remainder of the common to uncommon species were widely and evenly distributed in most parts of the OCS.

    Nephtys picta
    Lumbrineris sp.
    unidentified paraonid

The distributions of all these species are shown on plate 1.

SUMMARY

The five biological parameters described shared two common regional trends. First, the number of species, number of individuals, and biomass tended to be highest in the inner shelf and decreased with the increasing water depth. The opposite trend was indicated for equitability and probably was true for diversity as well. Second, the smallest numbers of species, numbers of individuals, and amount of biomass were located generally in the central sector of the OCS, and numbers or amount in each category increased to the north and south. The ancestral deltas of the Brazos-Colorado and Rio Grande generally had higher values than areas of comparable water depth in the central sector. Again, equitability and diversity appeared to vary inversely with water depth.

The spatial distribution of common to uncommon species did not appear to be random. Most species were most common in the area of the ancestral deltas of the Brazos-Colorado and Rio Grande and landward of midshelf in the central sector.

Overall, general trends for the biological characteristics of the infauna appeared to be most sensitive to water depth and sediment texture.

MACROBENTHIC INFAUNAL ASSEMBLAGES

The regional patterns of distribution (figs. 3, 4, 8, 9, 10) and large standard deviations from the means (table 4) of the biological parameters measured indicate that the biological makeup of the South Texas OCS is not homogeneous and imply that the macrobenthic infauna may occur in specific assemblages. To identify and differentiate macrobenthic infaunal assemblages from the data, a classification type of numerical analysis was

used. Such analysis has been applied in other studies with useful results (Day and others, 1971; Field, 1970, 1971; Field and McFarlane, 1968; Hughes and Thomas, 1971a, b; Stephenson and others, 1970; Santos and Simon, 1974).

The computer program for the analysis was supplied by Joseph L. Simon, Department of Biology, University of South Florida, with the permission of John G. Field of Capetown, South Africa, who developed the program. A description of the program is given by Santos and Simon (1974) and is briefly reviewed here. The classification normally consists of four main steps:

1. Compute a similarity matrix.
2. Sort the data into groups.
3. Test the statistical significance of the groups.
4. Express the results by a suitable means.

Czekanowski's coefficient (Bray and Curtis, 1957; Field and McFarlane, 1968) was used to measure the faunal similarity between stations (interindividual measure). The Czekanowski coefficient is defined as

$$C = \frac{2w}{(a+b)}$$

where a is the sum of the species scores from sample a; b is the sum of the species scores from sample b; and w is the sum of the lesser scores of the two samples for each common species. Several characteristics of Czekanowski's coefficient made it suitable for use. For example, large numbers of zeros in the data do not affect the coefficient, and it considers the relative abundance of each organism, rather than simply presence or absence. The sorting strategy used was group average sorting for Q or normal analysis, an agglomerative polythetic-type system used successfully by Field (1970, 1971). This sorting strategy was selected because the average level of similarity between stations was investigated, not the relations between individual organisms (Hughes and Thomas, 1971b; Orloci, 1967).

To determine if subsets generated by the similarity analysis differed significantly, the information statistic $2\Delta I$ (Williams and others, 1966; Field, 1969) was used. The results of the analysis are expressed in a hierarchical dendrogram. The number of species was log transformed ($\ln x+1$) to save computer time, and species not in at least 5 percent of the samples were eliminated from the analysis.

The results of the numerical analysis are shown in figure 11. Several major groups (assemblages I through IV), which may or may not be distinctive macrobenthic infaunal assemblages, are evident. The regional dis-

tribution of the macrobenthic infaunal assemblages, as defined by the clustering technique, can be mapped (fig. 12). If the macrobenthic infaunal assemblages are significantly different, the differences should be reflected in the biological characteristics of each assemblage.

In the following sections, macrobenthic infaunal assemblages are described and compared through a series of characteristics, including number of species and individuals, biomass, and faunal composition. For each of these characteristics, except faunal composition, the mean values were calculated by assemblage (table 5). The mean values of diversity (H'') and equitability are also listed in table 5. The faunal composition for each assemblage, in terms of the percent of the total species and individuals represented by each of the major taxa (Polychaeta, Crustacea, Mollusca), is shown in figure 13. Because of the interpretive problems associated with the derived data as previously discussed, they were not used in defining the macrobenthic infaunal assemblages.

TABLE 5.—*Characteristics of macrobenthic infaunal assemblages*

Parameters (averages)	Assemblages			
	I	II	III	IV
Number species/0.0125 m³	11.55	6.81	6.46	18.09
Number individuals/0.0125 m³	51.19	11.27	10.46	347.55
Biomass g/0.0125 m³	.73	.32	.25	10.39
Diversity/0.0125 m³	1.89	1.68	1.57	2.44
Equitability/0.0125 m³	.46	.68	.72	.47
Water depth (m)	30	50	100	60

ASSEMBLAGE I

Assemblage I occurs in a zone parallel to shore along the entire OCS and is confined generally to that part of the shelf shoreward of the 40-m isobath, except in the southern part of the shelf. This assemblage covers large parts of the two ancestral deltas and in the extreme south extends well beyond the 40-m isobath to depths of as much as 90 m.

Assemblage I has the second largest number of species, number of individuals, and biomass of the four assemblages (table 5). Of the total number of stations (264), 20 percent (53 stations) were clustered in Assemblage I (fig. 11).

Assemblage I (fig. 13) is characterized by high percentages of polychaetes in terms of both species (61 percent) and individuals (54 percent). Following polychaetes in order of abundance for number of species and individuals are crustaceans (19 and 38 percent) and mollusks (13 and 2 percent). Miscellaneous taxa account for 7 percent or less of the total number of species and individuals.

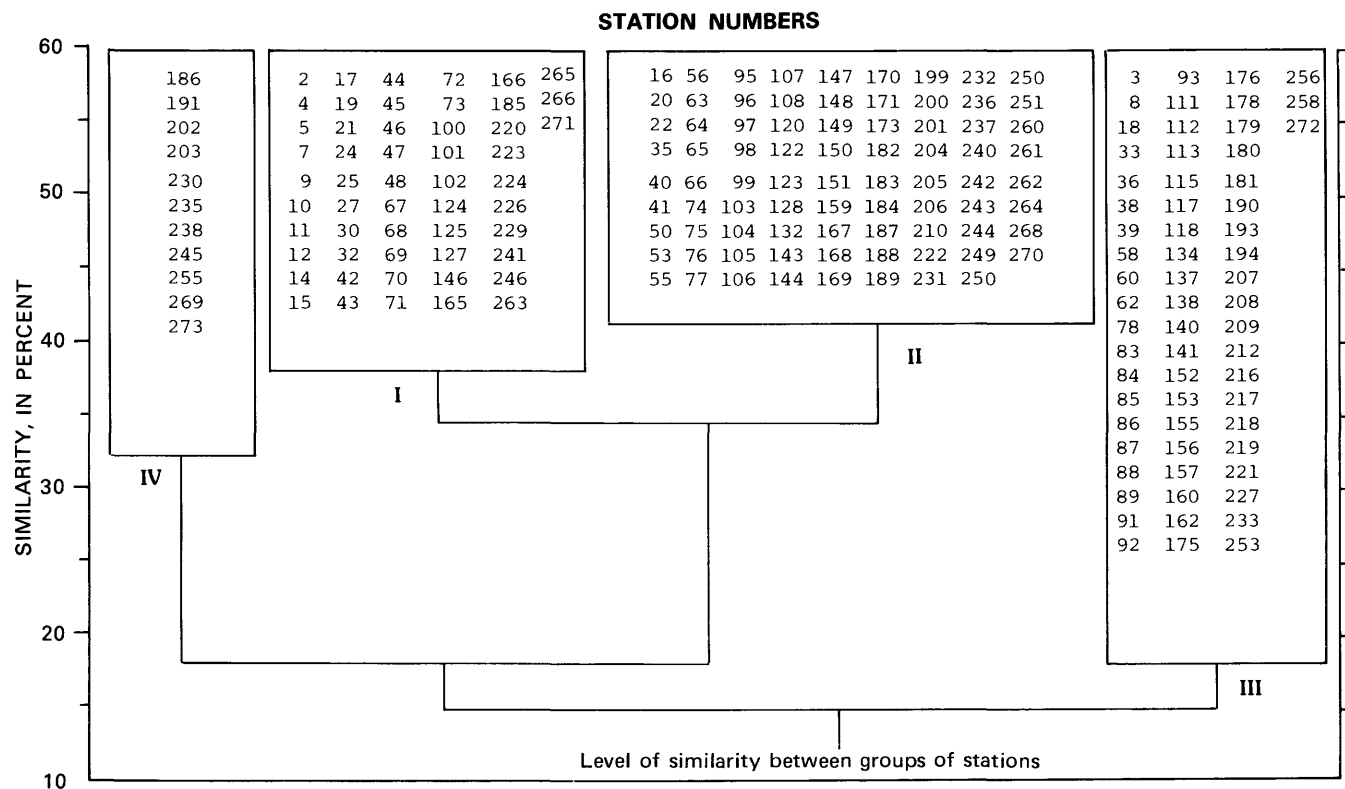The five most common species, in descending order,

STATION NUMBERS

FIGURE 11.—Dendrogram showing similarity of stations in terms of Czekanowski coefficient (see text; Bray and Curtis, 1957; Field and Mc-Farlane, 1968) and group average sorting for Q-mode analysis. See figure 12 for distribution of macrobenthic infaunal assemblages I-IV; see plate 1 for station localities.

are *Ampelisca* cf. *cucullata* (Crustacea, Amphipoda), *Paraprionospio pinnata* (Polychaeta), *Nephtys picta* (Polychaeta), a nereid polychaete, and *Ampelisca cristoides* (Crustacea, Amphipoda). These five species represent 67 percent of the individuals in assemblage I. A total of 88 species were collected from the samples in the assemblage.

ASSEMBLAGE II

Like assemblage I, assemblage II extends along the entire OCS, occupying a midshelf position that is generally bounded shoreward by the 40-m isobath. The seaward boundary is both irregular and eurybathic: in the central sector of the OCS, it approximates the 75-m isobath, but to the north and south on the ancestral deltas the assemblage extends in places to the shelf edge.

The mean values for numbers of individuals and species and biomass in assemblage II are the second lowest of the four assemblages. Approximately 30 percent (79 samples) of the total number of samples are clustered in assemblage II (fig. 11).

Polychaetes dominate assemblage II (fig. 13) as shown by the percentage of both polychaete species (59 percent) and individuals (63 percent). With respect to number of species, crustaceans ranked second (18 percent), mollusks third (14 percent), and other miscellaneous taxa fourth (9 percent). Crustaceans make up second largest group of individuals (16 percent), followed by miscellaneous taxa (14 percent) and mollusks (7 percent).

The five most common species in descending order are *Paraprionospio pinnata* (Polychaeta), *Nephtys picta* (Polychaeta), *Magelona* sp. (Polychaeta), nemerteans (Nemertinea), and *Eudorella monodon* (Crustacea, Cumacea). In assemblage II, 52 percent of the individuals belong to the five species. A total of 91 species are in assemblage II.

ASSEMBLAGE III

Assemblage III is found primarily along the outer part of the central sector of the South Texas OCS between the two ancestral deltas. The seaward boundary is the edge of the shelf (limit of area studied); the shoreward boundary is very irregular but approximates the 75-m isobath except in the southern and northern parts of the OCS. The assemblage also was found at shallower depths in
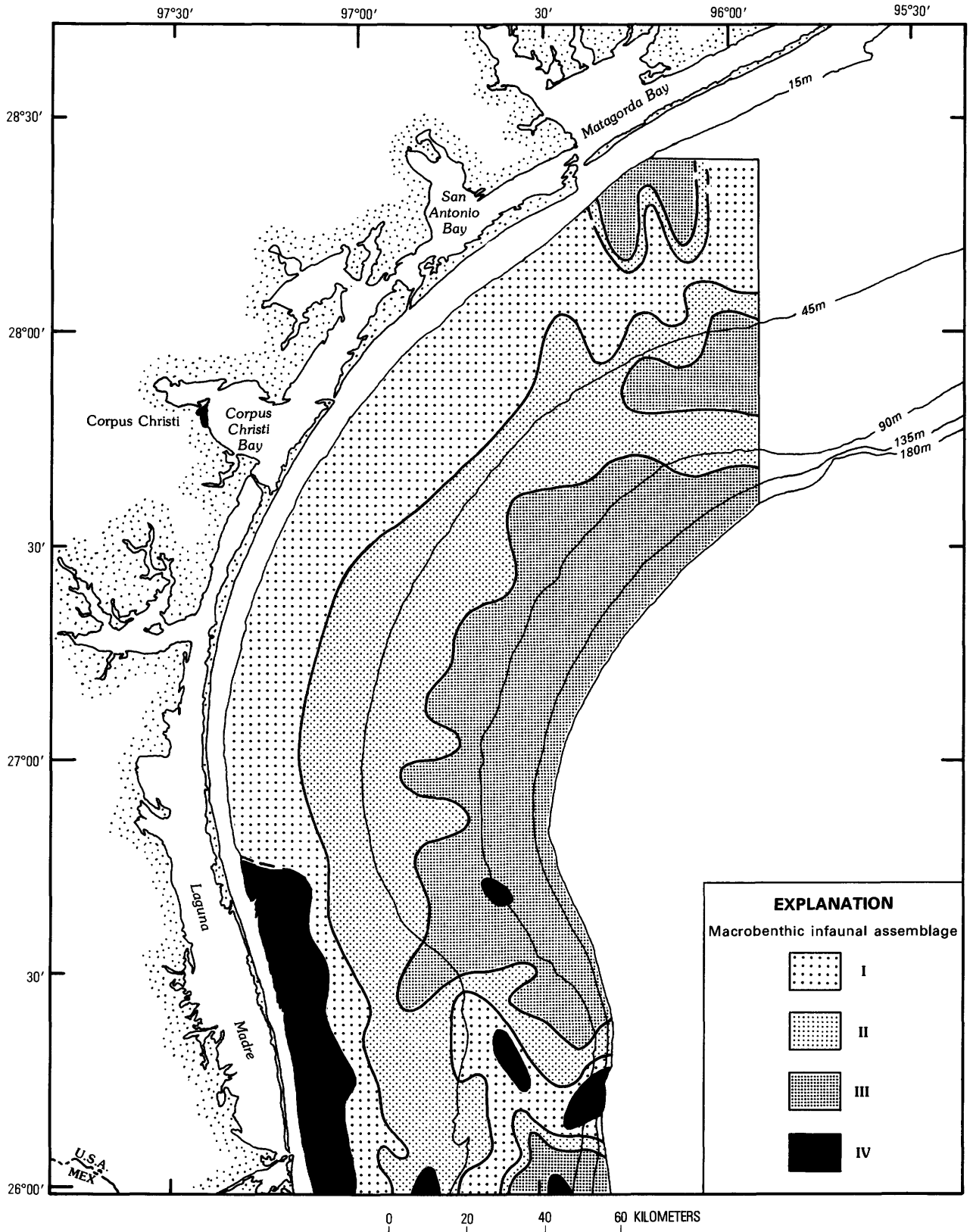
FIGURE 12.—Distribution of macrobenthic infaunal assemblages. Individual assemblages are numbered I–IV. (See fig. 11.)

NUMBER OF SPECIES, IN PERCENT

A

NUMBER OF INDIVIDUALS, IN PERCENT

B   EXPLANATION

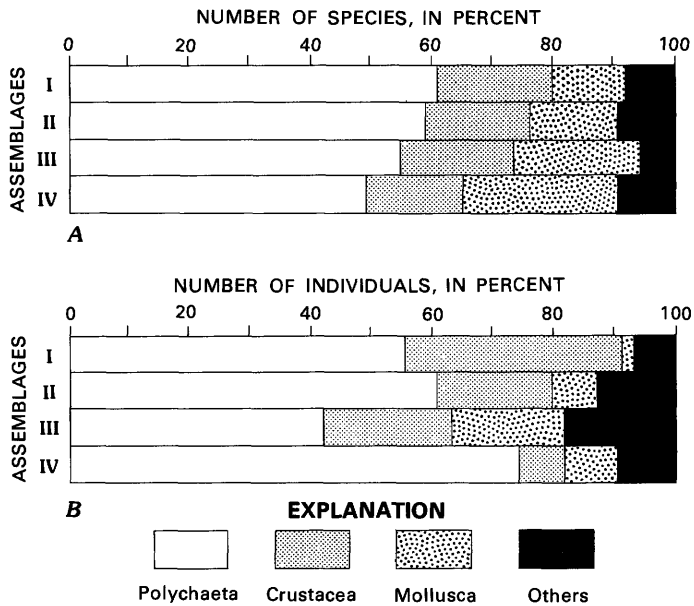Polychaeta   Crustacea   Mollusca   Others

FIGURE 13—Distribution among major taxa in four macrobenthic infaunal assemblages. A, Species. B, Individuals.

two areas in the northern sector of this study area, probably in response to local changes in sediment structure (fig. 12).

Assemblage III has the lowest average number of species and individuals and the smallest biomass of the four assemblages (table 5). Of the total 264 samples, 24 percent (63 samples) are clustered in assemblage III (fig. 11).

Polychaetes make up the largest part (55 percent) of the total number of species (fig. 13). They were followed by mollusks (21 percent), crustaceans (18 percent), and other miscellaneous taxa (6 percent). Polychaetes also represent the largest part (42 percent) of the total individuals, followed by crustaceans (21 percent), mollusks (19 percent), and miscellaneous taxa (18 percent).

The five most common species include *Diplodonta* sp. (Mollusca, Bivalvia), sipunculids (Sipunculida), *Ampelisca* cf. *A. vera* (Crustacea, Amphipoda), *Nephtys picta* (Polychaeta), and ophiurids (Echinodermata, Ophiuroidea). Thirty percent of the total individuals from this assemblage belong to these five species. Assemblage III contains 105 species.

ASSEMBLAGE IV

Assemblage IV has the most erratic and smallest areal distribution of the four assemblages (fig. 12). It occurs in the southernmost part of the South Texas OCS in a wide

range of water depths that extend from the inner to the outer shelf. The inshore boundary could not be determined because of the limitation of the study area. The assemblage is associated with gravelly (shelly) substrates that form low ridges from place to place across the ancestral Rio Grande delta. Most of the shell ridges are on the inner part of the ancestral delta.

Assemblage IV is the most densely populated and the most diverse (in number of species) of the four assemblages (table 5). Of the 264 sections, four percent (11 stations) were clustered in assemblage IV (fig. 11).

In terms of both species and individuals, polychaetes are most numerous (49 and 74 percent, respectively) followed by mollusks (26 and 9 percent) crustaceans (16 and 7 percent), and miscellaneous taxa (9 and 10 percent).

DISCUSSION

Assemblage IV in the southern part of the South Texas OCS is the most prolific of the assemblages. In the northern two-thirds of the OCS, the average biological parameters (table 5) decrease systematically seaward from assemblages I to III.

Regional trends are evident in the distribution of macrobenthic infaunal species and individuals among the major taxa in the different assemblages (fig. 13). Polychaetes are the dominant taxa with regard to both numbers of species and individuals, although their diversity and density generally decrease seaward. In contrast, the diversity and density of mollusks increase significantly as depth of water increases. Crustacean diversity is fairly constant across the shelf, but density decreases as depth of water increases and also decreases in the southern sector of the OCS. In shallow water, the individuals tend to be concentrated in a few species (table 6), particularly in assemblage I, where large numbers of amphipods are common. The individuals generally are more spread out among the species assemblages in deeper water and in assemblage IV. The percentage of species common to any two assemblages decreases with increasing spatial separation (table 7).

TABLE 6.—*Percentage of individuals in the most common 5, 10, 15, and 20 species for each macrobenthic infaunal assemblage*

Most common	Assemblages			
	I	II	III	IV
5 species	67	52	30	38
10 species	81	67	49	55
15 species	86	78	51	68
20 species	90	82	60	79

TABLE 7.—*Similarity of macro-benthic infaunal assemblages*

	I	II	III
II	67	---	---
III	47	53	---
IV	47	40	47

The only other study that attempted to recognize benthic assemblages on the South Texas OCS was that of Parker (1960). Of the several assemblages he described for the northwestern Gulf of Mexico, three are of particular significance to this study: the intermediate shelf assemblage (22–73 m), the outer shelf assemblage (73–119 m), and the upper continental slope assemblage (119–1,098 m). Parker concluded that the distribution of species followed certain ranges of bottom temperatures and major sediment types. His conclusions were based on the distribution of the molluscan fauna. Similar conclusions have been drawn for other parts of the U.S. Continental Shelf (for example, Cerame-Vivas and Gray, 1966). The assemblages defined in this study generally agree with Parker's assemblages. Differences in sampling technique, density of samples, and analysis, and the difficulty inherent in determining exact assemblage boundaries in gradational environments, preclude a detailed comparison of the two studies.

The differences in the biological parameters (table 5) used to characterize assemblages II and III are small but consistent. The results may be explained in the biological concept of the ecotone or boundary effect where two habitats overlap: The boundary zone is more favorable than either habitat alone (Odum, 1959). In the case of assemblage III, the texture of the bottom sediment is similar to that for adjacent assemblages, but the circulation of deep water from the Gulf of Mexico over the outer shelf in the central part of this study area (Parker, 1960; Berryhill and others, 1976) causes a change in the environmental conditions. As a result, the mixing of outer shelf and upper slope infauna increases both the number of species and the density of the fauna in assemblage III.

FACTORS CONTROLLING MACROBENTHIC INFAUNAL ZONATION

Variations in regional biotic patterns can be better understood by determining the controlling factors. Although the study was not designed specifically to identify factors that control faunal zonation, the variety of environmental aspects that we measured (sedimentological, biological, geochemical, and hydrological) can be assessed as to their role in observed biotic zonation. Two general relations are described with regard to their contribution in controlling zonation: interspecific relations and biologic-geologic-hydrologic relations.

INTERSPECIFIC RELATIONS

The importance of interspecific relations in zonation is measured by the ecological complexity of a community. Highly diverse populations that are relatively distinct and constant in their composition are said to exhibit a high measure of interspecific relations. The assemblages described are relatively low in taxonomic diversity, have many species in common, and, according to Holland (1976), fluctuate seasonally in composition. This may indicate that interspecific relations are a less significant factor than biologic-geologic-hydrologic relations in the control of macrobenthic infaunal zonation.

BIOLOGIC-GEOLOGIC-HYDROLOGIC RELATIONS

A series of regression analyses were performed to determine what relations existed between biologic, geologic, and hydrologic parameters. Stepwise regression was used to determine multiple correlation coefficients between individual biological parameters (dependent variables) and various combinations of physical parameters (independent variables) (table 8).

All the biological parameters correlated best with the sand-to-mud ratio. The correlations are significant, but the maximum variation explained is only 30 percent. As additional independent factors were introduced into the analysis, only depth of water made a significant increase (14 percent) in the proportion of variation explained.

The correlations might be poorer than expected from a visual comparison of the regional distribution maps for the various parameters. Part of the explanation lies in the absence of a strictly linear relation between the biological parameters and the physical parameter (par-

TABLE 8.—*Stepwise regression analysis for biological parameters versus physical parameters*

EXPLANATION OF VARIABLES

1. Number of species.	5. Mean grain size.
2. Number of individuals.	6. Standard deviation.
3. Biomass.	7. Water depth.
4. Sand-to-mud ratio.	

Biological parameters (dependent variables)	Physical parameters (independent variables)	Multiple correlation coefficient
1	4, 5, 6, 7	0.5217
1	4, 5, 7	.5200
1	4, 7	.5076
1	4	.4200
2	4, 5, 6, 7	.6710
2	4, 5, 7	.6707
2	4, 7	.6606
2	4	.5378
3	4, 5, 6, 7	.5871
3	4, 5, 7	.5870
3	4, 7	.5795
3	4	.5260

ticularly water depth), and the possibility that not all of the important physical parameters were considered. Poorer correlations may also have resulted from the variability inherent in the small samples taken from a large and diverse population.

The average values for three biological parameters were calculated for various classes of sand-to-mud ratios (table 9) and depths of water (table 10). These two physical parameters were selected because of their apparent influence on infaunal zonation in the study area as indicated by statistical analysis (table 9) and by visual comparison of the regional distribution maps for the various parameters (figs. 3–5, 8–10, 12). The number of species, number of individuals, and biomass increase with increasing sand-to-mud ratios. The most significant increase occurred where the sand-to-mud ratios exceeded 1.00.

TABLE 9.—*Some biological parameters of the South Texas OCS relative to sand-to-mud ratios*

Parameters	Sand-to-mud ratios		
	<0.12	0.12-1.00	>1.00
Number of samples	158	69	23
Average number of species	6.10	9.93	13.04
Average number of individuals	14.78	26.72	82.78
Average biomass (g)	.10	.64	8.14

TABLE 10.—*Some biological parameters of the South Texas OCS relative to water depth*

Parameters (per sample, 0.0125 m³)	Water depth (m)				
	0-40	41-80	81-120	121-160	161-220
Number of samples	87	105	42	14	7
Average number of species	10	6.8	5.3	5.5	6.9
Average number of individuals	37.3	11	7.1	7.0	12.6
Average biomass (g)	2.48	1.24	.31	.11	.23

One of the important aspects of water depth to biological communities is that bottom-water temperature changes with depth. The effect of bottom-water temperature on zonation of infauna within the study area was emphasized by Parker (1960). For our study, water temperature data were collected from expendable bathythermographs at 128 of the 264 bottom grab stations. For the winter of 1974, bottom-water temperatures reflect seasonally changing temperatures to about midshelf, with the bottom of the seasonal layer at about 70–80 m (fig. 14). These results agree with Parker (1960), who showed that at a depth of approximately 75 m the average winter and summer bottom-water temperatures differ, reflecting water mixing to the bottom (fig. 15). There is some indication in Parker's report that seasonal changes in temperature might occur to depths as great as 150 m. In this study the magnitude of the biological
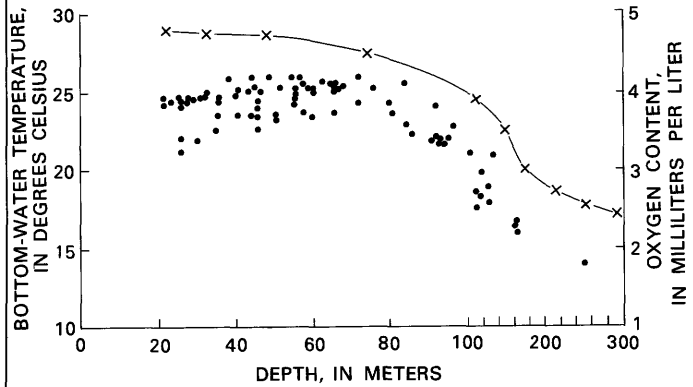

FIGURE 14.—Oxygen concentration (crosses) and winter bottom-water temperatures (dots) on the South Texas OCS. Oxygen data from Churgin and Halminski (1974).

parameters decreases down to about 120 m. Seaward of that depth, the biological parameters increase. The rough correlation of assemblage boundaries with the bottom of the seasonal water-temperature layer and with the increase in the magnitude of biological parameters in depth of relatively constant bottom-water temperatures indicates that water depth and bottom-water temperatures are probably important in controlling macrobenthic infaunal zonation.

Other factors related to water depth could also influence the distribution of biological parameters. For example, the bottom of the seasonal temperature layer may be the top of the oxygen-minimum zone. Churgin and Halminski's (1974) data on depth of the top of the oxygen-minimum zone for the western Gulf show the same general trend and depths as the bottom of the seasonal temperature layer (fig. 14). The oxygen levels
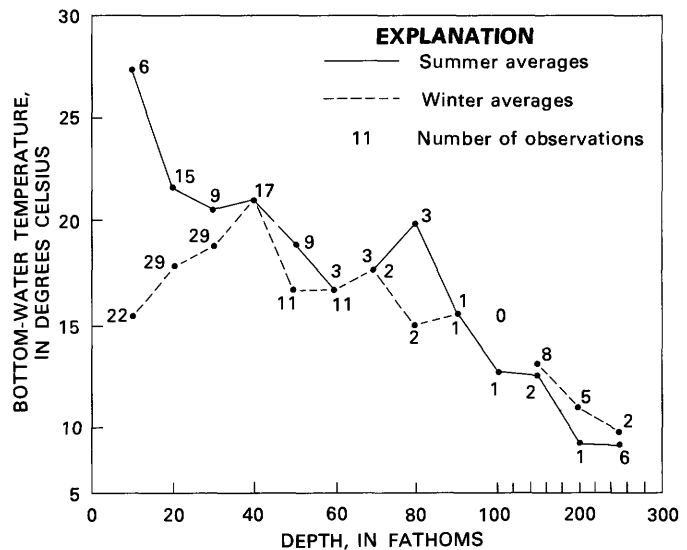

FIGURE 15.—Comparison of summer and winter average bottom-water temperatures in the northern Gulf of Mexico (1951-1955) (from Parker, 1960).

could be much more important than temperature on the distribution and density of organisms; however, we did not collect data that could be used to evaluate that factor.

DISCUSSION

Some knowledge of the factors that control zonation is important in classifying the assemblage observed. Depending on the gradients of environmental parameters and complexity of the communities involved, communities have been classified generally in other studies as discrete, discontinuous, or continuous gradations of one species assemblage into another (Gleason, 1939; Mills, 1969). Where environmental parameters are gradational, communities tend to be gradational as well (Beals, 1969). On the Continental Shelf, where such parameters as temperature, salinity, and light tend to vary in a continuous fashion, benthic communities on clastic substrates tend to be continuous and intergrading (Sanders and Hessler, 1969).

Another factor in classifying assemblages is the ecological complexity of the community. Communities characterized by low species diversity and by fluctuations in composition due to the physical environment are classified as immature or low grade; those characterized by high diversity and a relatively constant composition are mature or high-grade communities (Margalef, 1958). Sanders (1968) classified or graded communities in a similar manner. His classes are physically controlled (low grade) and biologically accomodated (high grade) communities. Biologically accomodated communities evolve when physiological stresses are low for short periods of time. As physiological stress increases because of an increase in fluctuating or unfavorable physical conditions, a gradual change in the community takes place to a predominantly physically controlled community. In these classifications, assemblages with high interspecific relations are termed high grade or biologically accommodated, and those with interspecific relations are termed low grade or physically controlled.

The results of this study indicate that interspecific relations are probably less important than biologic-geologic-hydrologic relations; environmental gradients are generally continuous; and the level of ecological complexity is relatively low. Consequently, assemblages on the South Texas OCS are classified as continuous, low grade, and physically controlled. This classification agrees with Johnson (1971), who viewed the nature of shallow-water marine benthic communities as "low-grade communities, largely controlled by the physical environment."

The above conclusion must be conditioned in light of current studies into the importance of biological interactions on community structure. Recent studies of intertidal and shallow subtidal environments have found that competition and predation may be key factors in previously described "physically-controlled" environments (for example, Woodin, 1974). To determine the factors that regulate community structure more precisely would require more in-depth investigations, including life-history studies.

BIOGENIC SEDIMENTARY STRUCTURES

Biogenic sedimentary (bioturbation) structures on the South Texas OCS are useful in sedimentologic and overall environmental interpretations of Holocene processes and events. Bioturbation structures vary in type, size, and orientation, and they reflect variations in infaunal diversity, density, and behavior. Burrows are the most common bioturbation structure. Large burrows are commonly indicated by burrow walls or by infilling of sediment; smaller burrows are commonly seen only on X-ray radiographs. Intense burrowing destroys the original grain-size relation in the sediment as well as the depositional layering.

The distribution and variability of bioturbation were determined by studying the radiographs of the pipe cores and box cores taken as a part of the geologic studies over a two-year period (fig. 16). The extent and magnitude of bioturbation in the cores are shown by Berryhill and others (1976, figs. 48-58, 93-100). In addition, the density or degree of bioturbation in the cores was estimated for subsurface depth increments of 0-25 cm, 25-75 cm, 75-125 cm, and greater than 125 cm to see if changes in the amount of bioturbation with depth might indicate changes in the nature and distribution of infaunal assemblages with time.

ZONATION

Zonation of biogenic sedimentary structures is related to macrobenthic infaunal assemblages and sediment facies. The zonation can be defined in terms of distribution, density, and diversity.

The regional distribution map of bioturbation in the upper 25 cm of all pipe cores (fig. 17) shows that the intensity of bioturbation generally decreases seaward and that surficial sediments of the two ancestral deltas are highly bioturbated.

Assemblages of biogenic sedimentary structures (ichnocoenoses) (fig. 18) were studied by dividing the study area latitudinally into thirds. Changes with water depth within each sector were also noted. The majority
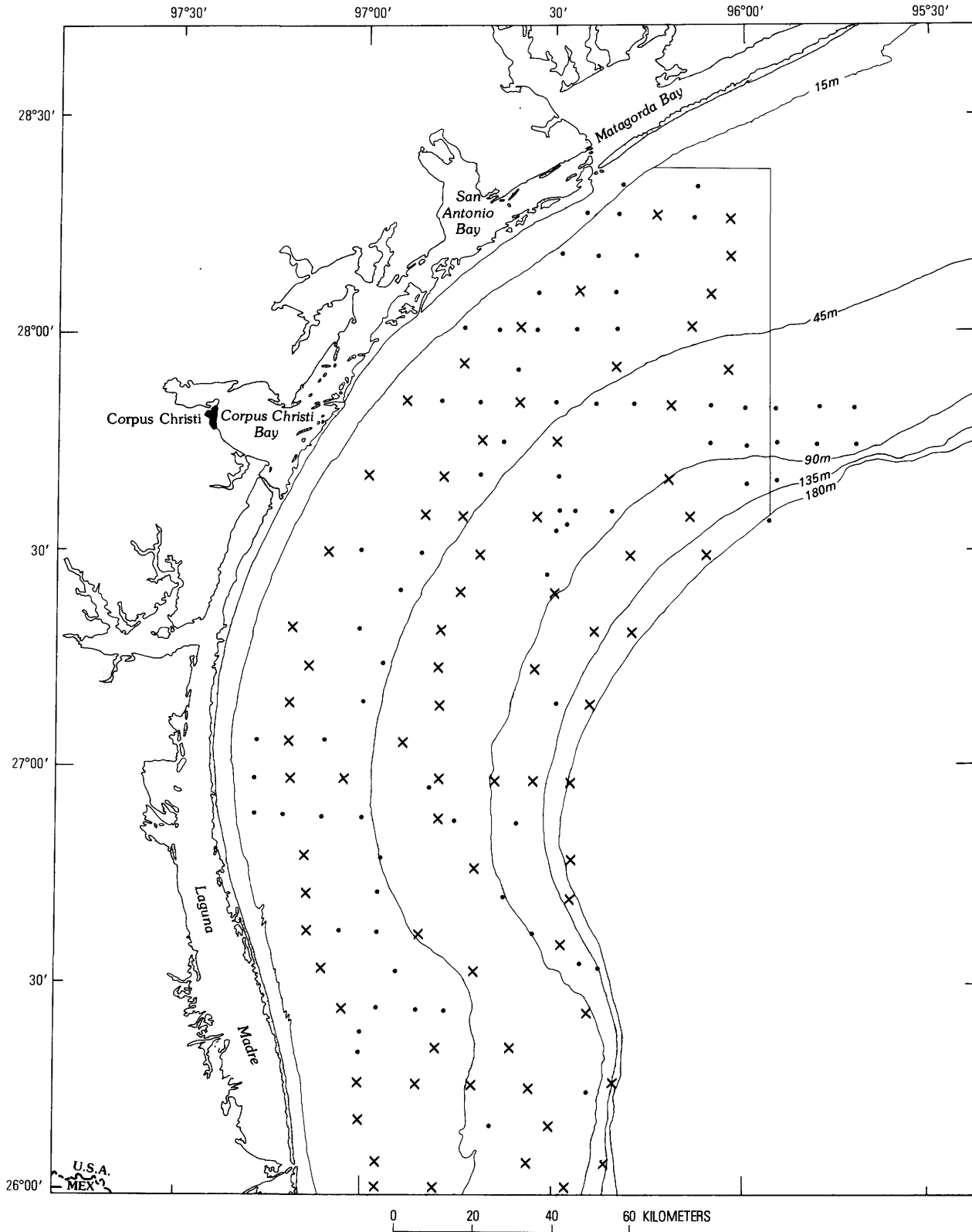
FIGURE 16.—Locations of pipe-core and box-core stations: dots are pipe core only; crosses are pipe core and box core.
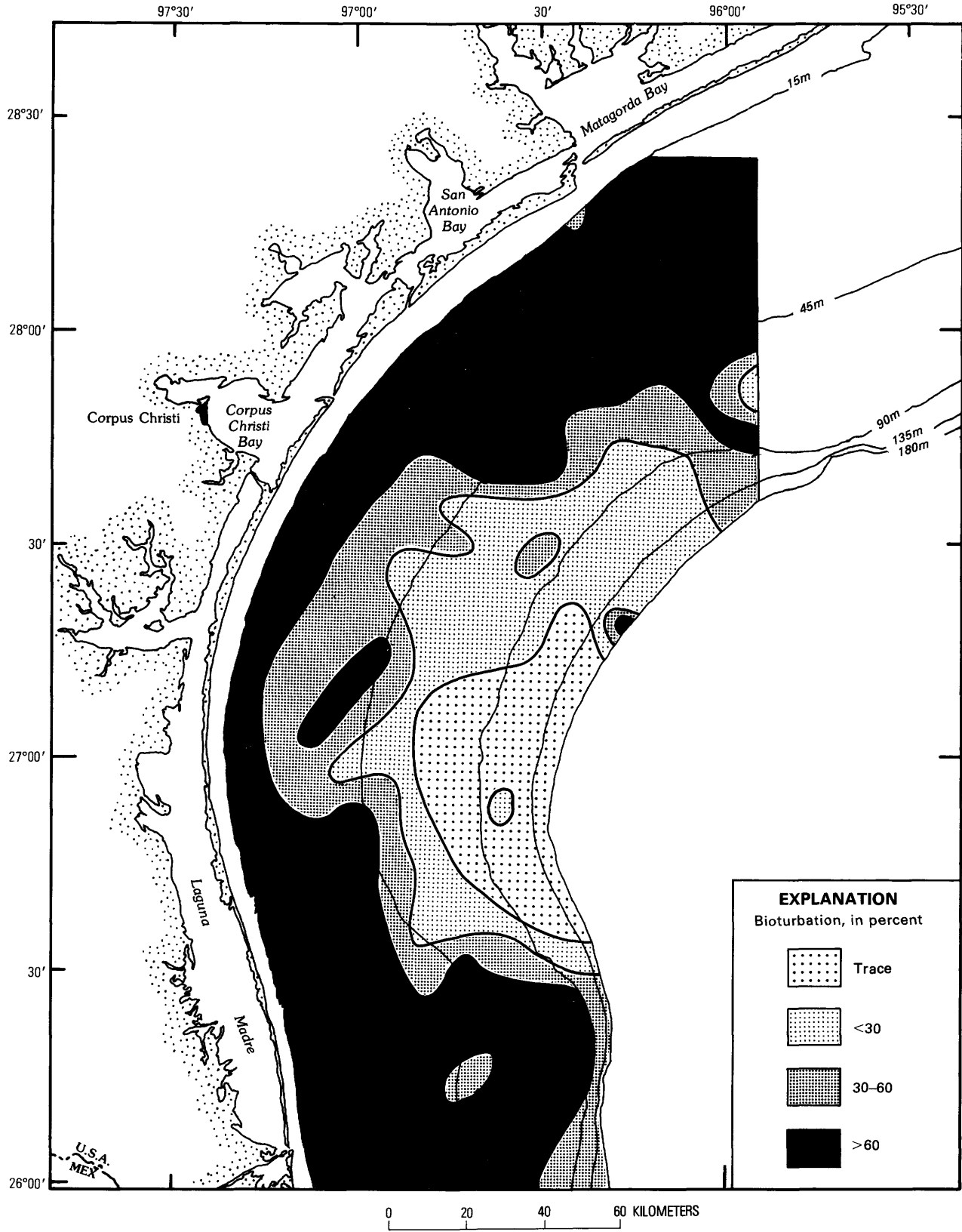
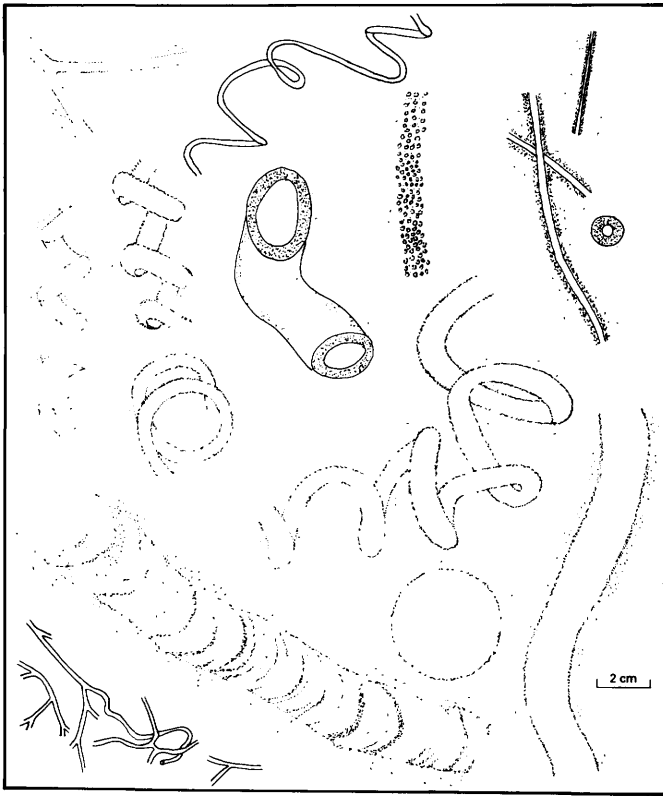FIGURE 17.—Bioturbation in the upper 25 cm of pipe cores.

FIGURE 18.—Examples of biogenic sedimentary structures observed in radiographs of box-core slabs. Structures represent various types of animal burrows and intrastratal trails.

of these biogenic sedimentary structures throughout the study area are the result of burrowing polychaetes and crustaceans.

The zonation (fig. 17) generally parallels the macrobenthic infaunal zonation (fig. 12). Substrates having relatively dense and diverse biogenic sedimentary structures are associated with infaunal assemblages characterized by more species and individuals, and larger biomass. Infaunal assemblages with these characteristics are found in shallower water and on both ancestral deltas.

Comparison of the regional distribution maps suggests a rough similarity between the zonation of biogenic sedimentary structures (fig. 17) and the physical characteristics of the sediments (figs. 5, 6, 7). Diversity and density of biogenic sedimentary structures decrease as mean grain size decreases; mean grain size generally decreases as water depth increases.

To determine whether biogenic structures are related to sediment characteristics, regression analyses for bioturbation (dependent variable) versus various biological and physical parameters (independent variables) were performed (table 11). In making these calculations,

the several classes of bioturbation intensity were given an arbitrary value (trace, 1; less than 30 percent, 2; 30–60 percent, 3; greater than 60 percent, 4). In the broadest perspective, the degree of bioturbation correlates best with water depth; as water depth increases, bioturbation decreases. As other physical and biological aspects are introduced into the analysis, the correlation improves; mean grain size of the sediment is the most significant addition. This analysis accounts for almost 70 percent of the variation observed in bioturbation.

In summary, the diversity and density of biogenic sedimentary structures generally decrease seaward across the shelf as the infaunal assemblages become less dense and diverse and the substrate finer grained with increasing water depth. Biogenic structures may be extremely useful in defining environments of deposition, in determining the extent to which original textural relations within a sediment have been altered by burrowing organisms, and in predicting the extent to which pollutants might become concentrated in seafloor sediments as a result of infaunal activity.

TABLE 11.—*Stepwise regression analysis for bioturbation versus biological and physical parameters*

EXPLANATION OF VARIABLES

1. Number of species.	5. Mean grain size.
2. Number of individuals.	6. Standard deviation.
3. Biomass.	7. Water depth.
4. Sand-to-mud ratio.	8. Bioturbation.

Dependent variable	Independent variable(s)	Multiple correlation coefficient
8	1, 2, 3, 4, 5, 6, 7	0.8179
8	1, 2, 4, 5, 6, 7	.8176
8	1, 4, 5, 6, 7	.8153
8	1, 4, 5, 7	.8104
8	1, 5, 7	.8054
8	5, 7	.8004
8	7	.7608

VARIATIONS IN ICHNOCOENOSES

The extent of bioturbation was mapped for deeper core intervals (25–75 cm; 75–125 cm; >125 cm) to determine if changes in the spatial distribution of bioturbation have occurred through time, assuming deposition has been continuous (figs. 19–21). The maps indicate that with passage of time that areas of greater than 60 percent bioturbation have increased in size, and that areas of little bioturbation have diminished. Although the variation in bioturbation is pronounced, the general regional pattern of distribution for deeper core intervals is basically similar to that indicated by the upper 25 cm (fig. 17); the intensity of bioturbation generally
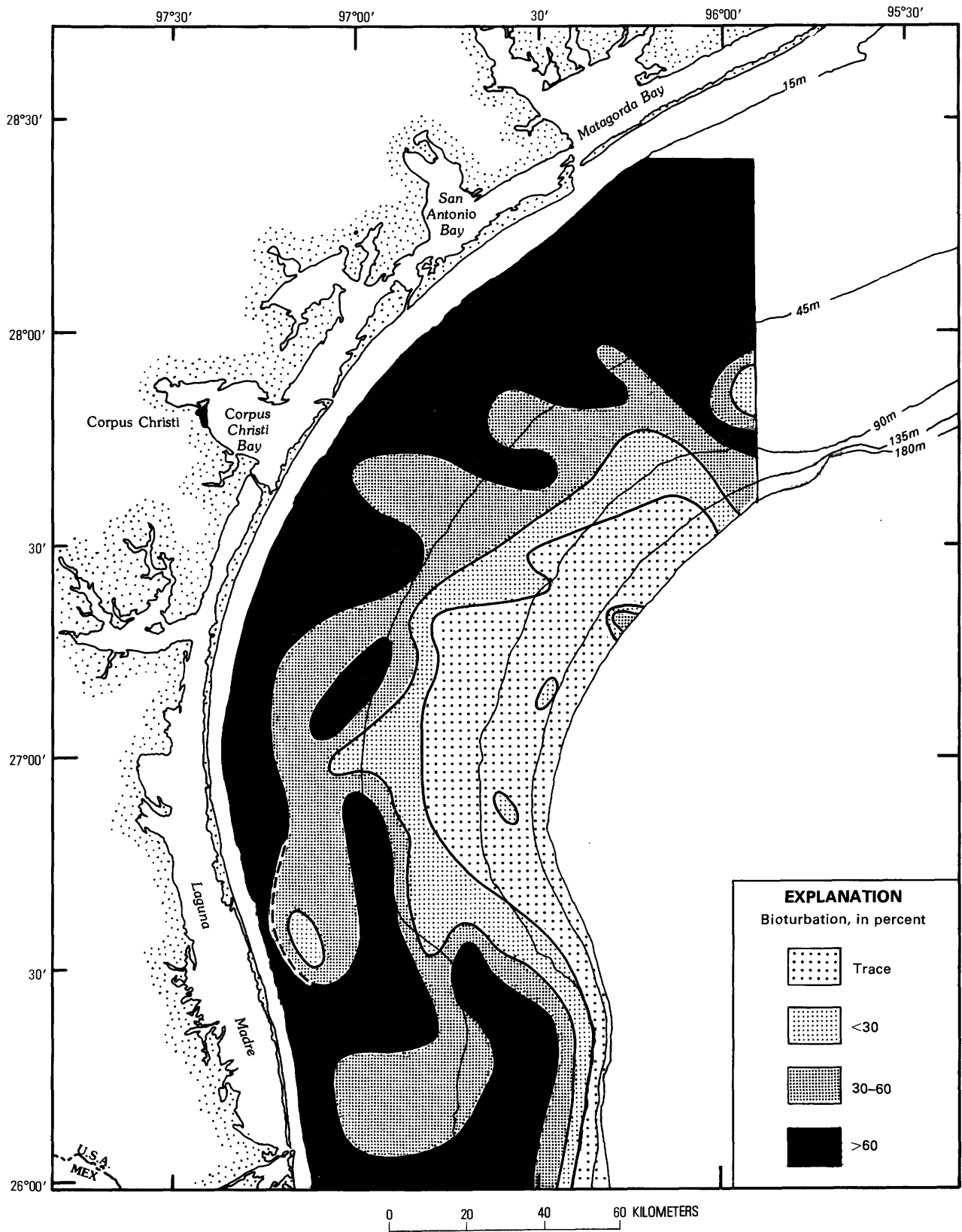
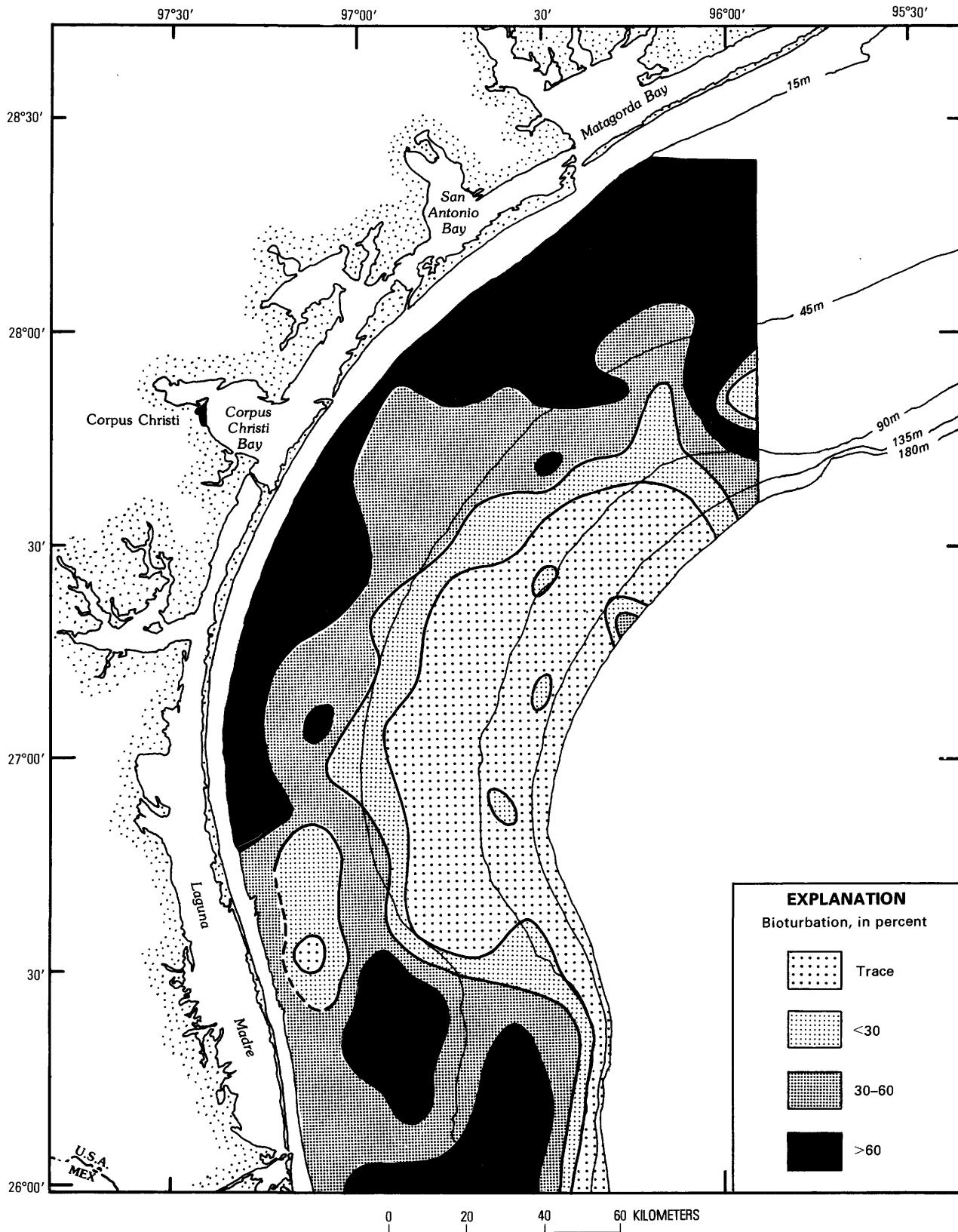FIGURE 19.—Bioturbation in the pipe-core interval 25–75 cm.

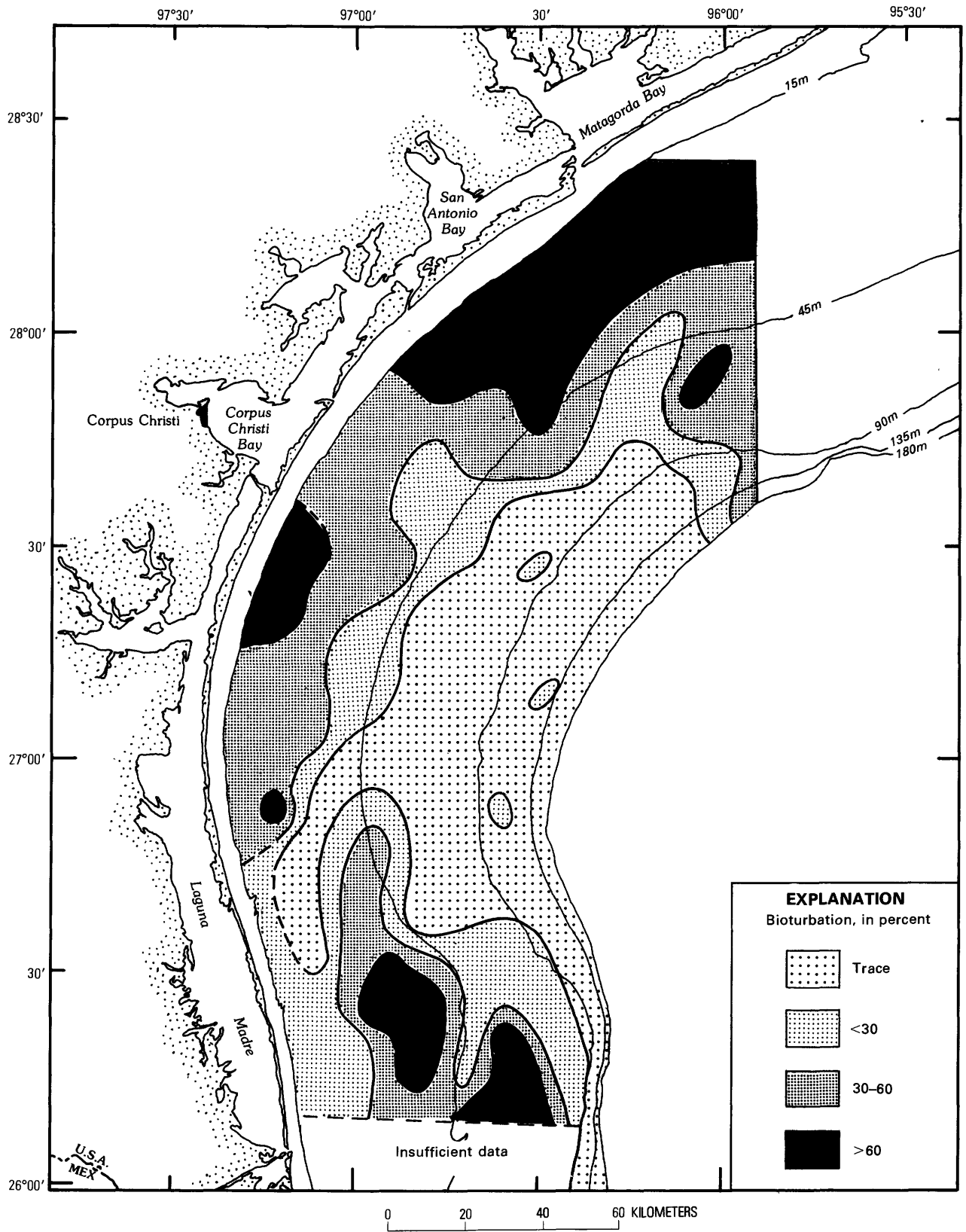FIGURE 20.—Bioturbation in the pipe-core interval 75–125 cm.

FIGURE 21.—Bioturbation in the pipe-core interval greater than 125 cm.

decreases as water depth increases, and the central sector of the study area has little bioturbation relative to other parts of the OCS.

The spatiotemporal variations in bioturbation may be related to changes in biological and physical processes during the time interval represented by the length of the pipe cores. According to Berryhill and others (1976) the "sediments contained in the longer pipe cores would seem to represent an average of approximately 2,000 to 1,500 years." Both the time estimate and the interpretations of the spatiotemporal variations are tentative.

Determination of the original diversity and density of fossil assemblages is virtually impossible using biogenic sedimentary structures alone; however, the structures do permit at least an estimation of the assemblages involved (Frey, 1971). The observed variation in bioturbation through time could indicate changes in the benthic infauna. If this were true, a variation in diversity and composition of ichnocoenoses would accompany density changes, using the similarity between patterns in recent zonation of infaunal assemblages and bioturbation as a guide. The cores indicate that the most significant change has been in the density of bioturbation and not in the diversity, composition, or zonation of ichnocoenoses. This finding implies little change in macrobenthic infaunal zonation but at least a minor change in the physical processes.

Our study has shown that intensity of bioturbation appears to relate best with animal distributions and these, in turn, appear related to water depth and sediment texture. Changes in these physical parameters in the past could have produced the observed variation in bioturbation. For the study area in general, ample evidence (position of barrier islands and reefs, for example) indicates little if any change in water depth during the last few thousand years.

Changes in sediment texture might explain the variation in bioturbation. In the upper 25 cm of sediment, bioturbation was most dense in relatively sandy areas. If sand were more limited in areal distribution in the older Holocene sediment, and the fauna changed accordingly, a decrease in the density of bioturbation might be expected. The relative areal distribution of the sand and mud facies in the cores (fig. 22) indicates, however, that sand is more widely distributed in the deeper sediment than in the more recent surficial sediments (Berryhill and others, 1976).

It may be that the variations in density of bioturbation through time are caused by changes in the rate of sediment deposition. The overall increase in the density of bioturbation in the younger Holocene sediments probably is caused by a decrease in rates of deposition within the study area, particularly in the central part of the shelf. The conclusion is supported by results of sedimentation-rate studies discussed in Berryhill and others (1976), which indicate that the lowest rate of sedimentation during the past 150 years has been in the central part of the shelf. Furthermore, data on the overall thickness of the Holocene sequence reported by Berryhill and others (1976) indicate that the current area of low sedimentation rate previously had a much higher rate of sedimentation.

CONCLUSIONS

1. In South Texas OCS, numbers of species and individuals and amount of biomass generally decrease with increasing water depth. Equitability increases across the shelf as water depth increases. The central sector has generally fewer dense and diverse populations than do the areas of the ancestral Rio Grande and Brazos-Colorado deltas to the south and north.

2. Four macrobenthic infaunal assemblages in the study area can be defined on the basis of species distribution and density. The most dense and diverse assemblage (IV) is located in the southern third of the study area; whereas, assemblages near the shelf edge in the central sector are low in density.

3. Polychaetes, crustaceans, and mollusks are the dominant infaunal taxa. As water depth increases, the percentage of polychaete species and individuals decreases. In contrast, the number of mollusk species and individuals increased seaward. The number of crustacean individuals significantly decreases with increasing water depth, primarily because of a large reduction in number of amphipods.

4. Overall, macrobenthic infaunal zonation on the South Texas OCS is best described as continuous, low grade, and physically controlled. Water depth and sediment texture are particularly important in controlling infaunal zonation.

5. Bioturbation ranges greatly in degree. Diversity and density of biogenic structures decrease as mean grain size decreases and water depth increases, most likely in response to the concomitant decreases in species number, individuals, and biomass.

6. Zonation of biogenic sedimentary structures generally parallels macrobenthic infaunal zonation in terms of diversity, density, and distribution of specific types of structures. Bioturbation patterns are useful in identifying spatiotemporal variations in macrobenthic infaunal zonation.
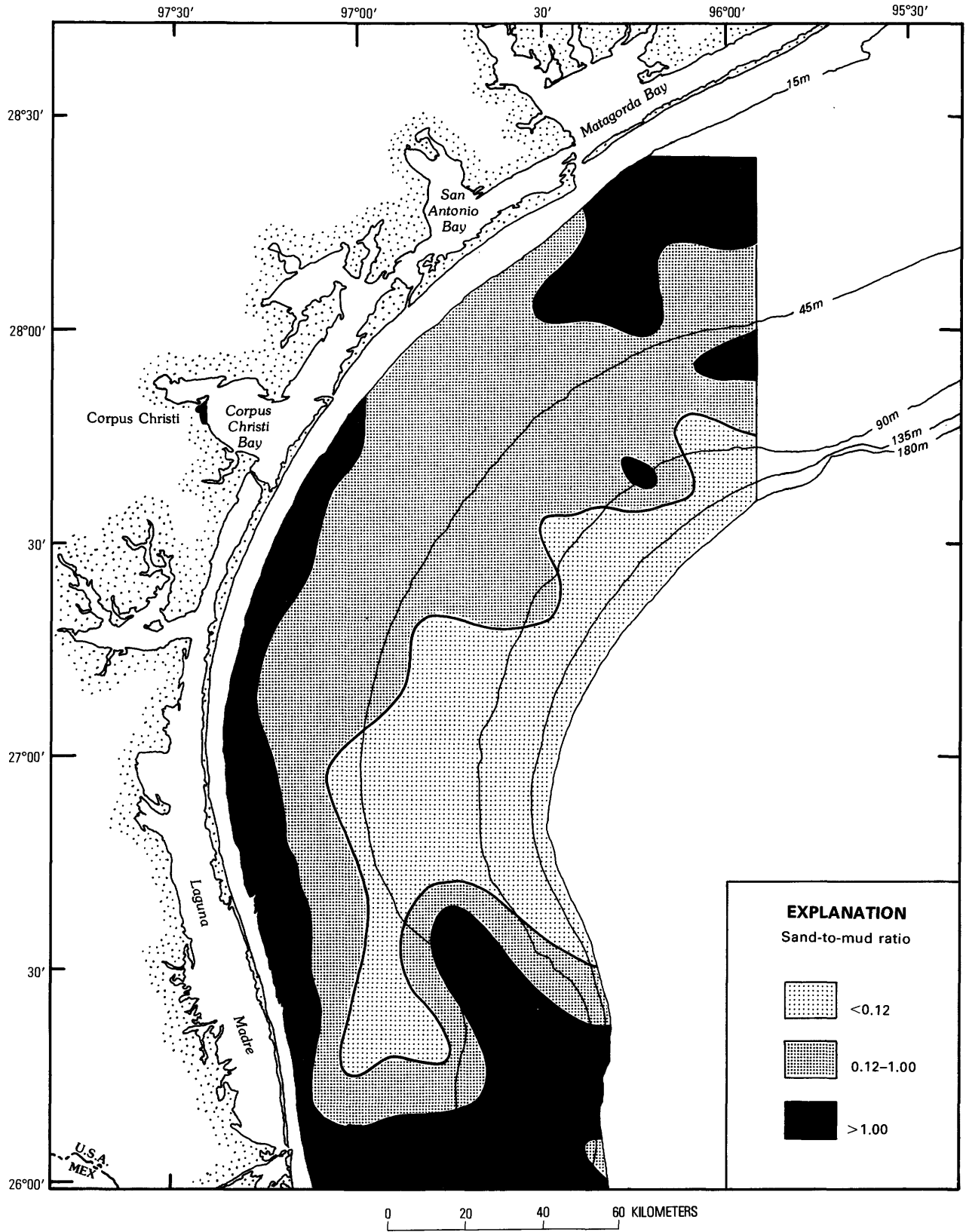
FIGURE 22.—Sand-to-mud ratios in the pipe cores (modified from Berryhill and others, 1976).

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