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Benthic Invertebrate Communities of the Eastern Gulf of Mexico*

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Although a number of studies of benthic invertebrate groups, or communities of such organisms, have been published from various areas of the Eastern Gulf of Mexico, few attempts have been made to pull together information necessary to understand distributions and relative differences of these communities. The first major attempt was "Gulf of Mexico, its origin, waters, and marine life" (Galtsoff, 1954). While it contains some very worthwhile studies, in retrospect many of its papers have proven highly inadequate. Whatever its merits, it was an up-to-date summary of existing knowledge when published.

After this collection of papers appeared, nearly twenty years passed before the State University System Institute of Oceanography (SUSIO) called together a group of specialists to produce a synthesis of opinion regarding the location and composition of dissimilar hydrobiological zones of the Eastern Gulf. From these meetings have come at least three very impressive compendia integrating existing knowledge of physical and chemical oceanography, geology, climatology, and biology to bring us an up-to-date "Summary of Knowledge" of these various zones. It is our opinion that, if this were a competitive endeavor, the biologists lost.

The task of these biologists was to pull together existing information, primarily from published literature, to produce this summary. For some, information was both available and comparable, and is reflected in their reports. The benthic invertebrate report for inshore, estuarine areas is far better than comparable information of 20 years ago. However, accounts of offshore shelf communities are nowhere as definitive, because much of the needed information has not been analyzed or published.

This does not mean that collecting trips have not been conducted nor observations made. Though certainly not to the degree of accessible inshore locales, offshore areas are being and have been studied, both by conventional collecting techniques and, in accessible areas, by scuba. Despite several thousand such collections, we have yet to see published a species list of the collective contents of a single dredge haul, much less attempts to pull together information from many such collections. The few published scuba observations are not adequate to define these

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invertebrate communities. Sponges and corals have long been acknowledged as very important basic constituents of allegedly highly diverse Eastern Gulf Shelf communities, but no serious attempt has been made to adequately define composition or dynamics of such communities.

This treatment of benthic invertebrates of the Eastern Gulf of Mexico follows that of Collard and D'Asaro (1973), in that a community approach is used to divide the region into recognizable biotopes defined by change in species composition. However, some divisions differ from those of the previous authors. These are related principally to subdivisions of the shelf fauna resulting from more than eight years of observations by one of us (WGL) on materials collected during the Hourglass Project and other West Florida Shelf programs.

Biological and geological factors dictate that the Eastern Gulf Shelf area be divided into two subregions, the Mississippi-Alabama Shelf extending from the eastern Mississippi Delta to Cape San Blas, and the West Florida Shelf extending from Cape San Blas southward to the Florida Keys. Subdivisions of these subregions, except estuarine and slope faunas, will be discussed separately. Physical and biotic characters serving to subdivide the subregions are hereafter discussed beginning at the land-water interface and proceeding ever deeper to the base of the continental slope. Collard and D'Asaro have summarized factors controlling composition of benthic invertebrate communities of the region. Briefly, these amount to temperature, salinity, substrate, wave action, and nutrients. Each factor is very important, and it is differences in these factors that create different communities.

Estuaries

The single category "Estuary" contains much of the first four of Collard and D'Asaro, i. e., "Low Salinity Communities," "Oyster Reef Communities," "Oyster, Mangrove and Hard Substrate Communities," and "Bays, Channels, and Sounds." The authors also recognized various subdivisions within most categories, based on salinity, temperature, vegetation, and substrate.

It is sufficient here to state that these areas, located along most of the Eastern Gulf coast, are characterized by salinity gradients generally ranging from 0 to ca. 34 ‰, with broad fluctuations caused by rainfall (or lack thereof), tides, and other factors. Temperature fluctuations are usually much greater than in other marine environments. Substrates may vary considerably, both within a single estuary and between estuaries. Nutrient values are generally higher than in other marine environments.

Of these factors, perhaps temperature and salinity fluctuation and high nutrient values are most characteristic in separating estuaries from other marine communities. However, substrate and vegetation are just as important in determining composition of communities. All factors are, to some degree, interrelated.

A remarkably high number of benthic invertebrates are adapted to exist under the rigorous conditions of Eastern Gulf estuaries. Cooley (ms) has listed more than 500 species in the Pensacola Bay area, Menzel (1971) has noted at least that many estuarine species in the Alligator Harbor area, and certainly more than 600 species occur in the Tampa Bay estuarine system (Taylor, 1971; Hall and Lyons, ms; other unpublished data). Much of the Florida West Coast may be considered "ecotonal" between the temperate Carolinian and tropical Caribbean zoogeographic provinces. Such areas, generally high in species diversity, result from occurrence of hardier types from each province. Constituents of both provinces occur throughout the area, although naturally more species of temperate affinity are found in the north and more of tropical origin occur in the south. There is also a small Gulf endemic element. However, most estuarine species are not easily assignable to any of these categories. Instead, as noted by Lyons et al. (1971), they belong to a broadly ranging, eurytolerant group found at least from North Carolina to the southern Caribbean. Broadly fluctuating salinities and, to an extent, temperatures, are characteristic of habitats through much of their range. They are the basic elements of most estuaries, while the "provincials" and endemics, more sensitive species, serve to characterize individual estuarine differences. These subtleties result in "northern" and "southern" communities.

A. Low Salinity Communities (Marshes and Deltas; Marshes and Mangrove Swamps): Each of these is characterized by low salinity and organically rich sediments. Mangrove communities are dominant in the south but entirely absent in the north, primarily due to low temperature intolerance. Spartina-Juncus marshes occur extensively in the north, but much less so in the far south. Both occur south of Cedar Key, but with mangroves increasingly dominant to the south.

B. Oyster Reef-Hard Substrate Communities: This is the major sessile invertebrate community of Eastern Gulf estuaries. It is based upon Crassostrea virginica throughout the region, but widely diverse temperatures and salinities dictate different species associations at different localities.

C. Bays, Channels, Sounds: Though still characterized by broadly fluctuating salinities and temperatures, overall mean values may be higher than in the previously mentioned areas. These factors are still important in determining local species composition, but substrate, vegetation, and depth are also major factors.

Substrates may vary from muds, terrigenous sands, and mixtures thereof in the north to vegetable debris and calcareous sands in the far south. Terrigenous sands are not important south of Cape Romano. Quartz sandshell mixtures dominate most of west Florida, but muds become important west of the Apalachee Bay area.

Pure or mixed stands of seagrasses occur in estuaries throughout the region. Species include Thalassia, Syringodium, Halodule, and Ruppia. Two species of Halophila are less common. Most of these

grasses reach their greatest densities in estuaries, but in this area are generally limited to depths less than 2 m because of poor light penetration. This leaves greater estuarine depths as non-vegetated substrate inhabited by species not tied to a "grassbed" existence.

Aside from oyster reefs and grassbeds for epiphytes, most estuarine substrate may be characterized as "soft." Because "hard" substrate is rare to nonexistent in the Carolinian Province, there are few "hard" substrate Carolinian species. It seems, therefore, that except for certain grassbed or oyster reef species, Eastern Gulf estuaries have been surrendered to "soft bottom" Carolinian species by default. Exceptions may occur where introduced objects such as pilings or jetties provide setting space for Caribbean species, but even these objects are usually occupied by species from oyster reef or grass communities.

Generally, estuaries are herein considered as coastal invaginations, often separated from the Gulf of Mexico by barrier islands. However, certain shallow offshore areas of low wave energy display typical estuarine characteristics. These include extensive shorelines from Apalachee Bay to the Anclote Keys and, further south, the Ten Thousand Islands area from Cape Romano to Cape Sable. These seem to represent estuaries intergrading directly into shallow shelf communities.

West Florida Shelf

The following delineations (Figure 1) are based upon observed faunal variation in more than 700 dredge and trawl tows from the Hourglass program, supplemented by many comparable collections and some scuba observation in other areas of the shelf. The degree of faunal change is the criterion used for suggesting separations. Obviously, each zone intergrades into its neighbors without sharply defined boundaries, and areas of intergradation are difficult to categorize. Nevertheless, central areas of these zones seem distinctive. Geological and hydrological features coincident with the zones are suggested as basic factors of community composition. Suggested depths for each zone are mean estimates; these depth limits may vary somewhat in response to geologic and hydrographic variation.

1. Shoreward Zone (0-10m): This zone is defined as the area extending from the land-water interface to depths of approximately 10 m. The latter is the mean depth where rocky outcrops become important substrate elements along much of the Florida west coast. Salinities fluctuate several parts per thousand in response to runoff from nearby rivers and bays. Temperature variations are nearly as severe as in adjacent estuaries. Nutrients are generally quite high. Four subdivisions are proposed for the shoreward zone.

A. Ten Thousand Islands: Extending northward from Cape Sable to Cape Romano, this area is characterized by grassbeds and scattered sand bottom blending the mangrove estuary smoothly into the offshore rocky communities. Many shallow water tropical species from the Keys occur

here, especially in grassy portions, but many temperate species are also common, especially in sand communities. Beaches are scarce.

B. Coastal Barrier Islands: Moderate wave energy beaches of quartz sand and shell fragments are the dominant shoreward feature of this zone which extends northward to Anclote Key. Bottom composition is also largely of these materials, with little hard substrate except dead shells of large mollusks. Seagrasses are scarce to absent. The quartz-shell sediments actually extend far to sea off Tampa Bay and the Charlotte Harbor area. In the latter area, influence of these sediments is quite strong in the next seaward zone, and possibly even beyond. Large temperate mollusks and echinoderms are characteristic faunal elements. Species diversity is generally lower than in adjacent estuaries or offshore areas.

C. Big Bend Area: This may be best defined as a huge, seagoing estuary extending from near Anclote Key to the vicinity of Alligator Harbor. Oyster reefs are common parallel to the shore, and vast beds of seagrasses are characteristic of the area. A thin veneer of quartz sand and organic debris overlies the limestone plateau of the Ocala-Middle Ground Arch. Occasional limestone outcrops protrude through this veneer to provide hard substrate. Species composition is predominantly the same found in estuarine seagrass or oyster reef communities. The shoreline receives only low energy waves.

D. Cape San Blas Area: Moderate wave energy quartz sand beaches are characteristic of the area from Alligator Harbor, and comparably composed sediments extend some distance offshore. The fauna is similar to that of the Coastal Barrier Islands area in that it is predominantly a temperate sand community. Most common species are represented in both areas.

2. Shallow Shelf (10-30 m): This is the first major zone of tropical species intrusion into the Eastern Gulf. Rock substrate allows establishment of many scleractinian, alcyonarian, molluscan, crustacean, and other invertebrate species common in shallower waters in the Florida Keys. Sand dwellers are represented by some species from more inshore waters but with many tropical species as well. Sediments are still largely of quartz sands, with increasing percentages of biogenically derived carbonates seaward. Overlying green, relatively turbid, coastal waters are usually well mixed, but cooler bottom waters are often separated by a low thermocline, especially during warmer months.

3. Middle Shelf I (30-60 m): Two apparent physical characters separating this zone from the shallow shelf are widespread carbonate sediments and an overlying mass of blue, offshore water. The intersection of this water mass with coastal green water is usually very visible in depths of about 30 m. Widespread rock outcrops are lower in the central and southern portions than on the Florida Middle Grounds, where they may rise 12 m above the surrounding bottom. Loggerhead sponges, corals, and tropical algae form communities supporting many other tropical species. Appearance of many tropical sand dwellers is probably due to largely carbonate sediments. Communities are highly diverse, containing many more species

than found in inshore zones.

4. Middle Shelf II (60-140 m): Few rock outcrops are found in this zone. Sediments are almost entirely carbonate, being composed of coralline alga (Lithothamnion), bryozoan and molluscan fragments; foraminiferal tests begin to contribute noticeably to sediments. Scattered sponges, bryozoans, ascidians, and alcyonarians attached to small rocks and shells form the dominant sessile epifauna. Many small molluscan and crustacean species are very common. Bottom water temperatures seldom exceed 22°C, are warmest in late fall, and are usually distinctly separated from warmer surface waters except during winter when mixing may occur. This zone receives waters from the Florida Loop Current, and salinities greater than 36.5 ‰ occur seasonally. The fauna is essentially tropical or tropically derived; some data suggest a small number of endemic northeastern Gulf mollusks at these depths.

5. Deep Shelf (140-200 m): It is problematical that a separation exists between 60 and 200 m. Sediments seem generally similar throughout; naturally water temperatures are depressed and little light penetration prevents most algal growth in deeper waters. Species diversity apparently decreases in these greater depths, but many species of the Middle Shelf II zone occur here. Changes in species composition noticeable at about 140 m in both fish and mollusks prompt designation of this depth as the intersection between zones. Pequegnat (1970) noted a number of brachyurans most common in depths corresponding to the deep shelf zone.

Mississippi-Alabama Shelf

The authors have little direct familiarity with this area beyond the estuaries and shoreward zone. A major physical feature influencing community compositions here is proximity to the nearby DeSoto Canyon, with a resultant steeply sloping shelf and nearshore intrusion of oceanic waters to high wave energy beaches. Mississippi Delta sediments are characteristic of the area from Mobile Bay westward.

As on the West Florida Shelf, far more collections have been taken than have been reported; most reports consist of individual species records rather than compendia of collections.

1. Shoreward Zone: Quartz sand is the dominant sediment element to depths of approximately 20 m from Cape San Blas to near Mobile Bay. The fauna is characteristically temperate sand dwellers. Many species common here are uncommon to absent in other Eastern Gulf sand communities. Moreover, many species found elsewhere in the Eastern Gulf attain larger sizes in the zone west of Cape San Blas. Jetties and wrecks provide hard substrate for some tropical species which could not otherwise occur here. Muds become more important near the Mississippi Delta, with correspondent lowering of the number of species present.

2. Deeper Areas: Faunal zone demarcations beyond the shoreward zone are not clear. Rocky outcrops first occur commonly off Panama City and

Destin in about 20 m, but these diminish in number at comparable depths to the west. A highly diminished tropical fauna occurs on these outcrops. A zone of calcareous sediments occurs on deeper parts of the shelf, and even a few limestone reefs are known near the edge of the shelf. Species from these calcareous communities are essentially the same as from others further south, but diversity may be reduced.

As in shallower areas, these sediments merge into sands, muds, and silts from the Mississippi outfall to the westward. Faunal change and species diversity reduction accompany this transition to soft bottom communities.

Slope

Calcareous sands give way to foraminiferal sands and muds in this area where the bottom slopes steeply (200-3200 m) from the shelf to the Gulf floor. Many species are confined to these depths, forming a characteristic slope fauna. Obviously, in so great a depth-span most are not found throughout, but many do exhibit considerable bathymetric range. Species diversity of many groups is markedly lower than for shelf zones, but penaeid and large caridean shrimps and galatheids show their greatest diversity here.

In summary, benthic invertebrates of the Eastern Gulf are a highly diverse group with several dissimilar zones of distribution ranging from the estuaries to the continental slope. Whereas temperature and salinity fluctuations are limiting factors in estuaries, such values become more constant offshore. These narrow ranges of fluctuation are important for the dominantly tropical offshore fauna. Bottom substrates and overlying water masses seem to become more critical offshore. The northern limestone base, best expressed at the Middle Grounds, and the southern quartz sand extensions are contrasting features superimposed upon this basic scheme. However, differences are nowhere near as absolute as might be deduced from the previous geological charts. Scattered limestone communities occur as frequently to the south as do scattered sand communities in the north. Where these communities are found, species compositions are essentially the same within zones.

Many areas are open for investigation of invertebrate communities. However, emphasis should be given to the importance of working up the many collections already made in this region. To repeat some would merely constitute duplication of effort, and some collections, already made but not reported, could not possibly be duplicated before extensive drilling for oil is under way in the Eastern Gulf.

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FIGURE 1.

