ECOLOGY AND DISTRIBUTIONAL PATTERNS OF MARINE MACRO-INVERTEBRATES, NORTHERN GULF OF MEXICO[1]

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ABSTRACT

The macro-invertebrate assemblages in the northern Gulf of Mexico can be separated into those occurring in the shallow lagoons and estuaries and those on the continental shelf and slope. Distributional patterns of faunal assemblages in lagoons and estuaries are considerably modified by prevailing climates. Climatic control is exerted to a lesser degree in the shallow waters on the continental shelf.

Eleven macrofaunal assemblages are recognized in the lagoons and estuaries along the northern coast of the Gulf of Mexico. Within each climatic zone certain of these assemblages are predominant, whereas others may be completely absent. Those assemblages which tolerate extended periods of low salinity, such as fresh-water marsh, river-influenced, and low-salinity oyster-reef assemblages, cover extensive areas in the humid zone. The number of species is small and populations are high in these environments. High-salinity assemblages characterize the semiarid zone, and here, also, large populations and a small number of species are typical. Within the subhumid zone, and its corresponding wide range of physical factors, most of the eleven macrofaunal assemblages are present. The extent of these assemblages in the subhumid zone is dependent entirely upon the prevailing climate at the time of sampling; during droughts, high salinity, open bay and sound assemblages predominate, and during wet periods, oyster reef and inter-reef assemblages are the most extensive.

Eight macrofaunal assemblages occur on the continental shelf and upper continental slope to 500 fathoms. Although six of these assemblages appear to be confined to rather narrow depth ranges, they are considerably modified by sediment type and average bottom-water temperature conditions. The general limits of the six level-bottom assemblages are (1) surf zone, (2) 2–12 fathoms, on the open coast, (3) 2–12 fathoms off the Mississippi Delta, (4) 12 to 30–40 fathoms, (5) 40–65 fathoms, and (6) 65–500 fathoms. One assemblage is restricted to rocky or calcareous bottom regardless of depth, and another consists of pelagic mollusks which indicate offshore surface waters.

Changes in climate and associated shallow-water environments are demonstrated for the Holocene transgression across the continental shelf of the northwestern Gulf of Mexico by using carbon-14-dated shells of species with restricted depth and environmental range, and temperature restrictive geographic ranges. At about 11,000 and again 9,000 years before present, the distribution of dated mollusk shells indicates that the climate along the now submerged shore lines changed from warm-temperate to subtropical and tropical. These conditions were synchronous with major circulation changes in the northern Gulf of Mexico as deduced from other evidence. The presence of extensive deposits of low salinity and surf-zone shells on the continental shelf also permits an interpretation of the location of large lagoons and estuaries and extensive stretches of barrier beaches during various periods of the Holocene transgression.

INTRODUCTION

The northern Gulf of Mexico is an excellent region for the study of the patterns of macro-invertebrate distribution in relation to a variety of ecological factors. This region (Fig. 1) is in warm-temperature latitudes and is characterized by climates ranging from humid, warm-temperate in the east, to semiarid, subtropical in the southwest. The central portion of the coast has the most extreme climate, with freezing temperatures

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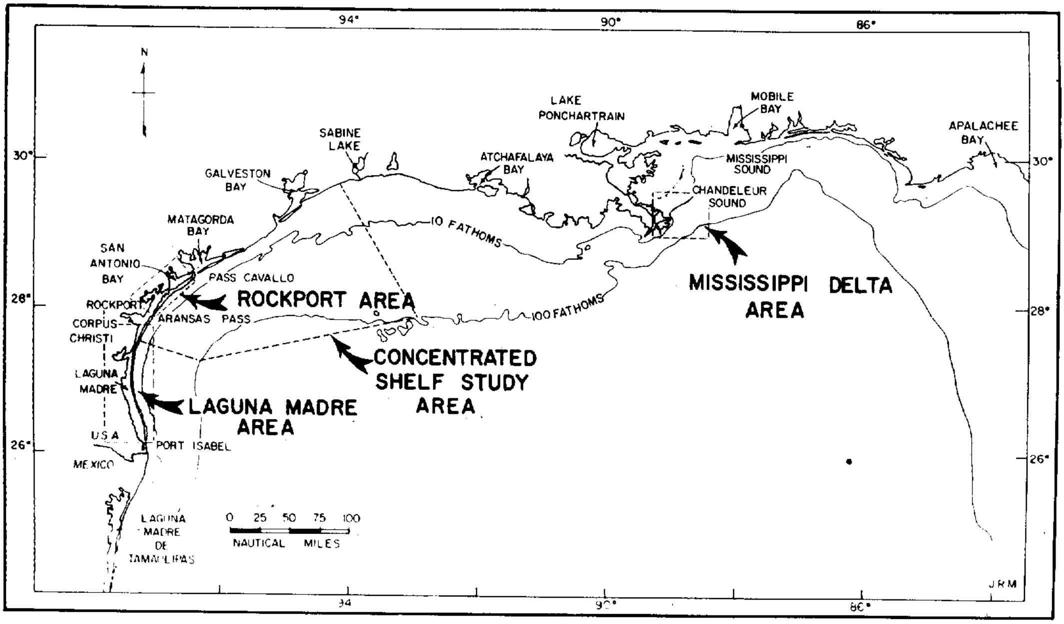


FIG. 1.—Northern Gulf of Mexico, areas of concentrated study. Smaller amounts of biological and physical data obtained from other named lagoons.

in the winter and tropical conditions in the summer. This diversity of climate and consequent wide range of ecologic factors have resulted in a great diversity of marine invertebrates and an unusually large number of assemblages associated with several terrigenous sedimentary environments.

The primary purpose of this paper is to assess the relationship between the living and dead invertebrates, and their relationships to sediments. An attempt is made to evaluate the ecological processes which affect them.

The macro-invertebrates of the northern Gulf of Mexico have received more intensive study than those in most of the shallow-water regions of the world. Except for the discussions of the assemblages found in the enclosed waters of Alabama, western Lousiana, and east Texas, the discussion of the lagoonal assemblages constitutes a review of earlier comprehensive papers, summarizing most of the published regional studies (Hedgpeth, 1953; Ladd, Hedgpeth, and Post, 1957; Parker, 1955, 1956, 1959a, and 1959b).[3]

Less is known about the ecology and distribution of marine invertebrates on the continental shelf and slope. There were only two expeditions in these waters for the study of marine invertebrates, both prior to 1900. Most of the discussion on the distribution and ecology of macro-invertebrates of the shelf and slope is based on new material, obtained both from American Petroleum Institute Project 51 field work and from unpublished data of other Gulf Coast investigators.

METHODS

The region sampled extends from Mobile Bay, Alabama, on the east, to Port Isabel, Texas, on the southwest, and offshore to approximately 100 fathoms (Fig. 1). Detailed sampling was done in the east Mississippi Delta area, the lagoons in the vicinity of Rockport, Texas, and Laguna Madre, Texas. A reconnaissance study of the shelf faunas was made from off Mobile Bay to the Mexican border, with most of the stations between Galveston and Aransas Pass, Texas, at depths of 5–60 fathoms. Areas of intense sampling are indicated on Figure 1. Less detailed information was available from Lake Pontchartrain, and Galveston and Matagorda Bays (Darnell, 1958; Suttkus, Darnell and Darnell, 1953–54; Pulley, 1953; and Marland, 1958).

Although nearly 2,000 samples were examined, the results cannot be considered conclusive. It

[3] See pages 368–81 for list of references.

will be necessary to sample at frequent intervals, over a considerable length of time, in order to place exact environmental limits for the assemblages used in this paper, inasmuch as these boundaries shift with the changes in climate and associated ecological factors (Parker, 1959a).

Most of the samples were taken with various grab samplers (van Veen and the orange peel, see Hedgpeth, *et al.*, 1957, pp. 62 and 69–70). The sediments were washed through 1-mm screens and all living and dead animals were identified and counted. Emphasis in the analyses was placed on the invertebrates containing hard parts likely to be preserved in the fossil record. Larger and more motile animals were collected with the otter trawl (figured in Hedgpeth *et al.*, *ibid.*, p. 76), and various types of bottom dredges. Most of the biological samples were taken at the same time as sediment samples and physical data (salinity, water temperature, currents, and depths). Sampling patterns, analyses of the individual samples and other basic information can be found in Parker (1955, 1956, 1959a), and Parker and Curray (1956). Unpublished data are on file at the Scripps Institution of Oceanography. Hydrography, distribution of sediments and microfauna, and geologic history of the areas sampled are discussed in other papers of this volume.

Abundances of each species with more than 10 living specimens per station were plotted on charts of each region studied in detail. These distributions were compared with the areal distribution of sediment type, salinity, temperature, bathymetry, and current patterns. From these data it was possible to ascertain the faunal composition of the primary assemblages from the complex distributions of the many species. As there are few very abundant species, geomorphic or environmental designations are applied, rather than the conventional community names (*Macoma*, *Venus*, and *Cardium* communities) as used by quantitative ecologists (Petersen, 1913, 1915; Thorson, 1957; and Jones, 1950).

LAGOONS AND BAYS

There are two major macrofaunal assemblages —one in lagoons or enclosed, protected waters, the other in open or unprotected, shelf waters. These major assemblages can be subdivided into animal communities living on level, sediment-covered bottoms and communities living on rock, coral, or dissected bottoms (Thorson, 1957). This study is concerned primarily with the distribution and ecology of the level-bottom assemblages, as rock or coral bottoms are rare in the northern Gulf of Mexico. The fauna of the rocky or dissected bottoms of the northern Gulf has been discussed by Puffer and Emerson (1953), Parker (1955), and Parker and Curray (1956).

DESCRIPTION OF THE ENVIRONMENTS

Annual rainfall in the northern Gulf of Mexico ranges from more than 90 inches in the Mississippi Delta region to less than 20 inches during prolonged dry periods on the south Texas coast. Surface-water temperatures may be as high at 42°C in some of the shallow lagoons in summer, to slightly below freezing in winter. Coastal physiography is diverse, providing enclosed waters ranging from deep estuaries to broad, shallow bays, nearly enclosed hypersaline lagoons, small deltas, one of the world's largest deltas, and open and enclosed sounds. It is convenient to divide the coast into climatic zones (Fig. 14).

The humid zone.—The coastal region from Florida to the Louisiana-Texas border may be considered a humid climate (Thornthwaite, 1948; Hedgpeth, 1953). Air temperatures range from those typical of warm-temperate to subtropical climates, and the coastal vegetation is similar to that found from North Carolina to Florida. Extensive marshes are present, and the large lagoons and estuaries have salinities permanently lower than the normal Gulf of Mexico salinity of 36 $^0/_{00}$.

Those lagoons from which considerable information has been collected are Mobile Bay (Austin, 1954), Mississippi Sound (Phleger, 1954b; staff of Gulf Coast Research Laboratory, personal communication), Lake Ponchartrain and Lake Borgne (Darnell, 1958), Breton Sound and Mississippi Delta region (Scruton, 1956; Phleger, 1955a; Parker, 1956; and Treadwell, 1955), and Atchafalaya Bay (Thompson, 1956).

The Mississippi Delta region is the best known area in the humid zone in terms of the physical factors (Fig. 2). The surface and bottom salinities in the vicinity of the Mississippi Delta are very low during periods of high river discharge in the spring and early summer, and water temperatures are generally colder than nearby sound or gulf waters. Conditions in the vicinity of the delta change considerably during late summer and fall, with warm and high-salinity gulf water often impinging directly upon the delta (Scruton, 1956). These seasonal differences, plus a complex system of currents caused by tides, wind, and river discharge, create an extremely variable environment which is unfavorable for most marine invertebrates.

Lake Pontchartrain, Mobile Bay, and Atchafalaya Bay represent the more stable, low-salinity conditions of the humid zone. Mobile Bay receives the least runoff and river discharge. The upper end of Mobile Bay has salinities low enough (8-11 $^0/_{00}$) to exclude most marine invertebrates (Austin, 1954). The central portion of this bay contains a large number of living oyster reefs, indicating that salinities usually range from 10 to 25 $^0/_{00}$. Lower Mobile Bay has salinities and temperatures near those of the nearshore Gulf of Mexico.

Most of Lake Pontchartrain and the shoaler portions of Lake Borgne have salinities of 6–9 $^0/_{00}$, too low for most marine invertebrates (Darnell, 1958). During droughts, however, the salinities in these large lakes and bays occasionally rise to more than 18 $^0/_{00}$. The more motile faunas, such as fish, shrimp, and crabs, invade these lakes under such conditions. Figure 3 shows the probable hydrography and range of physical factors for a low salinity estuary in the humid zone.

The subhumid or transition zone.—The climate of the coastal plain changes from humid to subhumid from the Texas-Louisiana border to Corpus Christi, Texas. The region from Sabine, Texas, to about Matagorda Bay can be considered moist, subhumid; and from Matagorda Bay to Corpus Christi the climate is dry, subhumid (Hedgpeth, 1953). Rainfall averages 30–50 inches in the

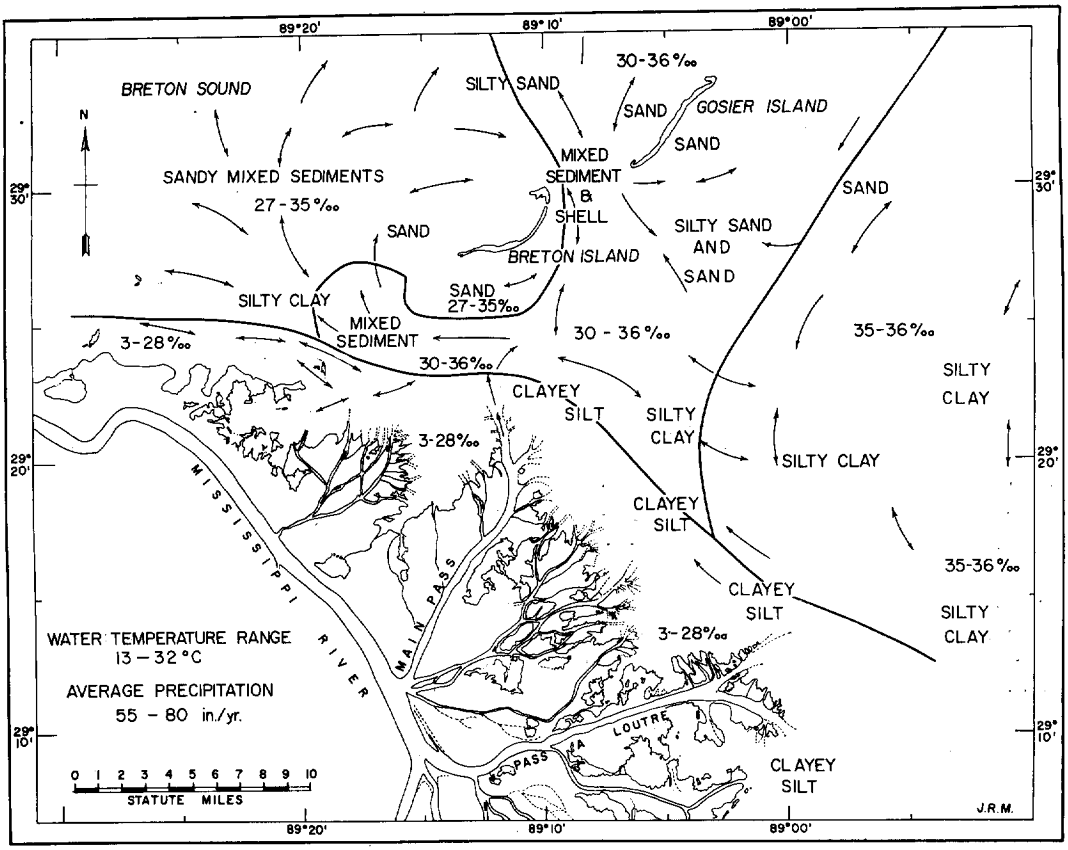


FIG. 2.—Generalized areal distribution of physical factors, east Mississippi Delta region. Salinity in ‰, water temperature, and currents from Scruton, 1956; sediment distribution from Parker, 1956; precipitation from Hedgpeth, 1953.

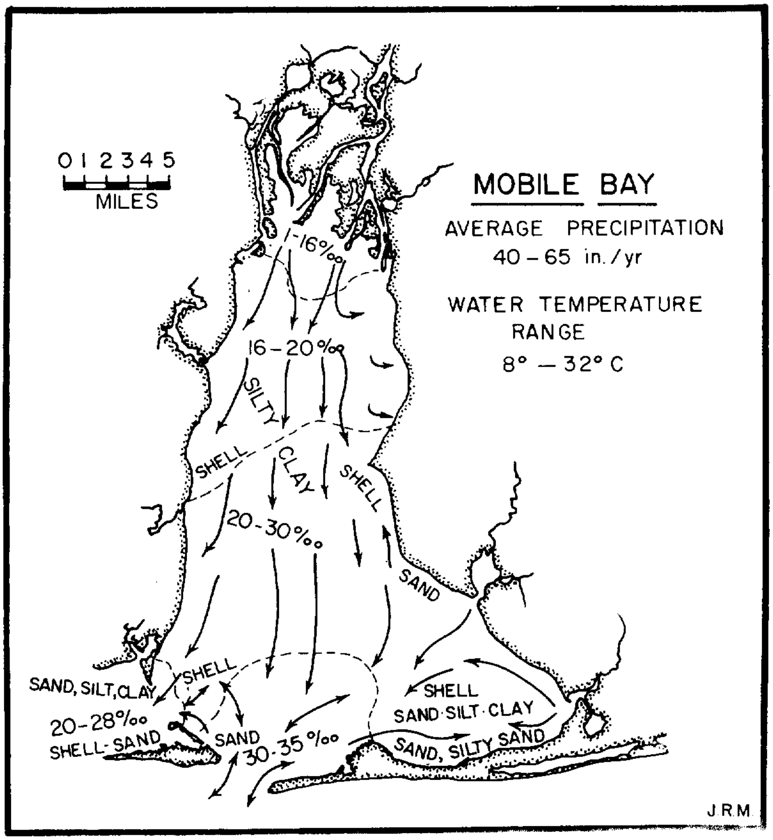


FIG. 3.—Generalized areal distribution of physical factors in Mobile Bay, Alabama. Salinity (‰) and currents from Austin, 1954; sediments from chart supplied by Alabama Department of Conservation; water temperature from Pulley, 1953; and precipitation from Hedgpeth, 1953.

moist, subhumid zone and as low as 10 to as high as 30 inches in the dry, subhumid zone. Rivers are small and contribute much less fresh water to the small, more enclosed lagoons than in the humid zone. Air temperatures are higher in the summer than in the humid zone, and in the winter the central portion may have the lowest air temperatures along the Gulf Coast. Large portions of the lagoons and estuaries in the moist, subhumid portion of this zone have reduced salinities. In the dry, subhumid portion where evaporation far exceeds runoff for extensive periods, on the other hand, the lagoons may temporarily have very high salinities even in the upper reaches.

Galveston Bay is the largest lagoon within the moist, subhumid zone. During the more prevalent wet years salinities throughout most of Galveston Bay are less than 20 $^0/_{00}$, although parts near the gulf entrances may approach 34 $^0/_{00}$ (R. Hoffstetter and T. E. Pulley, personal communication). During droughts only the upper half or third of Galveston Bay has low salinities, and the lower half approaches true marine conditions (Reid, 1955). Figure 4 illustrates the typical hydrography and range of conditions for a lagoon in the moist, subhumid zone.

The dry, subhumid zone includes the Matagorda Bay system, San Antonio, Mesquite, Copano, Aransas, Redfish, and Corpus Christi Bays (Figs. 1, 5). During infrequent high-rainfall years, salinities may be reduced to less than 5 $^0/_{00}$ throughout much of these bays. During droughts low salinities occur only near river mouths, and elsewhere salinities may be more than 40 $^0/_{00}$. Mass mortalities of macro-invertebrates occur when floods follow extended droughts. Figure 5 indicates the general patterns of hydrog-

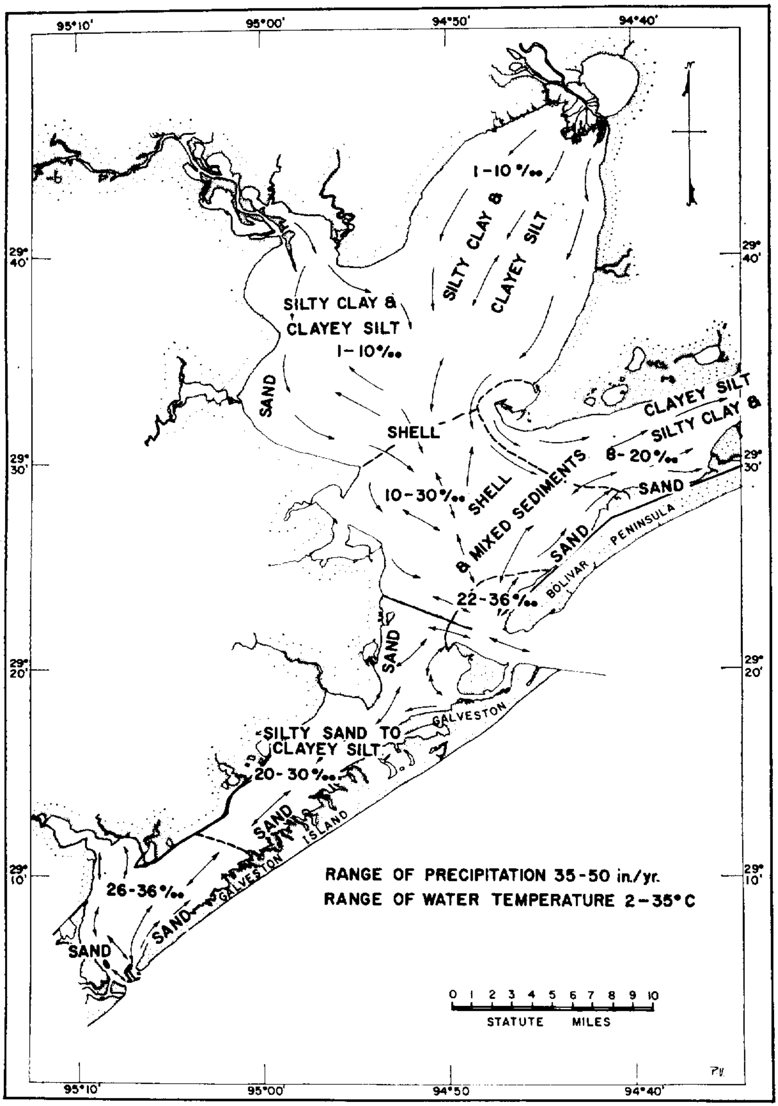


FIG. 4.—Generalized areal distribution of physical factors in Galveston Bay, Texas. Salinity (‰) from Galtsoff, 1931, and Reid, 1955; sediments from Reid, 1955, and A.P.I. studies; precipitation from Hedgpeth, 1953; water temperature from Pulley, 1953; and circulation hypothesized from salinity, sediment, and faunal distribution.

raphy and range of ecological factors for a typical lagoon in the dry, subhumid zone.

The semiarid zone.—This zone extends from Corpus Christi south and west almost to Tampico, Mexico. The principal coastal lagoons in this zone are Laguna Madre, Texas, and Laguna Madre de Tamaulipas, Mexico. These lagoons are hypersaline. No permanent rivers flow into the lagoons and rainfall is frequently less than 15–20 inches a year. Summer air temperatures and water temperatures are up to 42°C. There is excessive evaporation and salinities may rise to more than 100 ‰. Freezes do occur every 7-10 years, causing mass mortalities of lagoon faunas (Gunter and Hildebrand, 1951).

The hydrography of these lagoons has been discussed by Collier and Hedgpeth (1950), Simmons (1957), Breuer (1957), Parker (1959a),

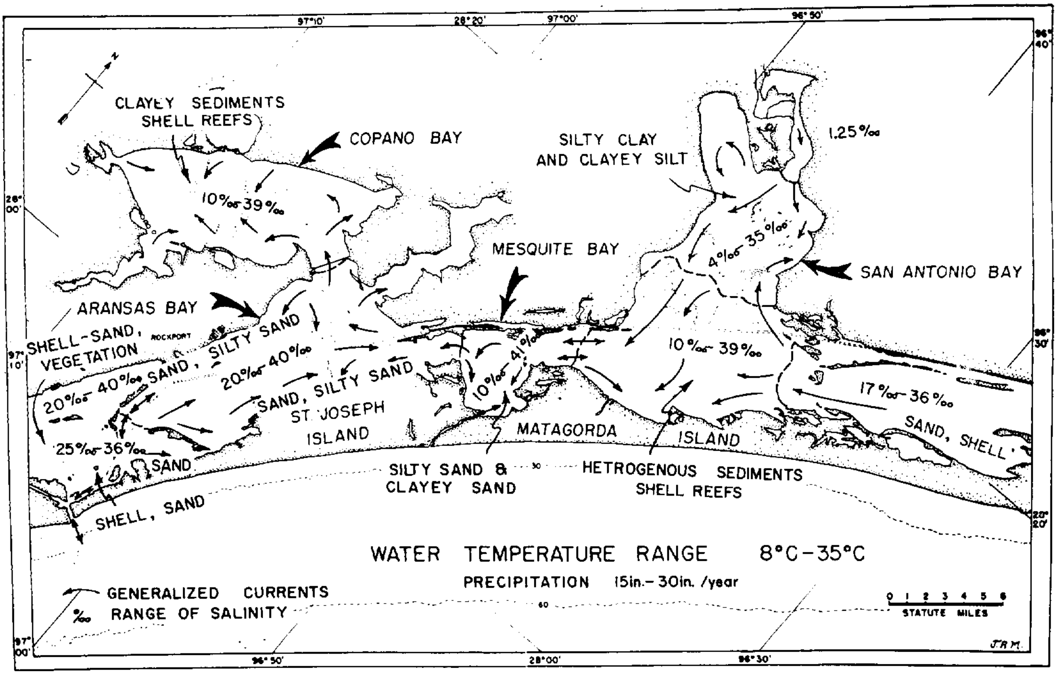


FIG. 5.—Generalized areal distribution of physical factors, Rockport, Texas region. Sediments from Shepard and Moore, 1955; precipitation and water temperature from Parker, 1955; and salinity and circulation from Parker, 1959a.

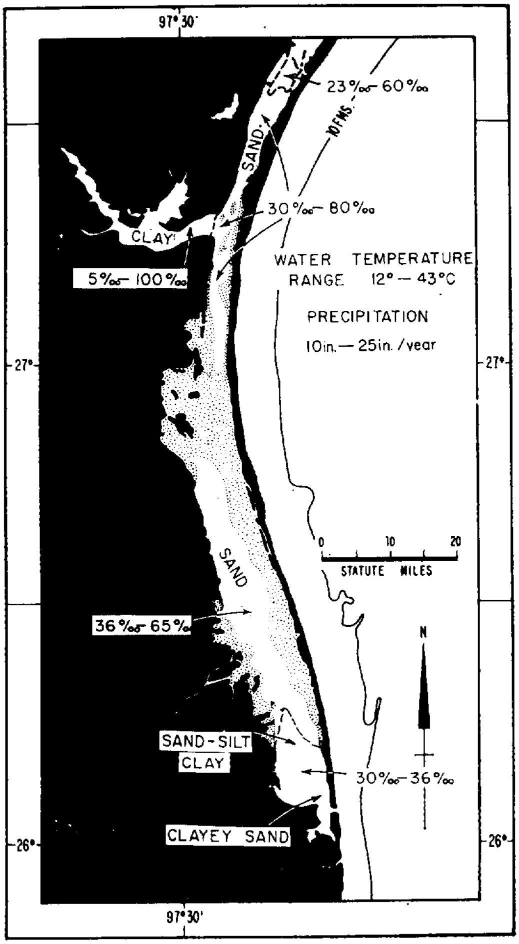


FIG. 6.—Generalized areal distribution of physical factors, Laguna Madre, Texas. Salinity and sediments from Rusnak, this volume; water temperature range from Pulley; 1953, and precipitation from Collier and Hedgpeth, 1950, and Hedgpeth, 1953.

and Rusnak (this volume, p. 159, ff.). The salinities in the lagoons of the semiarid regions range from below normal gulf values (30-36 $^{0}/_{00}$) in the portions adjacent to the dry, subhumid zone, to normal gulf salinities of 35–36 $^{0}/_{00}$) near the inlets, to continually hypersaline (40–80 $^{0}/_{00}$) in most of the enclosed portions of the lagoons. Although the conditions are adverse for most marine life, the factors are stable compared to those in most of the central Texas coastal lagoons. The normal hydrography of lagoons in the semiarid zone is shown in Figure 6.

MACROFAUNAL ASSEMBLAGES

There are many invertebrate species which appear to be confined to the enclosed coastal waters, especially when salinities are below normal sea water values of 34–36 $^{0}/_{00}$, but only a few genera are confined to lagoons and estuaries. Besides salinity, some of the limiting factors which may restrict lagoonal species are shallow water, permitting turbulence to the bottom by a minimum amount of wave action, high turbidity from runoff, and possibly nutrients and growth substances available from runoff.

I. FRESH WATER AND LOW-SALINITY MARSH ASSEMBLAGE

Species	*Comparative Abundance; Size*
GASTROPODS	
Littorina irrorata (Say, 1822)	Abundant at water's edge; small (½ in.)
Neritina reclivata (Say, 1822)	Abundant, but prefers lower salinity; small (½ in.)
CRUSTACEANS	
Uca pugilator (Bosc)	Common where tidal waters keep mud flats moist; medium (2–3 in.)
Cambarus, species	Abundant in fresh water coastal marshes; medium (3–5 in.)

This assemblage is most characteristic of the humid zone, especially in marshes between the Mississippi Delta (Fig. 7) and the Texas-Louisiana border. It also occurs sporadically in small areas as far as San Antonio Bay, Texas, but is missing from the semiarid zone. The characteristic substrate is sandy silt with a vegetational cover. The species are unique to this environment and are always found associated with abundant plant fibers. Typical species are on Plate 1.

(Plates and explanations on pages 332–337)

II. RIVER-INFLUENCED, LOW-SALINITY ASSEMBLAGE

Species	*Comparative Abundance; Size*
PELECYPODS	
Rangia cuneata (Gray, 1831)	Common in beds. Tend to have largest size in lowest salinity; medium (2–4 in.)
Rangia flexuosa (Conrad, 1840)	Less abundant. Prefers higher salinity and shallower water; medium (2–3 in.)
Polymesoda carolinensis (Bosc, 1830)	Missing from Mobile, east, and Matagorda Bay, west and south, not in fresh water as *R. cuneata;* medium (2-3 in.)
Macoma mitchelli Dall, 1895	Common in all low salinity lagoons and estuaries; small (¼–½ in.)
GASTROPODS	
Littoridina sphinctostoma Abbott and Ladd, 1951	Common in some localities. Replaced by other small hydrobiids elsewhere; tiny (1/16 in.)
CRUSTACEANS	
Callinectes sapidus Rathbun	Very common at certain seasons. Ranges to nearshore gulf; large (6–12 in.)
Macrobrachium (various species)	Range some distance up rivers; few; very large (1–2 ft.)

This assemblage is characteristic of areas surrounding permanent river mouths, where salinity is always less than 10 $^{0}/_{00}$. The assemblage is best developed in the upper and middle portions of bays and lagoons in the humid and moist, subhumid zones (Figs. 8–10), but is absent from the semiarid climatic zone. Characteristic forms are on Plate 1.

III. DELTA-FRONT DISTRIBUTARY AND INTERDISTRIBUTARY ASSEMBLAGE

Species	*Comparative Abundance; Size*
PELECYPODS	
Rangia cuneata (Gray, 1831)	Not as abundant as in river-influenced assemblage
Rangia flexuosa (Conrad, 1840)	More abundant, especially in interdistributary bays
Macoma mitchelli Dall, 1895	Rare, mostly in channels
Crassostrea virginica (Gmelin, 1791)	Very abundant in higher salinity interdistributary bays; large (2–6 in.)
Petricola pholadiformis Lamarck, 1818	Common on distributary submerged levees; medium (1½–2½ in.)
GASTROPODS	
Littoridina or *Amnicola*, species	Not very common; small (1/16 in.)

This assemblage is characteristic only of the major river deltas, such as the Mississippi Delta. The distributional pattern of this assemblage is on Figure 7. Most species are on Plate 1.

IV. LOW-SALINITY OYSTER REEF ASSEMBLAGE

Species	*Comparative Abundance; Size*
PELECYPODS	
Crassostrea virginica (Gmelin, 1791)	Predominates, forms base of reef; medium to large (2–6 in.)
Brachidontes recurvus (Rafinesque, 1820)	At times very abundant, missing at higher salinities; medium (1–4) in.)
GASTROPODS	
Crepidula plana Say, 1822	Common when reef in upper salinity range; medium (½–1½ in.)
CRUSTACEANS	
Balanus eburneus Gould, 1841	Barnacle, common at intermediate salinities; small (¼–½ in.)
Balanus amphitrite niveus Darwin, 1854	Common at slightly higher salinities; small (½–1 in.)

Oyster reefs are abundant in the humid and subhumid regions, where salinities are 10–30 ‰. Oyster reefs cease normal growth during high salinities (36 ‰) and can be killed by fresh water. This assemblage seldom occurs in the semiarid zone, although a few individuals survive hypersalinities for a time. These reefs do not thrive in water temperatures permanently more than 20°C, and commonly die if temperatures stay at 30–40°C. For oyster reefs to grow actively on the northern Gulf Coast, water temperatures should drop below 15°C for several months of the year to reduce reproductive activities and permit growth of new shell (Gunter, 1942).

Oyster reefs generally are perpendicular to the circulation in an estuary or lagoon, as shown in Figures 8, 9, and 10, and thrive in depths of about 8 feet on a firm bottom of old shell. Characteristic species are on Plate 1.

V. ENCLOSED LAGOON OR INTER-REEF ASSEMBLAGE

Species	*Comparative Abundance; Size*
PELECYPODS	
Nuculana acuta (Conrad, 1832)	Few in clayey sand; small (3/16 in.)
Nuculana concentrica (Say, 1824)	Common in clay; small (3/16–½ in.)
Mulinia lateralis (Say, 1822)	Abundant in all types sediment, especially clays; small (¼–½ in.)
Tagelus plebeius (Solander, 1786)	Common along bay margins; medium (1–3 in.)
Ensis minor Dall, 1899	Common along bay margins; medium (1–3 in.)
GASTROPODS	
Retusa canaliculata (Say, 1827)	Common dead, rare alive; small (¼ in.)
ECHINODERMS	
Amphiodia limbata (Grube)	Common in clayey sediments; small (disk—¼ in.; legs —2 in.)

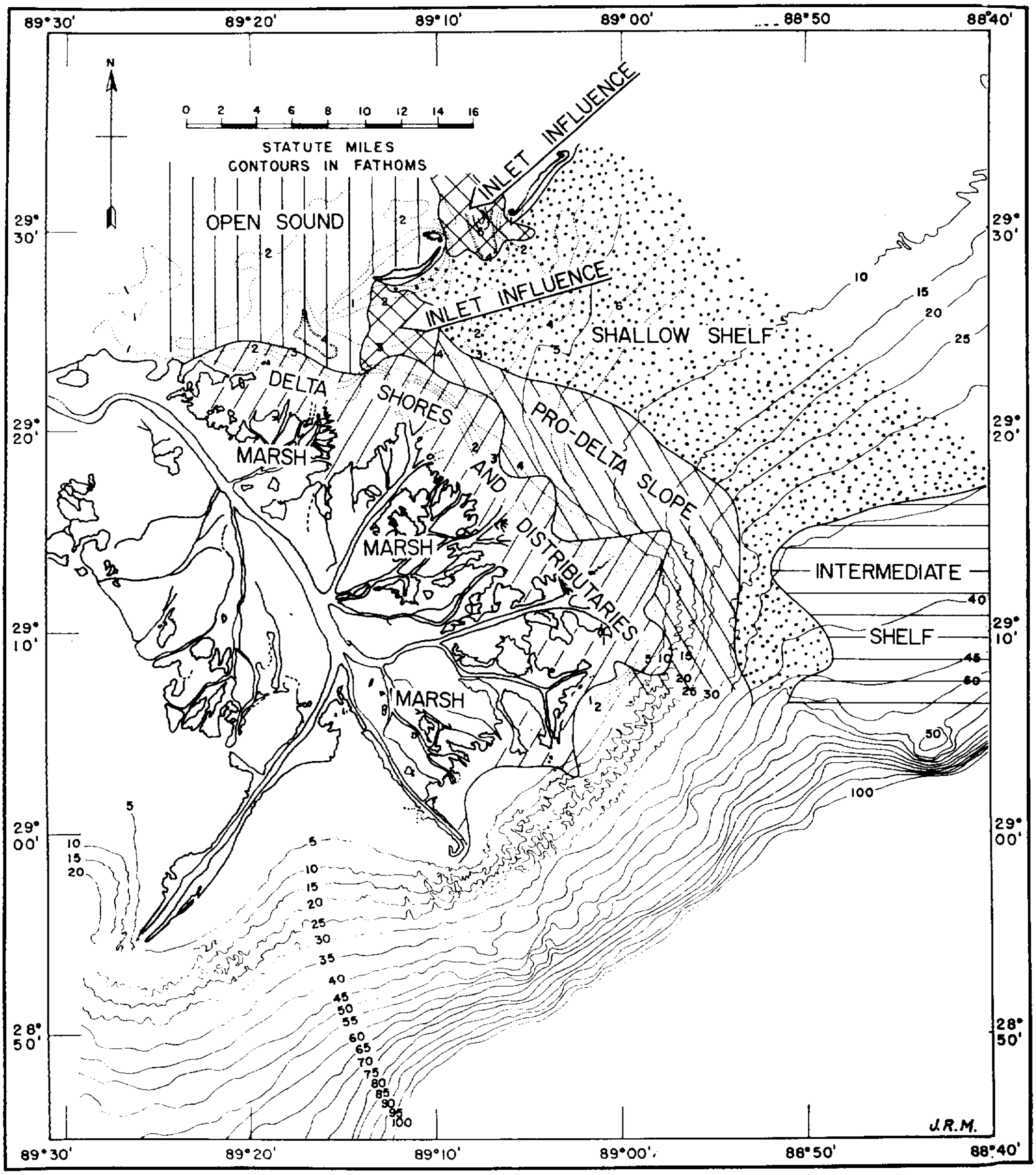


FIG. 7.—Areal distribution of macrofaunal assemblages in east Mississippi Delta region, modified from Parker, 1956.

The enclosed lagoon assemblage is characteristic of level bottoms between the oyster reefs from Mobile Bay to Corpus Christi Bay, but is not present in the semiarid zone. The environment in which this assemblage is found is a stable one in the humid zone (Fig. 8) and in small portions of the wet, subhumid zone (Fig. 9). In the dry, subhumid zone (Fig. 10), the environmental boundaries and assemblage composition shift rapidly with periods of high rainfall and drought (Parker, 1959a). Most of the species are tolerant of environmental changes, and they occur over a greater range of salinity, temperature, and sediment type than those in other assemblages. Some of the more characteristic forms are on Plate 1.

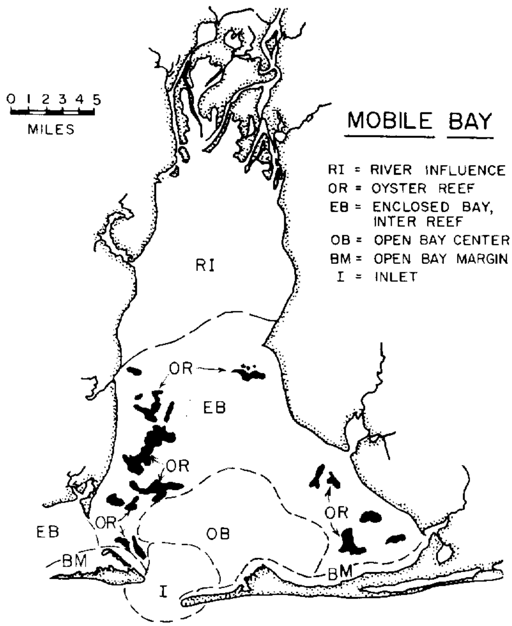


FIG. 8.—Areal distribution of macrofaunal assemblages in Mobile Bay, Alabama, determined from A.P.I. collections, and Ritter, 1896. Note large extent of low-salinity river-influenced assemblage and enclosed bay assemblage, as compared to small area of open bay and inlet.

VI. OPEN SOUND OR OPEN LAGOON MARGIN ASSEMBLAGE

Species	*Comparative Abundance; Size*
PELECYPODS	
Aequipecten irradians amplicostatus (Dall, 1898)	Abundant in beds at inlet end of lagoons; medium (1–2½ in.)
Trachycardium muricatum (Linné, 1758)	Abundant, but more scattered than clams or scallops; medium (1–2½ in.)
Mercenaria mercenaria campechiensis (Dall, 1902)	Abundant in dense beds at inlet end of lagoons; large (1-5½ in.)
Chione cancellata (Linné, 1767)	Abundant as scattered individuals; medium (½–2 in.)
Tagelus divisus (Spengler, 1794)	Abundant; medium (1–2 in.)
GASTROPODS	
Nassarius vibex (Say, 1822)	Common in certain localities; small (¼ in.)
Neritina virginea (Linné, 1758)	Few directly at margin of lagoons of semiarid zone; small (¼ in.)
Melampus bidentatus Say, 1822	Common under vegetation rafted on shore, goes into water only to breed; small (¼ in.)

These species are the more common ones found in this environment; at least 20 genera and as many as 40–50 species occur along the bay-margin areas of the dry, subhumid zone. The open-bay or lagoon-margin assemblage is in the humid zone from Breton Sound to Mobile Bay. It is the predominant margin assemblage of the dry, subhumid zone (Fig. 10), and within the inlet-influenced portions of the semiarid zone. The number of genera and species increases as the average salinity increases (Parker, 1955).

This assemblage may be difficult to recognize as a separate facies unit in older sediments, as it lives in a narrow band likely to be missed in sampling by coring or drilling. Large beds of clams, cockles, and scallops should furnish the best evidence. Representative species are on Plate 2.

(*Plates and explanations on pages 332–337*)

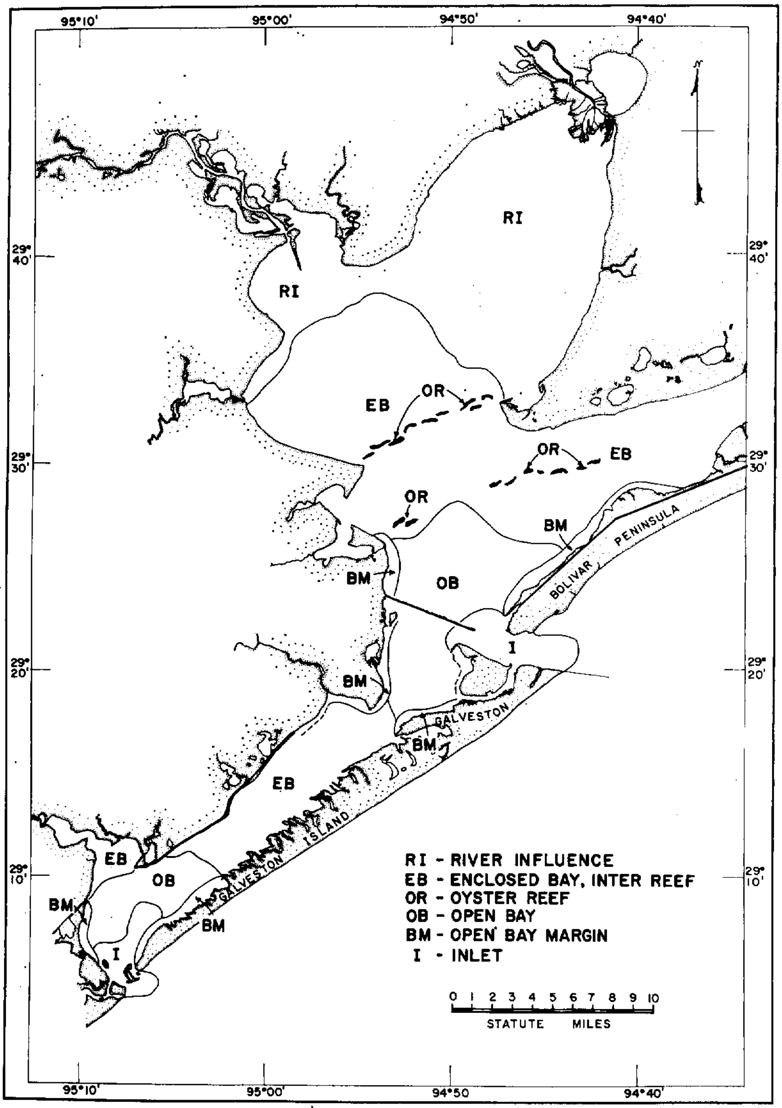


FIG. 9.—Areal distribution of macrofaunal assemblages in Galveston Bay, Texas, determined from Pulley, 1953, Galtsoff, 1931, Reid, 1955, and A.P.I. collections. Note large extent of river-influenced and enclosed-bay assemblages, as well as alignment of oyster reefs.

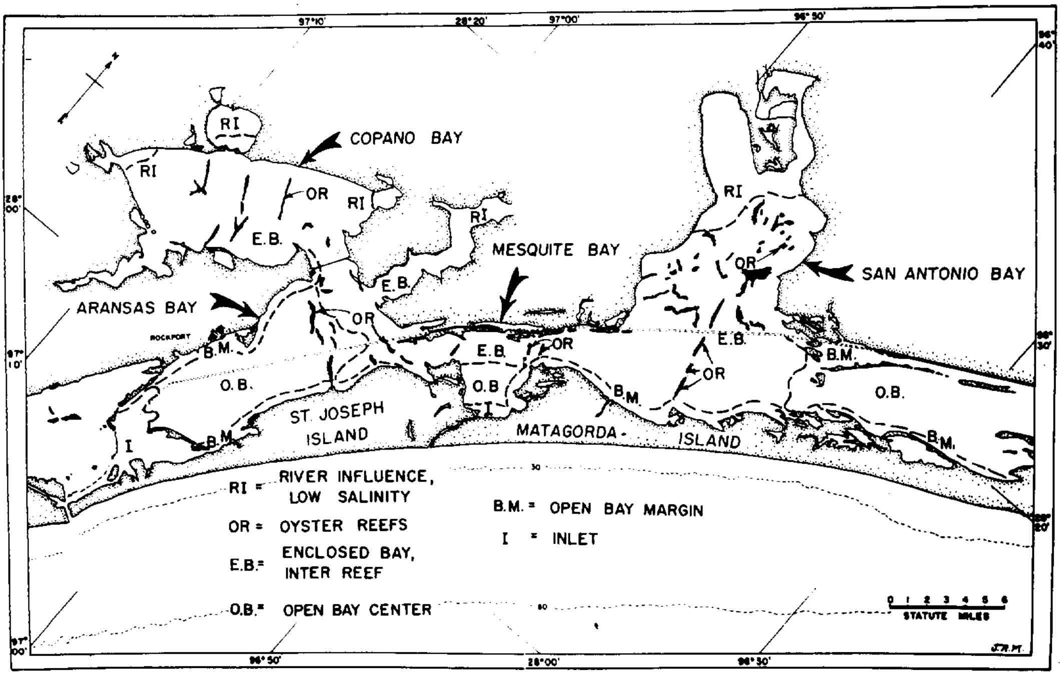


FIG. 10.—Areal distribution of macrofaunal assemblages, Rockport, Texas region, modified from Parker, 1959a. Note reduction of river influenced, and increased area of open-bay assemblages.

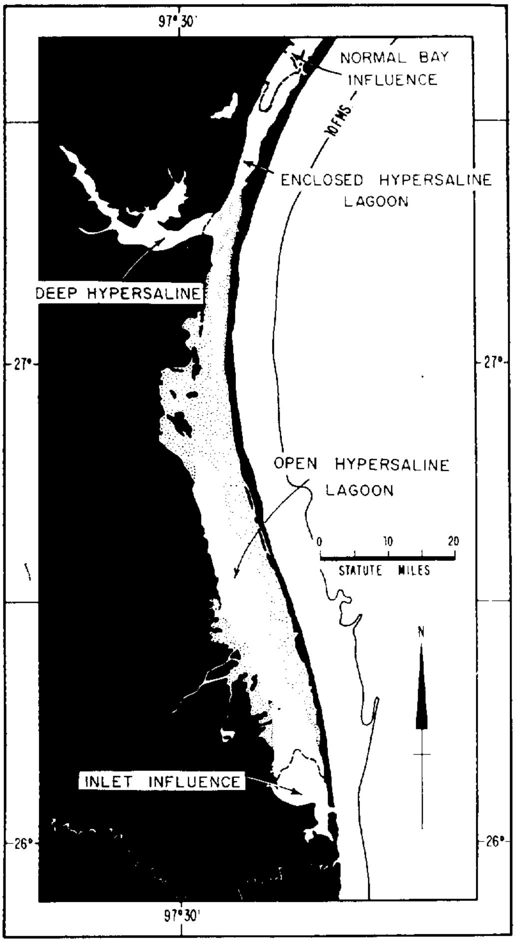


FIG. 11.—Areal distribution of macrofaunal assemblages, Laguna Madre, Texas, modified from Parker, 1959a. Note absence of river-influenced, enclosed-bay, and oyster-reef assemblages dependent upon lowered salinity.

VII. OPEN SOUND OR OPEN LAGOON CENTER ASSEMBLAGE

Species	*Comparative Abundance; Size*
PELECYPODS	
Abra aequalis (Say, 1822)	Abundant in clayey sediments; small (¼–½ in.)
Corbula contracta Say, 1822	Common on sandier sediments; small (¼ in.)
Diplodonta punctata (Say, 1822)	Few in mixed sediments; small (½–1 in.)
Mulinia lateralis (Say, 1822)	Abundant in clayey sediments, not restrictive; small (¼–½ in.)
Nuculana concentrica (Conrad, 1834)	Common in clayey sediments; small (¼–½ in.)
Pandora trilineata Say, 1822	Few in mixed sediments; medium (½–1 in.)
Periploma fragile (Totten, 1835)	Few, in sandy sediments; small (¼ in.)
GASTROPODS	
Nassarius acutus (Say, 1822)	Common in clayey sediments; small (¼ in.)
Retusa canaliculata (Say, 1827)	Common, dead; small (¼ in.)

The above species are the most common and characteristic of lagoon centers, although many more, less abundant species have been collected from this environment. The higher the salinity, the more species and the fewer the individuals of each species. The salinity range for this assemblage in the humid zone is 20–35 $^{0}/_{00}$, whereas in the dryer climatic zones, the salinity range is 25–39 $^{0}/_{00}$. Water temperatures are 9-30°C in the eastern Gulf and 8–36°C in the western Gulf. The sediments are predominantly silty clay and clayey silt in the Rockport area (Parker, 1959a), and slightly sandier in the Mississippi Delta region (Parker, 1956). The typical distributional patterns of this assemblage in bays, lagoons, and sounds for each of the climatic zones is shown in Figures 7–11. Typical species are on Plate 2.

VIII. HIGH SALINITY OYSTER OR MOLLUSK REEF ASSEMBLAGE

Species	*Comparative Abundance; Size*
PELECYPODS	
Anomia simplex d'Orbigny, 1842	Common. Sometimes forms small reefs; medium (1–2 in.)
Brachidontes exustus (Linné, 1758)	Common. Attaches to oyster valves; medium (½–1 in.)
Diplothyra smithi (Tryon, 1862)	Few. Bores into *Ostrea equestris* and *Crassostrea virginica;* small (½ in.)
Ostrea equestris, Say, 1834	Abundant. Replaces *C. virginica* when salinities rise above 30 ‰; medium (1–3 in.)
GASTROPODS	
Anachis avara semiplicata (Stearns, 1873)	Common, associated with algae on reefs; small (½ in.)
Anachis obesa (C. B. Adams, 1845)	Common, with algae on reefs; small (1/16–3/16 in.)
Mitrella lunata (Say, 1826)	Common, with algae on reefs; small (1/16–⅛ in.)
Thais haemastoma floridana (Conrad, 1837)	Common at high salinities. Preys on larger pelecypods (*Crassostrea* and *Ostrea*); large (1–4 in.)
CRUSTACEANS	
Crangon heterochelis (Say)	Common. Lives amidst dead shell; medium (½–2 in.)
Menippe mercenaria (Say)	Few, with dead shell. Feeds on live mollusks; large (3–6 in.)

High-salinity reefs form near inlets where there is relatively high-salinity water constantly being renewed by tides. The substrate is generally old shell, either brought in through the inlet, or derived from a pre-existing bay oyster reef. The assemblage is characteristic of the dry, subhumid, and the semiarid zone. Small, high-salinity reefs may be found in the inlets of the moist, subhumid zone and humid zone if the gulf salinities are normal (34–36 $^{0}/_{00}$). During droughts in the subhumid zone, *Ostrea equestris* and *Brachidontes exustus* may completely replace *Crassostrea virginica* and *Brachidontes recurvus* on the low-salinity reefs. This assemblage occurs in water depths of 1–30 ft. The high-salinity reefs are well preserved in Recent and Pleistocene sediments. Typical forms are on Plate 2.

IX. OPEN SHALLOW HYPERSALINE LAGOON NEAR INLET ASSEMBLAGE

Species	*Comparative Abundance; Size*
PELECYPODS	
Amygdalum papyria (Conrad, 1846)	Common, attached to shells and algae; medium (1–1½ in.)
Anomalocardia cuneimeris (Conrad, 1846)	Abundant, on sand bottom; small (¼ in.)
Laevicardium mortoni (Conrad, 1831)	Common, on sand bottom; medium (½–1 in.)
Phacoides pectinatus (Gmelin, 1790)	Few; medium (1–1½ in.)
Pseudocyrena floridana (Conrad, 1846)	Common on sand bottom; small (¼–½ in.)
GASTROPODS	
Bittium varium (Pfeiffer, 1840)	Abundant, with algae; small (1/16 in.)
Caecum pulchellum Stimpson, 1851	Common in sand; small (less than 1/16 in.)
Cerithidea pliculosa (Menke, 1829)	Common mostly close to shore; small (¼–½ in.)
Cerithium variabile (C. B. Adams, 1848)	Common on sand bottom with algae; small (½–¾ in.)
Haminoea succinea (Conrad, 1846)	Few, along shores; medium (1 in.)
Modulus modulus (Linné, 1758)	Few, rarely taken alive; small (½ in.)
Tegula fasciata (Born, 1780)	Few on shelly bottom; small (½ in.)
Vermicularia fargoi Olsson, 1951	Common, mostly along margins; small (½–1 in.)

This assemblage contains numerous species, especially small gastropods. It is characteristic of the open portions of lagoons and shallow tidal deltas in the vicinity of inlets in the dry, subhumid zone and semiarid climatic zone (Fig. 11). Salinities generally range from 32 to 45 $^0/_{00}$ and temperatures are usually high in summer, up to 40°C. The sediments are mostly sand and shelly sand with much vegetation. Some of the species are shown on Plate 3.

(Plates and explanations on pages 332–337)

X. ENCLOSED HYPERSALINE LAGOON ASSEMBLAGE

Species	*Comparative Abundance; Size*
PELECYPODS	
Anomalocardia cuneimeris (Conrad, 1846)	Exceedingly abundant (2,000/square meter); small (¼ in.)
Mulinia lateralis (Say, 1822)	Less abundant than *Anomalocardia,* but still abundant; small (¼–½ in.)
Tellina tampaensis Conrad, 1866	Less abundant than other two, most abundant in 6 in. water close to shore; small (½ in.)
GASTROPODS	
Cerithium variabile (C. B. Adams, 1848)	Few, close to shore; small (½ in.)

This assemblage is found only in the semiarid zone (Fig. 11), and especially where evaporation exceeds precipitation. Salinities are about 43–80 $^0/_{00}$ and temperatures may rise as high as 43°C. The hypersaline lagoon assemblage has been studied in detail in the Texas Laguna Madre by Parker (1959a), and has been reported from the Mexican Laguna Madre by Hildebrand (1958). The sediments are predominantly sand or shelly sand. The population of mollusks per square meter is the highest on the Gulf Coast, although individuals are much smaller than in other Texas bays. Most species are on Plates 1, 2, and 3.

XI. INLET AND DEEP CHANNEL ASSEMBLAGE

Species	*Comparative Abundance; Size*
PELECYPODS	
Atrina seminuda (Lamarck, 1819)	Few. In some areas form beds; large (4–10 in.)
Crassinella lunulata (Conrad, 1834)	Common on shelly bottom; small (1/16–3/16 in.)
Lucina amiantus (Dall, 1901)	Common on silty sands; small (⅛ in.)
Lucina crenella (Dall, 1901)	Common on silty sands; small (1/16–⅛ in.)
Tellidora cristata (Récluz, 1842)	Common on sandy bottom; medium (½–1 in.)
GASTROPODS	
Anachis avara similis (Ravenel, 1861)	Common to rare, on algae; small (¼ in.)
Polinices duplicatus (Say, 1822)	Common, preys on clams; large (1–2½ in.)
Sinum perspectivum (Say, 1831)	Few; medium (1–1½ in.)
SCAPHOPODS	
Dentalium texasianum Philippi, 1849	Common in stiff sediments; small (¾ in.)
ECHINODERMS	
Arbacia punctulata (Lamarck, 1816)	Few; large (2–4 in.)
Hemipholis elongata (Say, 1825)	Few; small (disc, ¼ in.)
Luidia clathrata (Say, 1825)	Common; large (5-6 in.)
Mellita quinquiesperforata (Leske)	Common; medium (1–2½ in.)
Ophiolepis elegans Lütken, 1859	Common; small (disc, ½ in.)
CORALS	
Astrangia astreiformis Milne-Edwards and Haime, 1849	Common on shell; small (¼ in.)
CRUSTACEANS	
Dromidia antillensis Stimpson, 1858	Few, inside pelecypod shells; medium (2 in.)
Heterocrypta granulata (Gibbes, 1849)	Few on shell; small (¾–1½ in.)

This list includes only a small part of the invertebrate species found in gulf coastal inlets. Most species listed are restricted to inlets, whereas the other 60–100 species present may range either from the nearshore gulf into the inlets or from the nearby lagoons into the inlets. Many of the larger invertebrates in the inlets are those which are dependent upon currents for planktonic food, or are attaching forms. There are also many motile forms which can move either in or out in response to the tidal flushing of the inlets.

This environment exists in all climatic zones where there are deep inlets extending from the open gulf into the bays (Figs. 7–11). Salinities in the inlets are usually within the normal gulf range, and bottom-water temperatures are more stable than those in the shallower lagoons. The sediments are sand and shelly sand. Depths of the inlets and channels range from 8 to 45 ft. Characteristic species are on Plate 3. Complete lists of the invertebrates, and illustrations of most of those found in the previous assemblages can be found in Parker (1956; 1959a).

CONTINENTAL SHELF AND UPPER CONTINENTAL SLOPE FAUNAS

More than 300 biological samples were collected on the continental shelf and upper continental slope from off Mobile, Alabama, to Port Isabel, Texas (Fig. 12). One-third of the samples were taken with the van Veen sampler, which gave a quantitative estimate of the larger bottom fauna. The different assemblages of the larger invertebrates are more homogenous on the continental shelf than in the adjacent bays.

DESCRIPTION OF THE ENVIRONMENTS

The Gulf of Mexico is considered a subtropical sea, as the mean annual surface temperatures range from a minimum of 18°C to approximately 30°C. The surface waters of the inshore portions of the northern Gulf from just east of the Mississippi Delta to Matagorda Bay (Fig. 1), however, are cold enough in the winter to be considered warm-temperate. Temperatures of the inner-shelf waters change from warm, subtropical in the eastern Gulf to cooler, temperate waters in the central region, and back to warm, subtropical on the southwestern coast near the Mexican border. There are also major differences in run-off, river discharge, and turbidity along major portions of the Gulf Coast.

Water circulation is an important factor in the Gulf of Mexico as a means of promoting and limiting the dispersal of marine invertebrate larvae. Leipper (1954) indicates that the major currents in the Gulf of Mexico originate from the Yucatan Straits. Most of the water flows northward and divides off the Mississippi Delta,

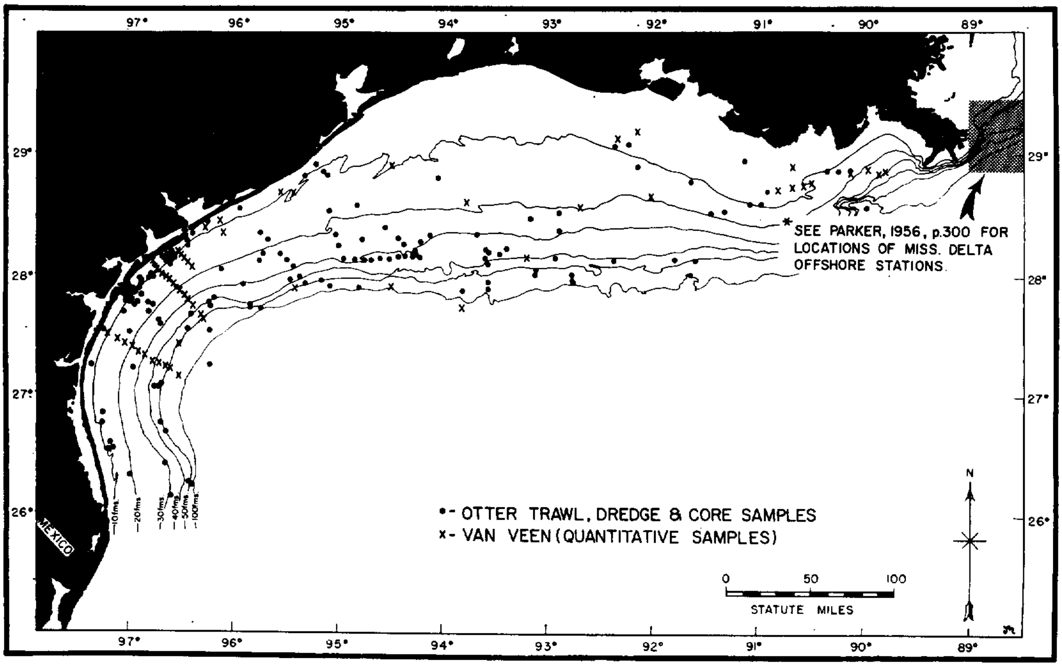


FIG. 12.—Location map of biological samples collected in the northwestern Gulf of Mexico from 1951 to 1957. About 100 samples were taken in the Mississippi Delta region, shaded area.

forming an eastward-flowing current which eventually becomes the Florida Current and a westward-flowing current which terminates off Padre Island, Texas, at the convergence with a current from the Gulf of Campeche (Fig. 13). Curray (this volume, p. 221) has plotted detailed current and wind information at various seasons on the Texas continental shelf. There are three portions of the northern Gulf coast, bathed by different currents—the north coast eastward from the Mississippi Delta; the area west of the Mississippi Delta to Padre Island; and the coast southwest of Corpus Christi, Texas.

The combination of circulation and climate, and the differences in predominant sediment off each portion of the coast create environments sufficient to separate faunas in the shallow shelf regions from east to west. These are recognized as zoogeographic provinces by Pulley (1953) and Hedgpeth (1953). The zoogeographic provinces (Fig. 14) correspond approximately to the climatic zones discussed above, although the humid zone contains two provinces—one east of the Mississippi Delta with a warm-water, sandy-shore fauna; and the other from the Mississippi Delta west to Sabine, Texas, with a cooler water, clayey-bottom fauna. The subhumid zone fauna is a transition one in shallow water, grading into the warm water, sandy shore fauna of the semiarid zone. The inshore environmental differences are the most striking in the region between the Mississippi Delta and Sabine, Texas. Salinities along this portion of the coast are always less than normal gulf values (Leipper, 1954, p. 135), and sand beaches are replaced by clay beaches and marshes growing directly into the Gulf of Mexico (Morgan, Van Lopik, and Nichols, 1953).

The surf zone is characterized by constant wave action, dessication of part of the zone at low tide, and a hard sand bottom. Outside this zone, from shore to 12 fathoms, there is considerable range of water temperature (Fig. 15). Pulley (1953) found that the water temperatures in the northern Gulf in winter approached the values found from North Carolina to Long Island; in the summer the temperatures were higher than those for the Caribbean. The 1–12 fathoms zone is constantly turbulent, the waters are virtually isothermal, and bottom temperatures reflect the prevailing air temperatures. Salinities may be less than the normal offshore values, especially in the vicinity of rivers. The bottom sediments are sandy inshore (except off western Louisiana) and grade into a mixture of sand and mud offshore (Fig. 16).

The second zone offshore extends to 30 or 40 fathoms. At 40 fathoms the average winter and summer bottom-water temperatures are the same, whereas inshore of that depth the wintcr and summer bottom-water temperatures differ, reflecting water mixing to the bottom (Fig. 15). At 12–40 fathoms there is less turbulence than on the inner shelf, less turbidity, and varying sediment types, depending upon sediment sources and the presence of relict sediments (Curray, this volume, p. 221, ff.).

At 40–60 fathoms the bottom-water temperatures reflect slightly the seasonal temperatures, and the bottom of the seasonal layer is at about 60 fathoms (Phleger, 1951). The minimum temperatures in this zone are higher than the minimum temperatures in the 0–12 fathoms zone. Sediments are mostly clayey silt and silty clay, although coarse sediments are common off Galveston, Texas. Fishermen report strong bottom currents at these depths, although the magnitude is not known. Some light penetrates to the bottom and the shallower banks on this portion of the shelf are often capped by algae.

The upper continental slope from 60 to at least 250 fathoms has virtually constant bottom temperatures and decreasing temperatures with increasing depth (Fig. 15). Below 150 fathoms water temperatures are permanently lower than the coldest inshore water temperatures. The sediments of the upper slope are mostly clayey silt

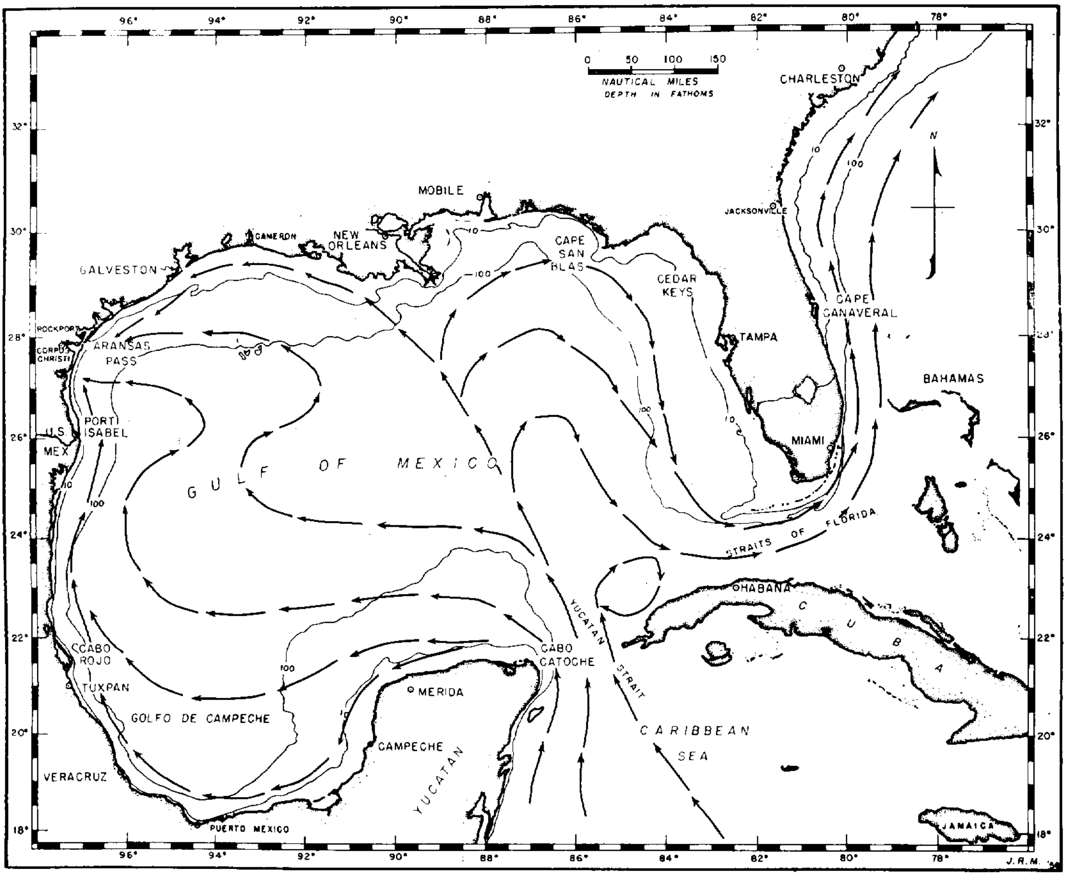


FIG. 13.—General surface water circulation in the Gulf of Mexico for month of June, after Leipper, 1954.

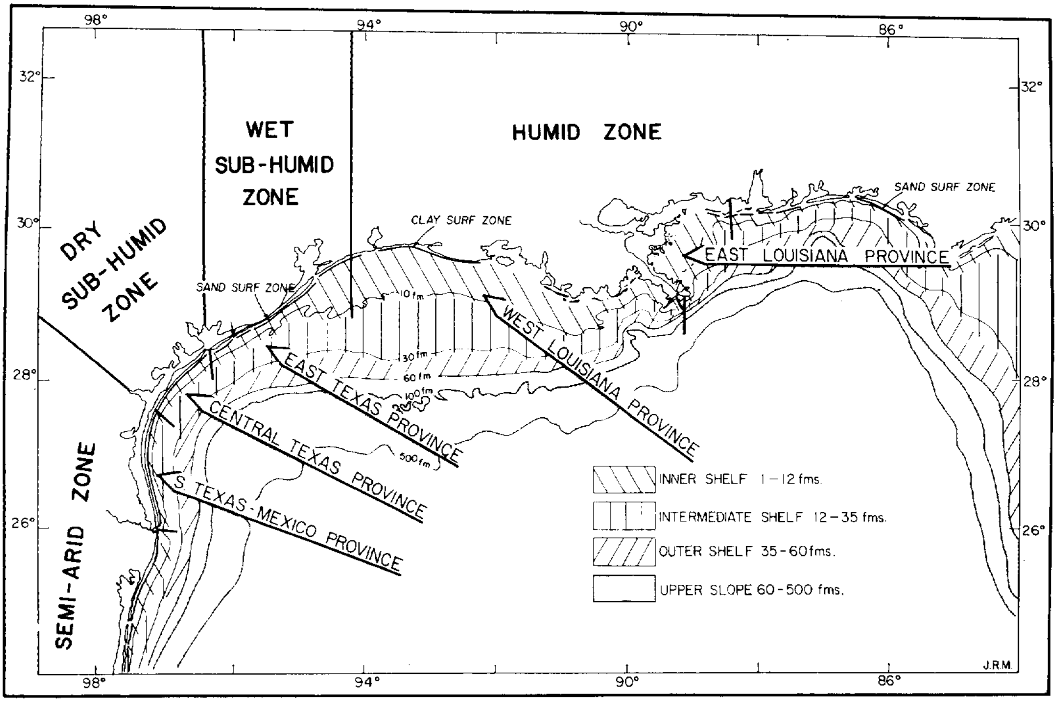


FIG. 14.—Areal distribution of macrofaunal assemblages, northern Gulf of Mexico, and climatic zones, modified from Hedgpeth, 1953. Faunal provinces, extending generally to depths of about 11 fathoms, based on breaks in mollusk distribution, related to climatic and physical boundaries. Based partially on data from Pulley, 1953.

or silty clay. Turbulence on the bottom below 100 fathoms is at a minimum; and all plant production ceases. The macrofaunal depth zones and inshore zoogeographic provinces are shown in Figure 14.

CONTINENTAL SHELF AND SLOPE MACROFAUNA

1. SURF ZONE OF SAND BEACHES

Species	*Comparative Abundance; Size*
PELECYPODS	
Donax variabilis variabilis Say, 1822	At times very abundant (Coe, 1957), ranges east of Mississippi Delta; small (½–1 in.)
Donax variabilis texasiana Philippi, 1847	Abundant, but ranges along Texas coast; small (½–1 in.)
Donax tumida Philippi, 1848	Common, lives somewhat deeper than *D. variabilis*, along whole coast; small (½–¾ in.)
GASTROPODS	
Olivella mutica (Say, 1822)	Common at times, not restricted to surf zone; small (3⁄16–⅜ in.)
Terebra cinerea (Born, 1778)	Abundant, when *Donax* is; medium (¾–1¼ in.)
CRUSTACEANS	
Emerita talpoida (Say)	Abundant, mostly in sand dampened by tide; medium (1–2 in.)
Ocypode albicans (Bosc)	Common, mostly in upper sand beach, rare in water; large (6–8 in.)

This assemblage is found throughout the world wherever there are sand beaches and heavy surf. It is virtually unchanged from east to west in the northern Gulf, except for the replacement of one subspecies of *Donax* with another east and west of the Mississippi Delta. The species are resistant to a very wide range in temperature, and prefer a substrate which is almost invariably a well-sorted very fine sand on the Gulf Coast. The predominant species are on Plate 4.

II. INNER SHELF, 2–12 FATHOMS

Species	*Comparative Abundance; Size*
PELECYPODS	
Atrina serrata (Sowerby, 1825)	Common, in sandier portions of zone; large (6–10 in.)
Chione intapurpurea (Conrad, 1849)	Common, only off western Louisiana; medium (1–1½ in.)
Dinocardium robustum (Solander, 1876)	Common, from east Mississippi Delta to Mexico, replaced by *D. r. vanhyningi* in eastern Gulf; large (4–6 in.)
Dosinia discus (Reeve, 1850)	Common, along whole Gulf Coast; large (1–3 in.)
Dosinia elegans Conrad, 1843	Rare off southern Texas, common to the south; large (2–3½ in.)
Labiosa plicatella (Lamarck 1818)	Few, along whole coast; large (2–3 in.)
Solen viridis Say, 1821	Common, only off western Louisiana; small (½ in.)
Spisula solidissima raveneli (Conrad, 1831)	Common, along whole coast on sand bottom; large (4–6 in.)
Tellina tayloriana Sowerby, 1867	Abundant along Texas beaches, replaced by *T. alternata* Say, east of Delta; medium (1–2 in.)
GASTROPODS	
Architectonica nobilis 'Bolten' Röding, 1798	Common, along whole coast; medium (1–2 in.)
Busycon plagosum texana (Hollister, 1959)	Common, along northern Gulf Coast; large 3–5 in.)
Oliva sayana Ravenel, 1834	Common, along whole Gulf Coast; medium (1–2 in.)
Phalium granulatum (Born, 1778)	Common, along whole Gulf Coast; large (2–3 in.)
Terebra dislocata (Say, 1822)	Abundant, in clayey sediments; small (½–1 in.)
ECHINODERMS	
Luidia clathrata (Say, 1825)	Common, on sand bottom along whole coast; large (5–6 in.)
Mellita quinquiesperforata (Leske)	Abundant, seasonally, on sand along whole coast; medium (1½–2½ in.)

The species listed are the larger and more conspicuous ones, but they represent only a part of the total of 40–60 common invertebrate species found in this zone. The depth zone 2 to 12 fathoms is the most productive of all in the Gulf of Mexico, having the largest number of living

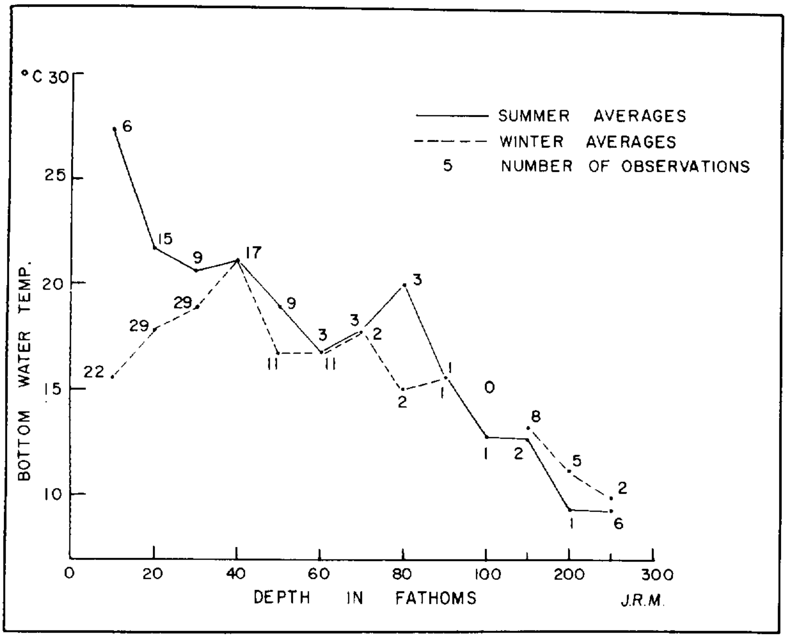


FIG. 15.—Comparison of summer and winter average bottom-water temperatures in the northern Gulf of Mexico (1951-1955), period of intense biological shelf collections. Data from Springer and Bullis, 1956. Note convergence of temperature values at about 40 fathoms and again at 60 fathoms.

individuals per unit area. Although this assemblage is quite constant from the eastern to western Gulf, a few species are distinct for the shelf off western Louisiana (*Chione intapurpurea* and *Solen viridis*), and a number of tropical or subtropical species such as *Dosinia elegans, Pecten raveneli, Aequipecten muscosus,* and *Murex cellulosus* are found in these shallow waters only off Padre Island, Texas. This assemblage is recognizable in Pleistocene deposits along the Texas coast, and in the Pleistocene-to-Miocene deposits in Florida (Gardner, 1947; and DuBar, 1958). Most of the species listed above are on Plate 4, and others are in Parker (1956, pp. 342, 345).

III. PRO-DELTA SLOPE, 2–11 FATHOMS+

Species	*Comparative Abundance; Size*
PELECYPODS	
Abra lioica (Dall, 1881)	Abundant, in silty clay sediments; small (3/16–3/8 in.)
Macoma tageliformis Dall, 1900	Common in silty clay and clayey silt sediments; medium (1½–2 in.)
Mulinia lateralis (Say, 1822)	At times abundant in clayey silts; small (¼–3/8 in.)
Nuculana concentrica (Say, 1824)	Common in clayey sediments; small (½ in.)
GASTROPODS	
Anachis avara semiplicata Stearns, 1873	Common, associated with algae and detritus; small (¼–3/8 in.)
Nassarius acutus (Say, 1822)	Common throughout environment; small (½ in.)
Polinices duplicatus (Say, 1822)	Common, also common in same depths along all Gulf Coast; large (1½–3 in.)
CRUSTACEANS	
Portunus gibbesi (Stimpson, 1859)	Common at certain times; large (6–8 in.)
Squilla empusa Say, 1818	Abundant at times; large (4–6 in.)

This association is peculiar only to the prodelta slope of the Mississippi where the deposition is very rapid and the sediments are clayey silt to silty clay (Parker, 1956, pp. 321–325). Salinities (18–36 $^0/_{00}$) differ from those at equivalent depths on the normal sandy coast. This assemblage has been recognized in older sediments near the Mississippi Delta, although it is not as distinct as most faunal assemblages, because many of the species range into the lagoons and sounds. The species are figured in Parker (1956, p. 322).

IV. INTERMEDIATE SHELF, 12 TO 35 FATHOMS

Species	*Comparative Abundance; Size*
On Mud Bottom	
PELECYPODS	
Nucula proxima Say, 1822	Common, found along whole coast; small (1/16–1/8 in.)
Nuculana concentrica (Say, 1824)	Common, along whole coast, occurs also in bays, but may be a different race; small (½ in.)
Pandora bushiana Dall, 1886	Common along whole coast; small (½ in.)
Pitar cordata (Schwengal, 1951)	Common, mostly off Texas; large (1–1½ in.)
Varicorbula operculata Philippi, 1848	Abundant, along whole coast; small (¼–3/8 in.)
GASTROPODS	
Anachis saintpairiana (Caillet)	Abundant, along whole coast; small (½ in.)
Nassarina glypta Bush, 1885	Common, along whole coast; small (3/16–3/8 in.)
Nassarius ambiguus (Montagu, 1803)	Common, along whole coast; small (3/16–3/8 in.)
On Sand Bottom	
PELECYPODS	
Aequipecten gibbus gibbus (Linné, 1758)	Common, along whole coast; medium (1½–2 in.)
Aequipecten muscosus (Wood, 1828)	Common, along whole coast; medium (1–1½ in.)
Chione clenchi Pulley, 1952	Abundant, along whole coast; medium (1–1½ in.)
Chione grus (Holmes, 1860)	Common, along whole coast, ranges deeper; small (½ in.)
Gouldia cerina (C. B. Adams, 1845)	Abundant, along whole coast; small (3/8 in.)
Laevicardium laevigatum (Linné, 1758)	Few, rare in central portion; large (2–3 in.)

Species	Comparative Abundance; Size
PELECYPODS (*Continued*)	
Lucina sombrerensis Dall, 1886	Common, along whole coast; small (⅛–¼ in.)
Pecten raveneli Dall, 1898	Few, rare in central portion; large (1½–2 in.)
Phylloda squamifera (Deshayes, 1854)	Common, along whole coast; medium (¾–1¼ in.)
Quadrans lintea (Conrad, 1837)	Common, along whole coast; medium (½–¾ in.)
Semele purpurescens (Gmelin, 1790)	Common, along whole coast; medium (¾–1 in.)
Solecurtus cumingianus (Dunker, 1861)	Few, along whole coast; medium (¾–1¼ in.)
Tellina georgiana Dall, 1900	Common, along whole coast; medium (¾–1¼ in.)
GASTROPODS	
Antilliphos cf. *candei* (d'Orbigny, 1842)	Common, western Louisiana to Mexico; medium (¾–1 in.)
Distorsio clathrata (Lamarck, 1816)	Common, along whole coast; medium, (1½–1¾ in.)
Fasciolaria hunteria (Perry, 1811)	Common, central Texas to Mexico; large (3–4 in.)
Murex fulvescens Sowerby, 1834	Common, along whole coast; large (3–6 in.)
Murex pomum Gmelin, 1790	Common, along whole coast; medium (1½–2 in.)
Strombus alatus Gmelin, 1790	Few, common to the south; large (2½–3½ in.)
Tonna galea (Linné, 1758)	Few, common to the south; large (4–10 in.)

Although the depth ranges of most of the species listed are within 12–40 fathoms, a few occur in lesser abundance inside and outside these depths. The above list is only a partial one, especially for the forms occurring on sand bottom. Relatively few species occur on the mud bottom at these depths, but most of those which do are more abundant than those found on sand bottom. Most of the species are illustrated on Plate 4, and others in Parker (1956, pp. 346, 348).

V. OUTER SHELF, 40–65 FATHOMS

Species	Comparative Abundance; Size
PELECYPODS	
Anadara baughmani Hertlein, 1951	Abundant, on mud bottom, whole coast; medium (1½–2 in.)
Cuspidaria ornatissima (d'Orbigny, 1846)	Common, mud bottom, rare alive; small (¼–½ in.)
Eucrassatella speciosa (A. Adams, 1852)	Common, mud bottom, whole coast; medium (1½–2½ in.)
Laevicardium fiski Richards, 1954	Common, on sandy bottom, rare alive; medium (½–1 in.)
Lyropecten nodosus (Linné, 1758)	Few, Texas to Mexico, sand bottom; large (3–6 in.)
Microcardium transversum Rehder and Abbott, 1951	Common, on sandy bottom, whole coast; medium (¾–1 in.)
Nuculana jamaicensis (d'Orbigny, 1842)	Abundant, whole coast, mud bottom, small (¼–½ in.)
Pecten papyraceus (Gabb, 1873)	Abundant, whole coast, mud bottom; large (2–3 in.)
Pitar cordata (Schwengel, 1951)	Abundant, northern Gulf Coast, mud bottom; medium (1½–2 in.)
Poromya granulata Nyst and Westendorp, 1839	Common, whole coast, sand bottom, not alive; small (3/16–⅜ in.)
Solecurtus sanctaemarthae (d'Orbigny, 1853)	Rare, south Texas, not alive, sand bottom; medium (1–1¼ in.)
Trigonicardia media (Linné, 1758)	Rare, Texas coast, not alive, sand bottom; medium (¾–1½ in.)
Verticordia ornata (d'Orbigny, 1846)	Common, whole coast, sand bottom; small (⅛–3/16 in.)
GASTROPODS	
Conus clarki Rehder and Abbott, 1951	Common, two forms of same species, slender form near Delta, mud bottom; medium (1–1½ in.)
Distorsio mcgintyi Puffer and Emerson, 1956	Rare, central portion, sand bottom, not alive; medium (1–2 in.)
Muricopsis hexagona Lamarck, 1822	Rare, not alive, common to the south, sand bottom; medium (1–1½ in.)
Natica canrena Linné, 1767	Common, whole coast, mud bottom; medium (1–2 in.)
Polystira albida (Perry, 1811)	Common, whole coast, mud bottom; large (2–3 in.)
Sconsia striata (Lamarck, 1816)	Common, whole coast, mud bottom; large (1½–2¼ in.)
Turritella exoleta (Linné, 1758)	Common, central Texas to Mexico, not alive, sand bottom; medium (1½–2½ in.)

Species	*Comparative Abundance; Size*
ECHINODERMS	
Astropecten duplicatus Sladen	Few, typical of Atlantic rather than Gulf Coast, mud bottom; large (4–6 in.)
Clypeaster prostratus (Ravenel)	Few, mud bottom, west of Delta; large (5–8 in.)
CRUSTACEANS	
Rhaninoides louisianense Rathbun	Common, whole coast, mud bottom; medium (1½–2½ in.)

Several of the species were not collected alive, but occur as dead shell in the sand deposits at these depths. They are found living in warmer and shallower waters to the south. Although most of the mud-bottom species are moderately common, they are not as abundant as the mud-bottom forms in shallower water. The deeper limit of the assemblage is at the approximate bottom of the seasonal layer (Phleger, this volume, p. 267). The above list represents only a portion of the total number of species known from these depths. Most of the species are figured on Plate 5.

VI. PELAGIC ASSEMBLAGE

No attempt is made to list all the pelagic mollusks living at or near the surface of the ocean in the northern Gulf of Mexico. There are a number of pteropod species such as *Cavolina longirostris* 'Leseuer' Blainville, 1821, *Cavolina uncinata* 'Range' d' Orbigny, 1836, and *Cavolina tridentata* (Linné, 1758); two gastropods, *Janthina janthina* (Linné, 1758) and *Atlanta peroni* Leseuer, 1817; and two cephalopods, *Argonauta argo*, Linné, 1758 and *Spirula spirula* (Linné, 1758) whose shells are deposited on the outer continental shelf and the deeper portions of the Gulf of Mexico. These mollusks are associated with offshore water masses and apparently never occur close to shore. Their shells occur in the surface sediments deeper than about 30 fathoms. A few are illustrated on Plate 5.

VII. UPPER CONTINENTAL SLOPE, 65–600 FATHOMS

Species	*Comparative Abundance; Size*
PELECYPODS	
Aequipecten glyptus (Verrill, 1882)	Few, mostly deeper than 100 fm.; large (3–4 in.)
Astarte nana Dall, 1886	Common, 50 to over 100 fm.; small (⅛–¼ in.)
Callista eucymata (Dall, 1889)	Few, mostly associated with shell or calcareous deposits below 65 fm.; medium (¾–1½ in.)
Cuspidaria granulata (Dall, 1881)	Common, many dead in shallower water, living in deeper than 65 fm.; small (½ in.)
Cyclopecten nanus Verrill and Bush, 1897	Common east of Mississippi Delta, rare west of Delta; small (¼ in.)
Limopsis antillensis Dall, 1881	Rare, chiefly west of Delta; small (¼ in.)
Limopsis sulcata Verrill and Bush, 1898	Common, along whole coast, 50–150 fm.; small (¼ in.)
Microcardium permabile (Dall, 1886)	Common, mud bottom, whole coast, mostly between 60 and 100 fm.; medium (¾ in.)
Nuculana cf. *carpenteri* Dall, 1881	Rare, differs from true *carpenteri* in shallower water; small (⅜–½ in.)
Pecten dalli E. A. Smith, 1886	Rare, deeper than most A.P.I. stations; medium (1½–2½ in.)
Thyasira trisinuata d'Orbigny, 1846	Few, ranges shallower to the south; small (3/16–⅜ in.)
Venericardia armilla (Dall, 1903)	Common, especially from 60–120 fm.; small (¼ in.)
Verticordia fischeriana Dall, 1881	Common, mostly in upper depth range of assemblage; small (¼ in.)
Verticordia sequenzae Dall, 1886	Rare, in deeper water than *fischeriana;* small (¼ in.)
Yoldia solenoides Dall, 1881	Common, occurs dead from 40 fm., living to at least 118 fm.; small (½ in.)
GASTROPODS	
Antemetula agassizi (Clench and Aguayo, 1941)	Rare, 80 fm. off central Texas; medium (1¼ in.)
Fusinus couei Petit, 1853	Few, mostly off south Texas to Mexico, and east of Delta; large (5 in. long)

Species	*Comparative Abundance; Size*
Gastropods (*Continued*)	
Gaza superba Dall, 1881	Rare, on middle slope; small (½ in.)
Mitra fulgarita Reeve, 1844	Rare, between 60 and 80 fm.; medium (1 in.)
Mitra swainsoni antillensis Dall, 1889	Rare, between 65 and 80 fm.; large (2½–3½ in.)
Murex branchi Clench, 1953	Rare, 80–100 fm.; large (3 in.)
Petrotrochus quoyana Fischer and Bernadi, 1856	Rare, middle slope depths; medium (1½–2 in.)
Polystira tellea (Dall, 1889)	Common, from 60–100 fm.; medium (1–2 in.)
Terebra dislocata rudis (Gray, 1834)	Rare, from 60–80 fm.; medium (¾–1½ in.)

Many of the species listed above from depths below 100 fathoms are cited from the literature (Springer and Bullis, 1956; and Dall, 1903). There are at least 50–100 additional species known from the upper slope of the Gulf of Mexico, but most are known from a single record. The number of individuals per species decreases rapidly below 65 fathoms. Some of the species collected by the A.P.I. Project 51 are shown in Plate 6.

VIII. CALCAREOUS BANK ASSEMBLAGE

Species	*Comparative Abundance; Size*
Pelecypods	
Arca umbonata Lamarck, 1819	Common, on banks from 10–60 fm., attaching; large (2–3 in.)
Barbatia candida (Gmelin, 1790)	Common, attaching, from 10–60 fm.; medium (1 in.)
Barbatia domingensis (Lamarck, 1819)	Common, attaching, 10–60 fm.; small (½ in.)
Chama congregata Conrad, 1833	Abundant, mostly on shallow banks; medium (½–¾ in.)
Chama macerophylla Gmelin, 1790	Common, mostly on deeper banks; medium (1–½ in.)
Corbula dietziana (C. B. Adams, 1852)	Abundant, free-living, mostly deeper banks; small (¼–½ in.)
Echinochama cornuta (Conrad, 1866)	Common, attaching, 10–60 fm.; medium (½–1 in.)
Lima tenera Sowerby, 1846	Common, attaching, 30–65 fm.; large (2–3 in.)
Papyridea soleniformis (Bruguieré, 1789)	Common, free-living, found with shell on level bottom also; medium (1 in.)
Plicatula gibbosa Lamarck, 1801	Abundant, mostly on deeper banks, attaching; medium (½–1 in.)
Pycnodonta hyotis (Linné, 1758)	Few, on deeper banks, attaching; medium (1–2 in.)
Gastropods	
Calyptraea centralis (Conrad, 1841)	Common, few alive, mostly deeper banks; small (3/16–⅜ in.)
Crucibulum auricula (Gmelin, 1780)	Common, attaching, 15–40 fm.; medium ½–1 in.)
Haliotis pourtalesii Dall, 1889	Rare, only on banks over 60 fm.; small (½–1½ in.)
Liotia bairdi Dall, 1889	Common, mostly on deeper banks; small (3/16 in.)
Nesta atlantica Farfante, 1947	Rare, attaching, on banks below 30 fm.; small (1/16–3/16 in.)

The above list contains only a few of the more than 150 species collected from banks in the northern Gulf of Mexico. Many of the species collected were dead, and appear to be related to lower stands of sea level. A more complete list of species from a few of the banks and a discussion of their importance can be found in Parker and Curray (1956). A few of the species are illustrated on Plate 6, and others are illustrated in Parker and Curray (1956).

GEOGRAPHICAL DISTRIBUTIONS

It is impossible to locate exact boundaries for the assemblages just discussed for each portion of the northern Gulf Coast. Species which are part of one depth assemblage in the southeastern Gulf or off Mexico may be part of a deeper assemblage off the central Texas coast. In general the species listed for the level-bottom assemblages in the northern Gulf have somewhat restricted depth ranges falling within those given for their respective assemblages. However, for every species listed there are two or three more which do not conform to this range throughout the gulf. So few living individuals were collected in this study as compared to dead shell that it is difficult to assess the true patterns of distribution.

An estimate of the relative abundance of living

TABLE I. RELATIVE ABUNDANCE OF LIVING INVERTEBRATES IN VARIOUS DEPTHS ACROSS SHELF

DEPTHS (FATHOMS)	*1–10*	*10–20*	*20–30*	*30–40*	*40–50*	*50–60*	*60–70*
Number of Samples	19	12	10	3	5	2	4
Average of living animals per station	18.8	2.2	3.2	1.6	3.0	2.0	4.0
Average of living species per station	5.7	1.0	1.7	1.6	1.2	.5	1.7
Greatest number of living animals per station	82	10	14	3	12	4	6
Greatest number of living species per station	23	4	6	3	3	1	3

invertebrates in various depths across the shelf, as gained from the study, is shown in Table I. This table includes mean values and greatest numbers of living invertebrates with hard parts per station for van Veen grab samples *only*. Dredge and trawl samples produced many more living animals per station, but the area sampled by these devices is much greater, and cannot be accurately determined. It can be seen in the table that, except for the inshore zone (1–10 fathoms), the numbers of living individuals and species are very low. The depth-faunal zones used in this paper, however, were not based on these samples alone, but were assessed from published and unpublished records of the most abundant species, plus the total living and dead populations gained from this study.

In general the species distributions follow certain ranges of bottom temperatures, and separate according to major sediment types. Hutchins (1947) discussed the relationships between maximum and minimum water temperatures and the survival of invertebrate larvae and adults. The principles outlined in his paper were utilized to establish zoogeographic regions in the Gulf of Mexico, based upon the inshore distribution of pelecypods (Pulley, 1953; Parker, 1956). The relationship between distribution of invertebrates and sediment types has been discussed by Thorson (1957). Clayey or firm sediments are generally inhabited by detritus feeders or scavengers, whereas, sandy sediments contain more filter feeders and predators.

The depth assemblages seem to be applicable from Florida to Mississippi, except that in the shallower zones there are a number of mollusks and crustaceans which do not occur off Louisiana and Texas but are common off southwestern Florida.

Off the Mississippi Delta and west to Sabine, Texas, the offshore assemblages follow the previously established depth-temperature zones, but the deeper assemblages are mostly those of mud bottom. Inshore, there is a slightly different fauna than that found either east of the Mississippi delta or west of Galveston. Climate and water-temperature records indicate this region to be somewhat colder than the rest of the Gulf Coast. This is substantiated by the fact that the mollusk species peculiar only to this region in the Gulf of Mexico are found in cooler waters along the Atlantic coast. Low-salinity faunas occur both in the vicinity of the Mississippi Delta and off the major bays in western Louisiana. These are maintained in depths to 5 or even 10 fathoms by the flow of fresh water directly into the gulf in these areas. The surf-zone sand-beach assemblage is missing from much of this coast, inasmuch as either the beaches are clay, or the coastal marshes grow uninterrupted into the open gulf. The clay beaches of western Louisiana are characterized by a number of large boring clams, especially *Petricola pholadiformis* and *Cyrtopleura costata*.

The shelf from Galveston Bay to Matagorda Bay also has depth assemblages following the depth-temperature zones (Fig. 14), but the assemblages are different from those off Louisiana because the sediments are predominantly sandy. The calcareous bank fauna is also characteristic of this region (Parker and Curray, 1956). Wherever clayey or muddy sediments occur, assemblages similar to those in muddy sediments off Louisiana are also found.

From approximately Matagorda Island to the southern part of Padre Island the offshore sediments are mostly clay and the assemblages are like those typical of the region off Louisiana. The surf-zone assemblage attains its best development off Texas, with the appearance of long stretches of sandy beach and high surf. Calcareous banks are few and apparently not as rich as those off Galveston, possibly because they have their tops in deeper water. The deeper assemblages follow the depths and isotherms closely in this region, and the faunas are quite uniform within each zone.

The region directly off the Rio Grande differs

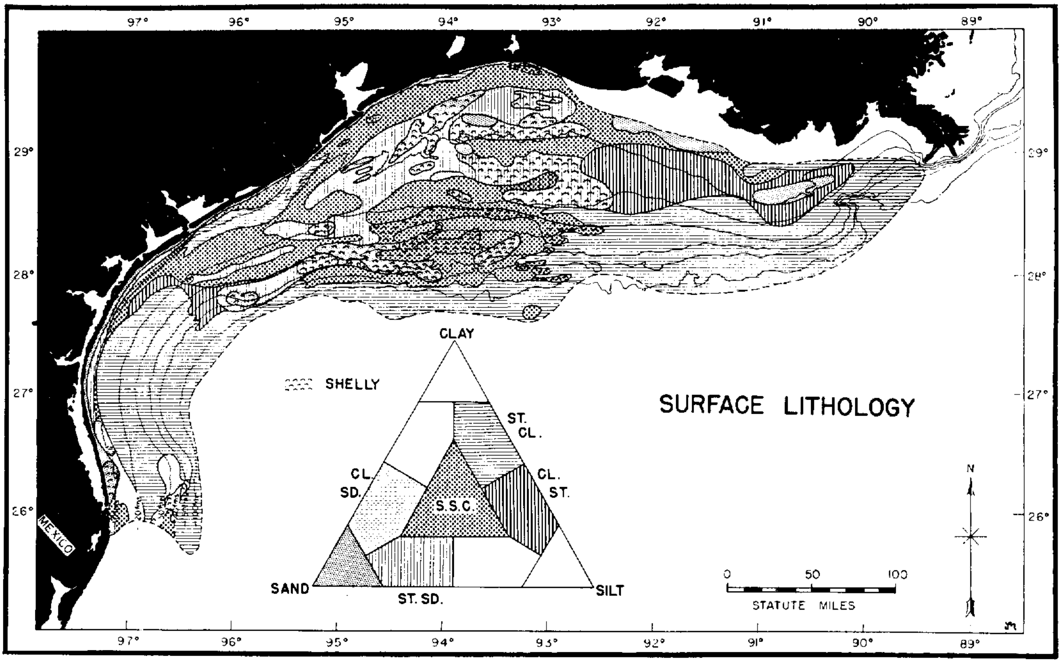


FIG. 16.—Areal distribution of sediments on continental shelf, northwestern Gulf of Mexico, from Curray, this volume.

from the clayey areas adjacent to it in two ways (1) the presence of sandy sediments and calcareous banks with their typical faunas; and (2) a decidedly warm-water element. Many species which are common off the coast of Mexico, including the Gulf of Campeche, are found in small numbers off southern Padre Island and the Rio Grande mouth. The warm-water species probably are transported by the Campeche water which flows northward to the Rio Grande (Fig. 13). The surf-zone assemblage is an important one in this region. The invertebrate fauna for the clayey bottoms in the last two zones is discussed in detail by Hildebrand (1954), and his zonation of fauna agrees closely with that given in this paper.

In general, the shallower the assemblage or depth zone the more variation in species from east to west or south to north. Only the upper continental slope zone shows no variation in species composition from the eastern to western Gulf. Although the faunal composition at depths of 12–40 fathoms is fairly consistent along the northern Gulf Coast, many of the same species are found in less than 12 fathoms in the Gulf of Campeche, the Florida Keys, and the Caribbean. It appears, therefore, that depth alone is not the critical factor.

MACROFAUNAL REMAINS ON CONTINENTAL SHELF AS A MEANS OF INTERPRETING HOLOCENE EVENTS

There are extensive areas of sand and shell debris over many portions of the continental shelf of the northern Gulf of Mexico (Fig. 16). These deposits have been interpreted as reworked sediments resulting from the regression and transgression of the sea during the last glacial stage of the Wisconsin (Curray, this volume, p. 258). A number of carbon–14 dates on shell material indicate little deposition on parts of the shelf in the past 15,000 years. To establish the sea level at various time intervals, only shells which presently live within very narrow depth ranges in shallow water were used for dating. The presence of certain species of mollusk shells in essentially nondepositional areas makes it possible to assess the probable water temperatures and climates which existed during the past 18,000 years.

More than 20,000 years before present.—The only evidence as to the probable climate before and during the regression are the submerged beachrock and coquina deposits off Freeport and Galveston, and Pleistocene outcrops along the Texas coast. Dates of 26,900 and 32,500 years B.P. were obtained on oyster and *Rangia* shell in the coquina banks at 10 fathoms. Both dates may be too young because of carbonate replacement and contamination. The coquina from the banks off Freeport, Texas, was composed of partially recrystallized shells of *Rangia cuneata, Crassostrea virginica,* and a few *Brachidontes recurvus.* These three species make up the bulk of the fauna in the warm-temperate, low-salinity regions today, and indicate a coast line similar to that of present-day western Louisiana.

20,000 to 18,000 years B.P.—During this period sea level is presumed to have been at −65 fathoms and perhaps lower (Curray, *op. cit.*). Samples from escarpments and shelly areas at depths of 60–66 fathoms indicate that at least part of this period was characterized by a temperate climate, as there were several valves of *Chione cancellata,* a few small valves of *Crassostrea virginica,* and many valves of the inlet species, *Crassinella lunulata.* Rutsch (1957) reported the same species in greater abundance from bioherms at approximately the same depths east of the Mississippi Delta.

The dominant shell material at the shelf break consists of large numbers of the warm water pelecypod genera *Barbatia, Arca, Chama, Echinochama, Pteria, Lima, Ostrea,* and *Plicatula,* and gastropod genera associated with a hard or rocky bottom, such as *Astraea, Murex, Diodora, Fissurella, Cypraea,* and possibly *Haliotis.* Few specimens were taken alive, and most of the shells are abraded, broken, and covered with fouling organisms and dead calcareous algae. Large amounts of old coralline algae, small ahermatypic corals, and bryozoa were present.

The presence of the many warm-water mollusk shells at this time can be explained in two ways. At the present time, bottom-water temperatures at the shelf break are warmer on the average than the winter inshore temperatures. A number of warm-water species usually restricted to rock bottom could become established there over a long period of time, especially as these rocky areas furnish the only suitable substrate along the northern Gulf Coast. The warm-water fauna could have become established during one of the changes in climate and circulation when sea level was much lower. These warm, shallow water animals have proliferated for a considerable time, and with increased depths and cooler climates would have been killed off. Certain individuals of a few species were able to survive these climatic and ecologic changes and continued to exist as isolated and slightly different populations (Parker and Curray, 1956).

18,000 to 16,000 years B.P.—According to Curray (this volume, p. 258), the sea level rose from at least 65 fathoms to about 45 fathoms, with about the same wind, current, and longshore-drift patterns as today. Most of the shallow-water species found in the sandy sediments between 65 and 45 fathoms are those presently living on the the outer coast from northern Florida to Cape Hatteras, and the environment seemed to consist of stretches of sandy bottom with water temperatures much like those of the central portion of the northern Gulf today. Typical species from these deposits are the pelecypods, *Aequipecten gibbus gibbus, Gouldia cerina,* and the gastropods, *Architectonica nobilis, Oliva sayana, Phalium granulatum,* and *Strombus alatus.* This is a typical assemblage tossed up on the beaches of Texas after storms. There were few warm water shells in these deposits.

16,000 to 14,000 years B.P.—Glaciers apparently advanced (corresponding to the Brady Interstadial) and sea level lowered slightly, or perhaps was stationary. The presence of *Crassostrea virginica* shell from several stations between 45 and 48 fathoms supports the existence of lagoons at this time.

14,000 to 12,000 years B.P.—The sea rose to about 25 fathoms below present sea level (Curray, this volume, p. 259). Faunal evidence indicates that climatic conditions may have been similar to those existing today, although more fresh water was available than during the preceding period. *Rangia* shells were collected from clayey deposits in depths of between 45 and 25 fathoms, which were dated at 12,000 to 13,000 years ago. No interpretation of the environmental conditions or geomorphology can be made for this period, as subsequent regression and transgression of the sea again nearly obliterated or reworked traces of the shore lines.

12,000 to 10,000 years B.P.—This period coincided with the readvance of the Mankato glaciers, causing a regression from a high of 22 to 25 fathoms to a low sea level of about 35 fathoms, as well as a change in wind and longshore-current direction (Curray, this volume, p. 221; and Fig. 17–*A*). The change in circulation from east to west could account for the large number of warm-water shells in what was then shallow inshore waters. These waters could have been warmed to a depth of 10 fathoms by the influx of Campeche water and warm surface water blown across the gulf by the southwest winds. There would also be a steady replenishment of warm-water planktonic mollusk larvae from south to north, once the population became established. Species flourishing at that time, and which are now either very rare, alive, in deeper water, or do not live in shallow water along the Texas coast today, include the pelecypods, *Antigona strigillina, Chama sarda, Laevicardium laevigatum, Laevicardium pictum, Lima lima, Lima tenera, Pitar albida, Solecurtus sanctaemarthae, Spondylus americanus, Tellina radiata,* and *Trachycardium magnum*; and the gastropods, *Anachis translirata, Calliostoma jujubinum rawsoni, Crassispira tampaensis, Distorsio mcgintyi, Erato maugeraei, Nassarius concensus, Oliva reticularis, Turritella exoleta,* and various species of tropical *Conus* and *Murex.*

The sand bodies associated with this stage contained large numbers of two species of *Donax* and various surf clams indicating sandy beaches. There were also extensive clayey areas containing many shells of *Crassostrea virginica, Rangia cuneata,* and *Mulinia lateralis,* which dated between 10,000 and 11,000 years B.P. These may represent embayed areas behind the barriers formed during the regression and halt of sea level. At the end of this period, circulation reverted to that similar to today's.

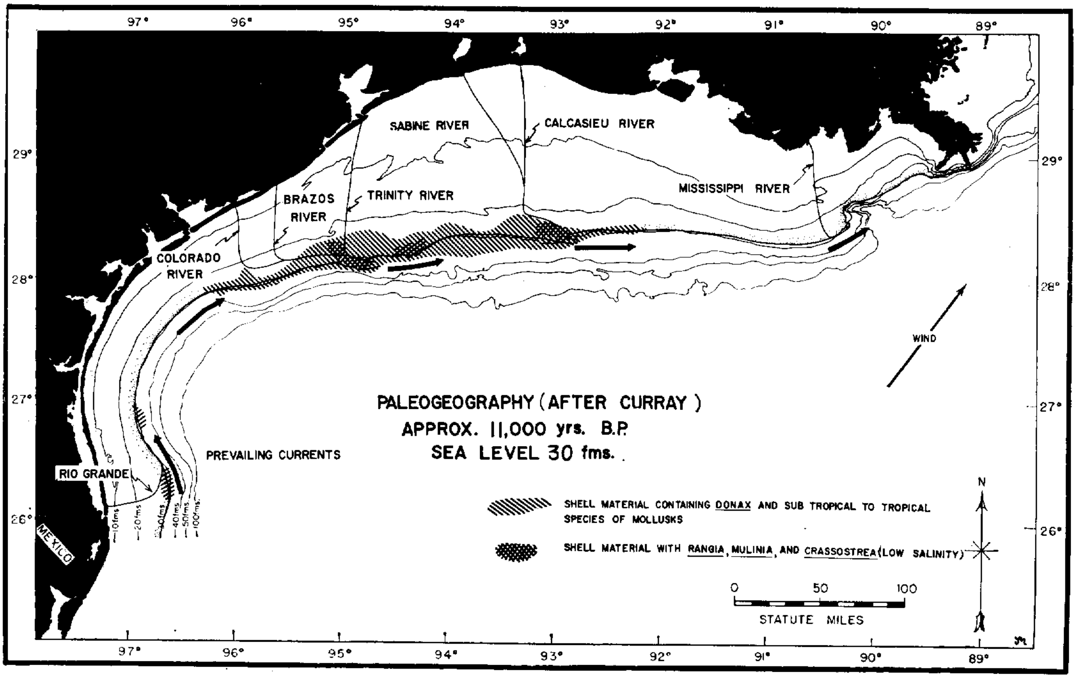
9,000 to 7,000 years B.P.—Evidence for a change in climate again, and another circulation reversal, is the presence of shells which have southern, shallow-water affinities (Fig. 17–*B*). Such warm-water species living in less than 10 fathoms were the pelecypods, *Aequipecten muscosus, Anadara lienosa floridana, Laevicardium laevigatum, Macrocallista maculata, Macrocallista nimbosa,* and *Pecten raveneli;* and the gastropods, *Crassispira ostrearum, Nassarius ambiguus,* and various species of *Trivia.*

Topographic highs along the 10-fathom contour contained large numbers of *Crassostrea virginica, Mulinia lateralis,* and a few *Rangia,* which dated at between 7,000 and 9,000 years B.P. (Fig. 17–*B*). Beds of old *Rangia cuneata* and *Rangia flexuosa* also exist at these depths off western Louisiana and eastern Texas, but have not been dated. Closer to the Mississippi Delta, the marsh snails *Neritina reclivata* and *Littorina irrorata* were found in 10-fathom deposits, although they are much younger, as oyster shell from the same deposits gave dates younger than 5,000 years. These deposits were originally marshes formed after sea level stabilized, and may have subsided with the general downwarping of the Mississippi Delta.

7,000 years B.P. to the present time.—It is difficult to describe the events and probable climates existing during the past 7,000 years from the shelf sediments and shell remains inshore of 10 fathoms, as they are continually agitated and reworked by wave action. There is an indication from two dates obtained from shells of an exclusively tropical species of tropical shallow-water oyster, *Crassostrea rhizophorae,* collected from between 30 and 40 fathoms, that at about 3,200–3,600 years ago there may have been either a change in circulation, again, or a distinct warming of the climate.

The effects of sea-level rise and eventual stabilization at the present level during the past 8,000 years are easier to trace in the history of deposition in some Texas bays. Analyses of borings in San Antonio, Mesquite, and Aransas Bays have been reported in Shepard and Moore (1955; this volume, p. 133, ff.), Shepard (1956b) and Parker (1959a). Shell material from various depths was dated by carbon 14, and the environmental conditions at 5- to 6-foot intervals throughout the borings were established from the lithology, coarse fractions, and the macrofaunal remains.

In general, the macrofauna indicates that between about 8,000 and 9,000 years ago low-salinity conditions were prevalent, with a river-influenced fauna present at the upper end of long narrow estuaries and oyster reefs at the seaward end of the estuaries. As sea level rose, the fauna



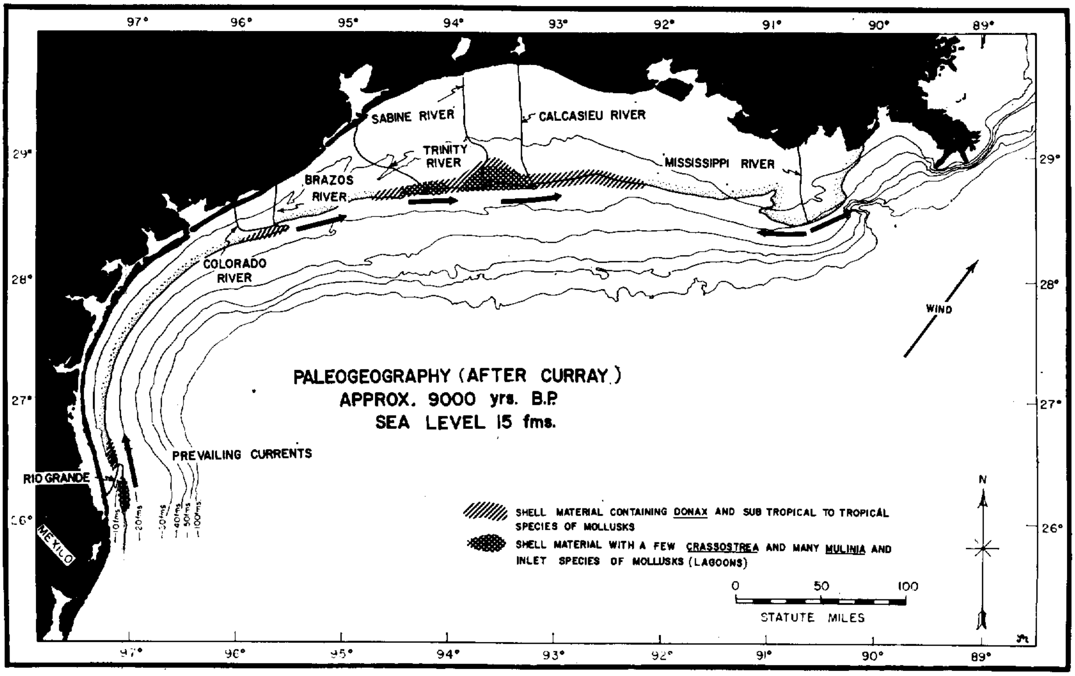


FIG. 17.—*A*—Paleogeography of northwestern Gulf Coast between 12,000 and 10,000 years before present, with the superimposed distribution of dated shell material used for climatic interpretation; *B*—Paleogeography of northwestern Gulf Coast at about 9,000 years before present, with distribution of shell material used for climatic interpretations. After Curray, this volume, p. 221, ff.

changed from a low salinity to a high salinity one. At about 6,000 to 5,000 years ago, many of the species from core depths of this age indicate a deep channel with access to the open gulf in the upper and central portions of the present bays, and open sound or lagoon conditions were indicated at the seaward end. The macrofaunas at this level (—30 feet in the cores) indicate that when sea level reached its present stand, only incomplete barriers existed where there are presently long stretches of islands and spits, and that larger and deeper lagoons and estuaries existed where San Antonio and Aransas Bays are now located. Salinity conditions approached those of the nearshore open gulf. As sea level stabilized, the barriers became better established and gradually extended along the coast, closing off the lagoons and estuaries. With the creation of barriers, the hydrographic conditions changed from an open sound to the present low-to-medium salinity inter-reef conditions at the upper and central portions of the bays, and high salinity open-bay environments only near the inlets.

(Plates 1–6 and Explanations follow)

EXPLANATION OF PLATE 1

MARSH, AND RIVER-INFLUENCED, LOW SALINITY ASSEMBLAGE

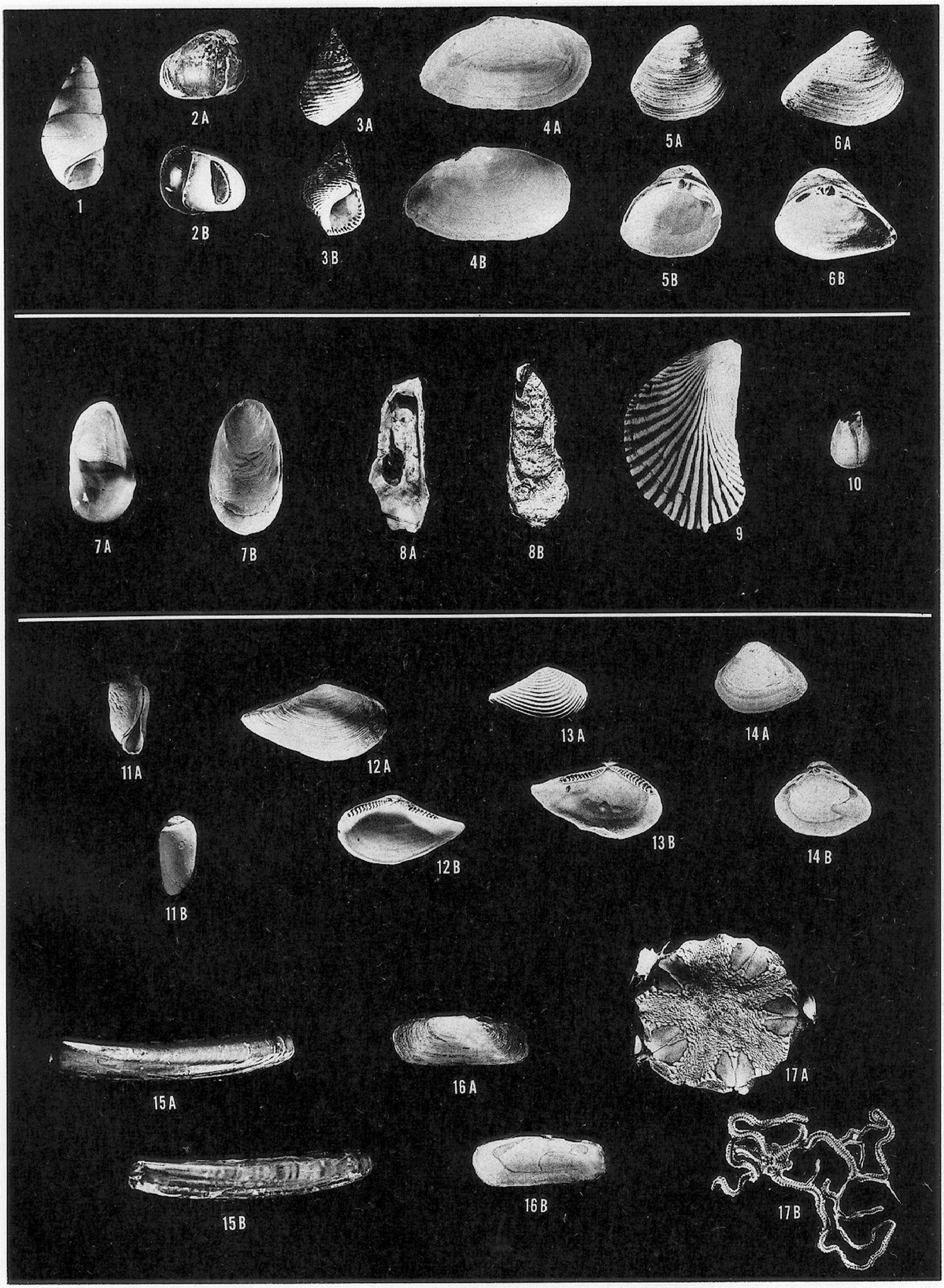
FIG. 1.—*Littoridina sphinctostoma.* Aperture, size–3×2 mm.
2.—*Neritina reclivata. A.* Back side, *B.* Aperture, size–11×13 mm.
3.—*Littorina irrorata. A.* Back side, *B.* Aperture, size–19×14 mm.
4.—*Macoma mitchelli. A* Interior, *B.* Exterior, size–21×12 mm.
5.—*Rangia cuneata. A.* Exterior, *B.* Interior, size–42×39 mm.
6.—*Rangia flexuosa. A.* Exterior, *B.* Interior, size–36×30 mm.

LOW SALINITY OYSTER REEF ASSEMBLAGE

7.—*Crepidula plana. A.* Interior, *B.* Exterior, size–22×12 mm.
8.—*Crassostrea virginica. A.* Interior, *B.* Exterior, size–170×70 mm.
9.—*Brachidontes recurvus.* Exterior, size–16×11 mm.
10.—*Balanus eburneus.* Exterior, size–5×7 mm.

INTER-REEF, ENCLOSED BAY ASSEMBLAGE

11.—*Retusa canaliculata. A.* Aperture, *B.* Back, size–6×3 mm.
12.—*Nuculana concentrica. A.* Exterior, *B.* Interior, size–11×6 mm.
13.—*Nuculana acuta. A.* Exterior, *B.* Interior, size–6×4 mm.
14.—*Mulinia lateralis. A.* Exterior, *B.* Interior, size–10×7 mm.
15.—*Ensis minor. A.* Exterior, *B.* Interior, size–54×10 mm.
16.—*Tagelus plebeius. A.* Exterior, *B.* Interior, size–42×16 mm.
17.—*Amphiodia limbata. A.* Disc, *B.* Whole, size–6 mm.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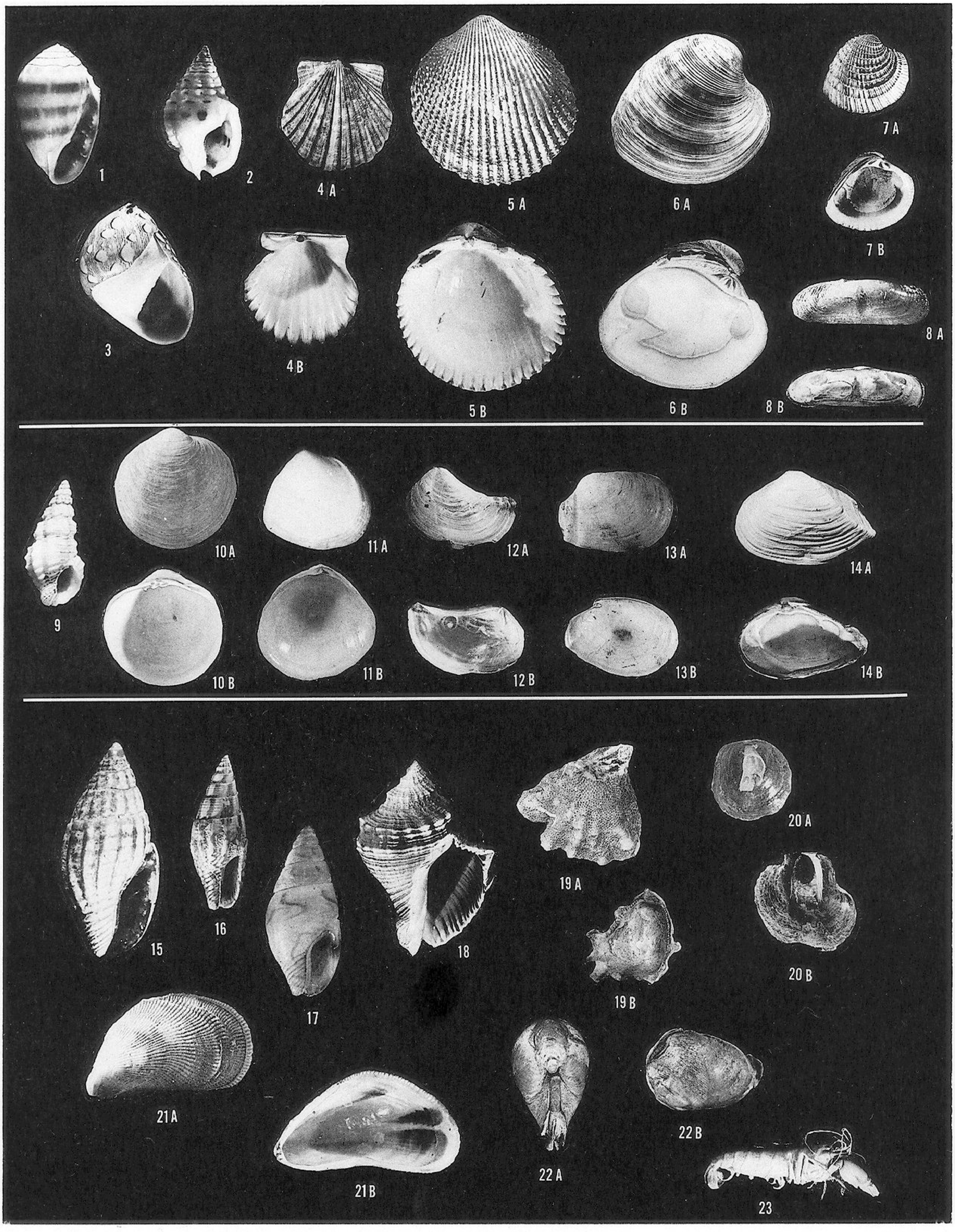
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EXPLANATION OF PLATE 2

OPEN BAY AND SOUND MARGIN ASSEMBLAGE

FIG. 1.—*Melampus bidentatus*. Aperture, size–11×7 mm.
2.—*Nassarius vibex*. Aperture, size–12×8 mm.
3.—*Neritina virginea*. Aperture, size–11×10 mm.
4.—*Aequipecten irradians amplicostatus*. *A*. Exterior, *B*. Interior, size–65×63 mm.
5.—*Trachycardium muricatum*. *A*. Exterior, *B*. Interior, size–42×44 mm.
6.—*Mercenaria mercenaria campechiensis*. *A*. Exterior, *B*. Interior, size–102×94 mm.
7.—*Chione cancellata*. *A*. Exterior, *B*. Interior, size–26×22 mm.
8.—*Tagelus divisus*. *A*. Exterior, *B*. Interior, size–27×9 mm.

OPEN BAY AND SOUND CENTER ASSEMBLAGE

9.—*Nassarius acutus*. Aperture, size–11×4 mm.
10.—*Diplodonta punctata*. *A*. Exterior, *B*. Interior, size–12×11 mm.
11.—*Abra aequalis*. *A*. Exterior, *B*. Interior, size–12×10 mm.
12.—*Pandora trilineata*. *A*. Exterior, *B*. Interior, size–20×11 mm.
13.—*Periploma fragile*. *A*. Exterior, *B*. Interior, size–12×8 mm.
14.—*Corbula contracta*. *A*. Exterior, *B*. Interior, size–7×5 mm.

HIGH SALINITY REEF ASSEMBLAGE

15.—*Anachis obesa*. Aperture, size–4×2 mm.
16.—*Anachis avara semiplicata*. Aperture, size–11×5 mm.
17.—*Mitrella lunata*. Aperture, size–4×2 mm.
18.—*Thais haemastoma floridana*. Aperture, size–47×29 mm.
19.—*Ostrea equestris*. *A*. Exterior, *B*. Interior, size–38×50 mm.
20.—*Anomia simplex*. *A*. Interior, *B*. Interior (other valve), size–21×20 mm.
21.—*Brachidontes exustus*. *A*. Exterior *B*. Interior, size–17×9 mm.
22.—*Diplothyra smithi*. *A*. Dorsal, *B*. Side, size–6×4 mm.
23.—*Crangon heterochelis*. Side, size–37 mm.

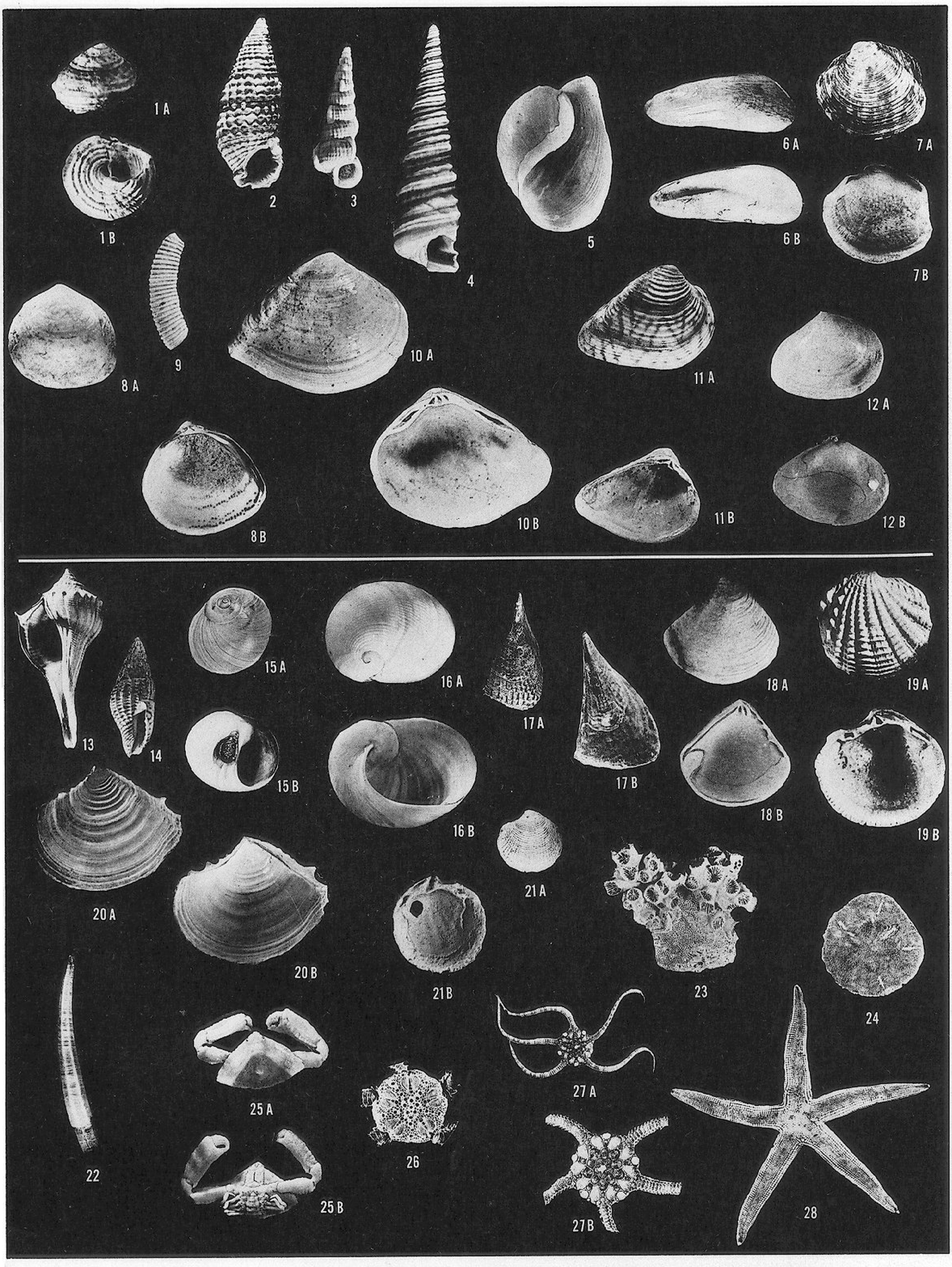
EXPLANATION OF PLATE 3

OPEN HYPERSALINE LAGOON ASSEMBLAGE

FIG. 1.—*Modulus modulus*. *A*. Back, *B*. Aperture, size–9×10 mm.
2.—*Cerithium variabile*. Aperture, size–12×5 mm.
3.—*Cerithidea pliculosa*. Aperture, size–32×11 mm.
4.—*Vermicularia fargoi*. Aperture, size–26×7 mm.
5.—*Haminoea succinea*. Aperture, size–12×9 mm.
6.—*Amygdalum papyria*. *A*. Exterior, *B*. Interior, size–23×9 mm.
7.—*Phacoides pectinatus*. *A*. Exterior, *B*. Interior, size–30×27 mm.
8.—*Laevicardium mortoni*. *A*. Exterior, *B*. Interior, size–15×14 mm.
9.—*Caecum pulchellum*. Side, size–3×1 mm.
10.—*Pseudocyrena floridana*. *A*. Exterior, *B*. Interior, size–18×13 mm.
11.—*Anomalocardia cuneimeris*. *A*. Exterior, *B*. Interior, size–11×7 mm.
12.—*Tellina tampaensis*. *A*. Exterior, *B*. Interior, size–10×5 mm.

INLET INFLUENCED ASSEMBLAGE

13.—*Busycon perversum*. Aperture, size–80×39 mm.
14.—*Anachis avara similis*. Aperture, size–8×3 mm.
15.—*Polinices duplicatus*. *A*. Top, *B*. Aperture, size–39×41 mm.
16.—*Sinum perspectivum*. *A*. Top, *B*. Aperture, size–31×31 mm.
17.—*Atrina seminuda*. *A*. Exterior, *B*. Interior, size–188×108 mm.
18.—*Crassinella lunulata*. *A*. Exterior, *B*. Interior, size–8×7 mm.
19.—*Lucina amiantus*. *A*. Exterior, *B*. Interior, size–6×6 mm.
20.—*Tellidora cristata*. *A*. Exterior, *B*. Interior, size–15×13 mm.
21.—*Lucina multilineata*. *A*. Exterior, *B*. Interior, size–5×5 mm.
22.—*Dentalium texasianum*. Side, size–20 mm.
23.—*Astrangia astreiformis*. Colony, size–25 mm.
24.—*Mellita quinquiesperforata*. Top, size–53×46 mm.
25.—*Heterocrypta granulata*. A. Dorsal, *B*. Ventral, size–15 × 10 mm.
26.—*Hemipholis elongata*. Disc, size–7 mm.
27.—*Ophiolepis elegans*. *A*. Whole, *B*. Disc, size–55 mm.
28.—*Luidia clathrata*. Whole, dorsal, size–95 mm.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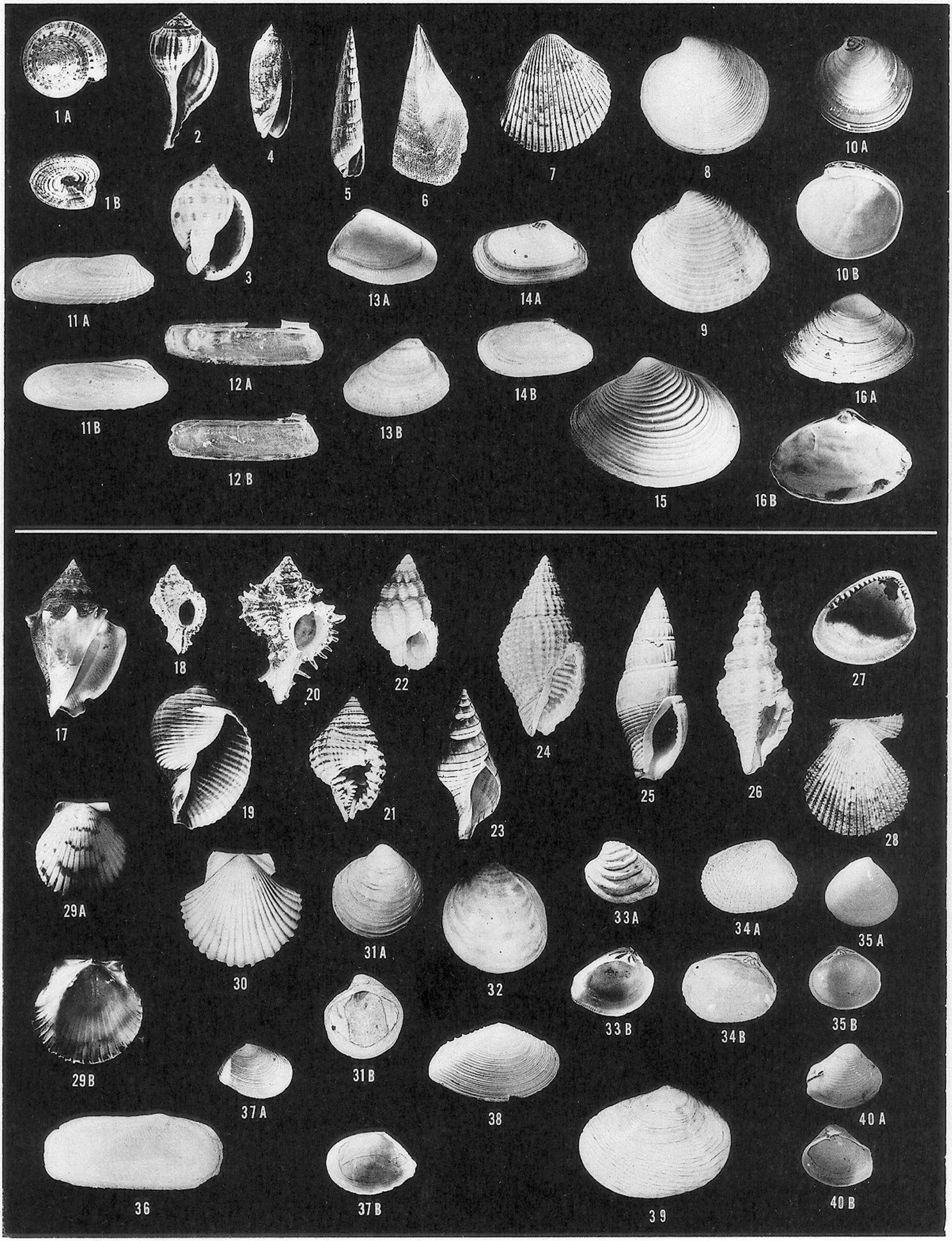
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EXPLANATION OF PLATE 4

INNER SHELF AND SURF ZONE, 0–12 FATHOM ASSEMBLAGE

FIG. 1.—*Architectonica nobilis*. *A*. Top, *B*. Aperture, size–49×31 mm.
2.—*Busycon plagosum*. Aperture, size–119×57 mm.
3.—*Phalium granulatum*. Aperture, size–59×40 mm.
4.—*Oliva sayana*. Aperture, size–43×17 mm.
5.—*Terebra cinerea*. Aperture, size–32×7 mm.
6.—*Atrina serrata*. Exterior, size–175×76 mm.
7.—*Dinocardium robustum*. Exterior, size–96×90 mm.
8.—*Dosinia elegans*. Exterior, size–66×60 mm.
9.—*Chione intapurpurea*. Exterior, size–25×21 mm.
10.—*Dosinia discus*. *A*. Exterior, *B*, Interior, size–73×71 mm.
11.—*Petricola pholadiformis*. *A*. Exterior, *B*. Interior, size–23×8 mm.
12.—*Solen viridis*. *A*. Exterior, *B*. Interior, size–10×4 mm.
13.—*A*. *Donax variabilis*, Exterior, size–20×28 mm.; *B*. *Donax tumida*, Exterior, size–10×7 mm.
14.—*Macoma tageliformis*. *A*. Exterior, *B*. Interior, size–44×25 mm.
15.—*Labiosa plicatella*. Exterior, size–68×50 mm.
16.—*Spisula solidissima raveneli*. *A*. Exterior, *B*. Interior, size–80×55 mm.

INTERMEDIATE SHELF, 12–40 FATHOM ASSEMBLAGE

17.—*Strombus alatus*. Aperture, size–85×54 mm.
18.—*Murex pomum*. Aperture, size–48×31 mm.
19.—*Tonna galea*. Aperture, size–51×36 mm.
20.—*Murex fulvescens*. Aperture, size–54×36 mm.
21.—*Distorsio clathrata*. Aperture, size–55×32 mm.
22.—*Nassarius ambiguus*. Aperture, size–8×5 mm.
23.—*Fasciolaria lillium*. Aperture, size–60×28 mm.
24.—*Antilliphos c.f. candei*. Aperture, size–29×19 mm.
25.—*Anachis saintpairiana*. Aperture, size–9×4 mm.
26.—*Nassarina glypta*. Aperture, size–4×1 mm.
27.—*Nucula proxima*. Interior, size–5×5 mm.
28.—*Aequipecten muscosus*. Exterior, size–43×41 mm.
29.—*Aequipecten gibbus gibbus*. *A*. Exterior, *B*. Interior, size–27×26 mm.
30.—*Pecten raveneli*. Exterior, size–30×38 mm.
31.—*Lucina sombrerensis*. *A*. Exterior, *B*. Interior, size–7×7 mm.
32.—*Laevicardium laevigatum*. Exterior, size–34×37 mm.
33.—*Chione clenchi*. *A*. Exterior. *B*. Interior, size–18×15 mm.
34.—*Chione grus*. *A*. Exterior, *B*. Interior, size–9×7 mm.
35.—*Gouldia cerina*. *A*. Exterior, *B*. Interior, size–8×7 mm.
36.—*Solecurtus cumingianus*. Exterior, size–25×11 mm.
37.—*Quadrans lintea*. *A*. Exterior, *B*. Interior, size–16×12 mm.
38.—*Phylloda squamifera*. Exterior, size–16×10 mm.
39.—*Semele purpurescens*. Exterior, size–18×13 mm.
40.—*Varicorbula operculata*. *A*. Exterior, *B*. Interior, size–9×7 mm

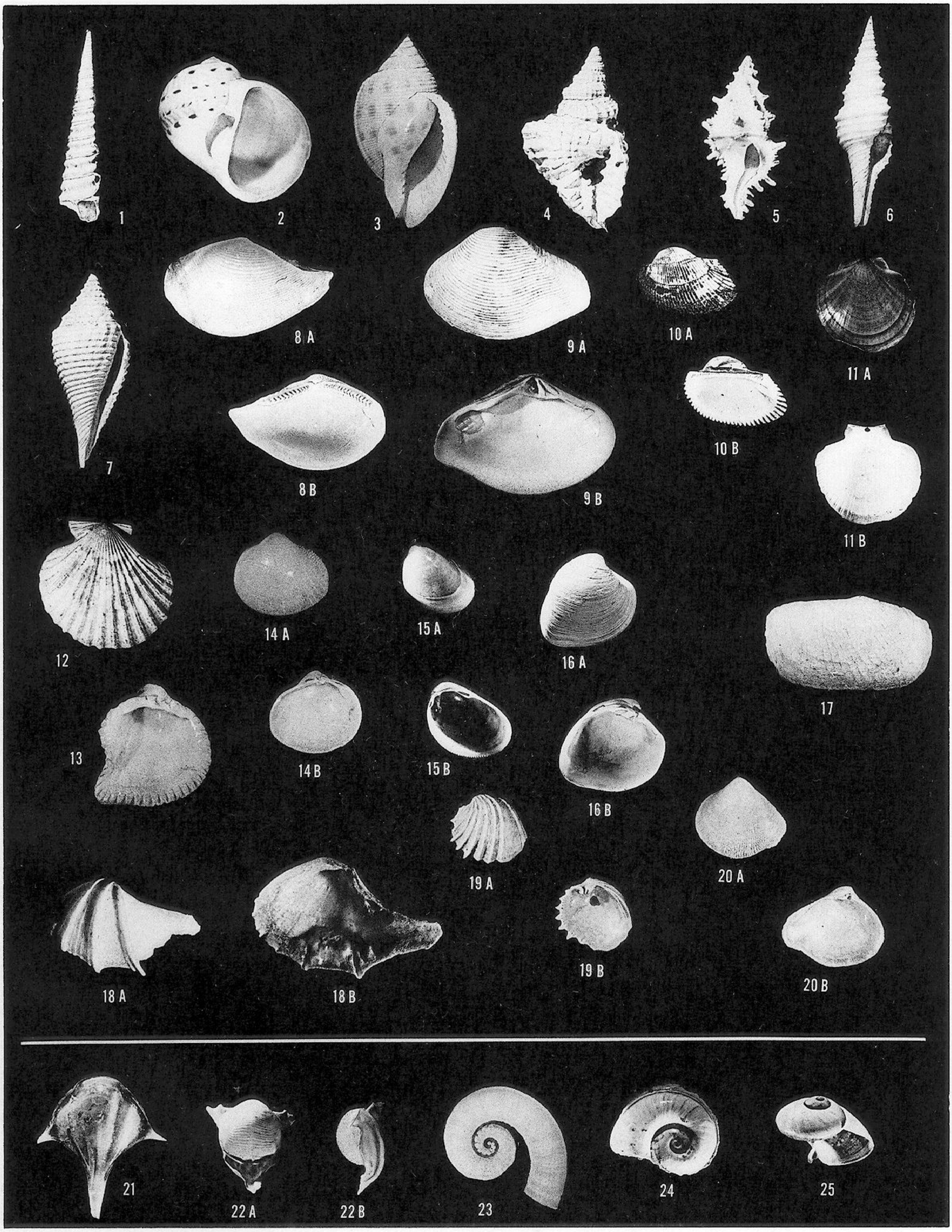
EXPLANATION OF PLATE 5

OUTER SHELF, 40–60 FATHOM ASSEMBLAGE

FIG. 1.—*Turritella exoleta*. Aperture, size–47×10 mm.
2.—*Natica canrena*. Aperture, size–43×43 mm.
3.—*Sconsia striata*. Aperture, size–45×25 mm.
4.—*Distorsio mcgintyi*. Aperture, size–34×21 mm.
5.—*Muricopsis hexagona*. Aperture, size–30×17 mm.
6.—*Polystira albida*. Aperture, size–59×18 mm.
7.—*Conus clarki*. Aperture, size–35×15 mm.
8.—*Nuculana jamaicensis*. *A*. Exterior, *B*. Interior, size–8×5 mm.
9.—*Eucrassatella speciosa*. *A*. Exterior, *B*. Interior, size–54×32 mm.
10.—*Anadara baughmani*. *A*. Exterior, *B*. Interior, size–33×21 mm.
11.—*Pecten papyraceus*. *A*. Exterior, *B*. Interior, size–58×54 mm.
12.—*Lyropecten nodosus*. Exterior, size–54×36 mm.
13.—*Trigonicardia media*. Interior, size–13×13 mm.
14.—*Microcardium transversum*. *A*. Exterior, *B*. Interior, size–14×13 mm.
15.—*Laevicardium fiski*. *A*. Exterior, *B*. Interior, size–12×17 mm.
16.—*Pitar cordata*. *A*. Exterior, *B*. Interior, size–43×48 mm.
17.—*Solecurtus sanctaemarthae*. Exterior, size–30×16 mm.
18.—*Cuspidaria ornatissima*. *A*. Exterior, *B*. Interior, size–9×6 mm.
19.—*Verticordia ornata*. *A*. Exterior, *B*. Interior, size–4×4 mm.
20.—*Poromya rostrata*. *A*. Exterior, *B*. Interior, size–7×6 mm.

PELAGIC MOLLUSKS

21.—*Cavolina trispinosa*. Back, size–7×7 mm.
22.—*Cavolina longirostris*. *A*. Aperture, *B*. Side, size–4×4 mm.
23.—*Spirula spirula*. Top, size–20×15 mm.
24.—*Atlanta peroni*. Top, size–6×4 mm.
25.—*Janthina janthina*. Aperture, size–16×21 mm.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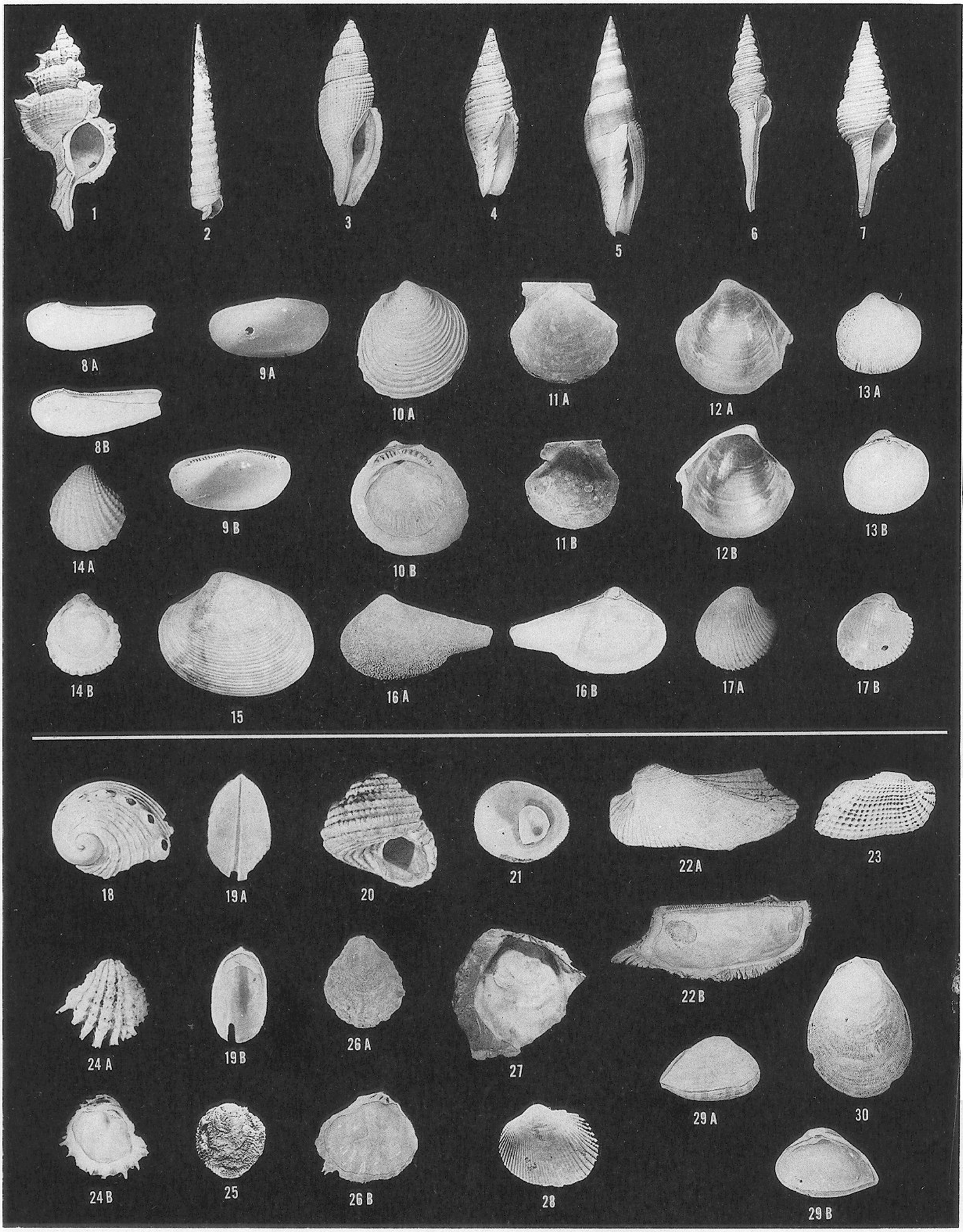
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Explanation of Plate 6

UPPER SLOPE, 60–500 FATHOM ASSEMBLAGE

Fig. 1.—*Murex branchi.* Aperture, size–123 × 61 mm.
2.—*Terebra dislocata rudis.* Aperture, size–68 × 10 mm.
3.—*Antemetula agassizi.* Aperture, size–27 × 9 mm.
4.—*Mitra fulgarita.* Aperture, size–24 × 8 mm.
5.—*Mitra swainsoni antillensis.* Aperture, size–70 × 20 mm.
6.—*Fusinus couei.* Aperture, size–130 × 30 mm.
7.—*Polystira tellea.* Aperture, size–52 × 15 mm.
8.—*Nuculana c.f. carpenteri. A.* Exterior, *B.* Interior, size–12 × 4 mm.
9.—*Yoldia solenoides. A.* Exterior, *B.* Interior, size–13 × 7 mm.
10.—*Limopsis sulcata. A.* Exterior, *B.* Interior, size–11 × 10 mm.
11.—*Cyclopecten nanus. A.* Exterior, *B.* Interior, size–6 × 5 mm.
12.—*Thyasira trisinuata. A.* Exterior, *B.* Interior, size–4 × 5 mm.
13.—*Microcardium permabile. A.* Exterior, *B.* Interior, size–15 × 14 mm.
14.—*Venericardia armilla. A.* Exterior, *B.* Interior, size–8 × 7 mm.
15.—*Callista eucymata.* Exterior, size–31 × 25 mm.
16.—*Cuspidaria granulata. A.* Exterior, *B.* Interior, size–13 × 7 mm.
17.—*Verticordia fischeriana. A.* Exterior, *B.* Interior, size–6 × 6 mm.

CALCAREOUS BANK ASSEMBLAGE

18.—*Haliotis pourtalesii.* Exterior, size–5 × 4 mm.
19.—*Nesta atlantica. A.* Exterior, *B.* Interior, size–5 × 3 mm.
20.—*Liotia bairdi.* Aperture, size–6 × 5 mm.
21.—*Crucibulum striatum.* Interior, size–28 × 24 mm.
22.—*Arca umbonata. A.* Exterior, *B.* Interior, size–60 × 28 mm.
23.—*Barbatia domingensis.* Exterior, size–8 × 5 mm.
24.—*Echinochama cornuta. A* Exterior, *B.* Interior, size–18 × 18 mm.
25.—*Chama congregata.* Exterior, size–14 × 13 mm.
26.—*Plicatula gibbosa. A.* Exterior, *B.* Interior, size–15 × 13 mm.
27.—*Pycnodonta hyotis.* Interior, size–35 × 30 mm.
28.—*Papyridea soleniformis.* Exterior, size–30 × 26 mm.
29.—*Corbula dietziana. A.* Exterior, *B.* Interior, size–14 × 9 mm.
30.—*Lima tenera.* Exterior, size–51 × 38 mm.