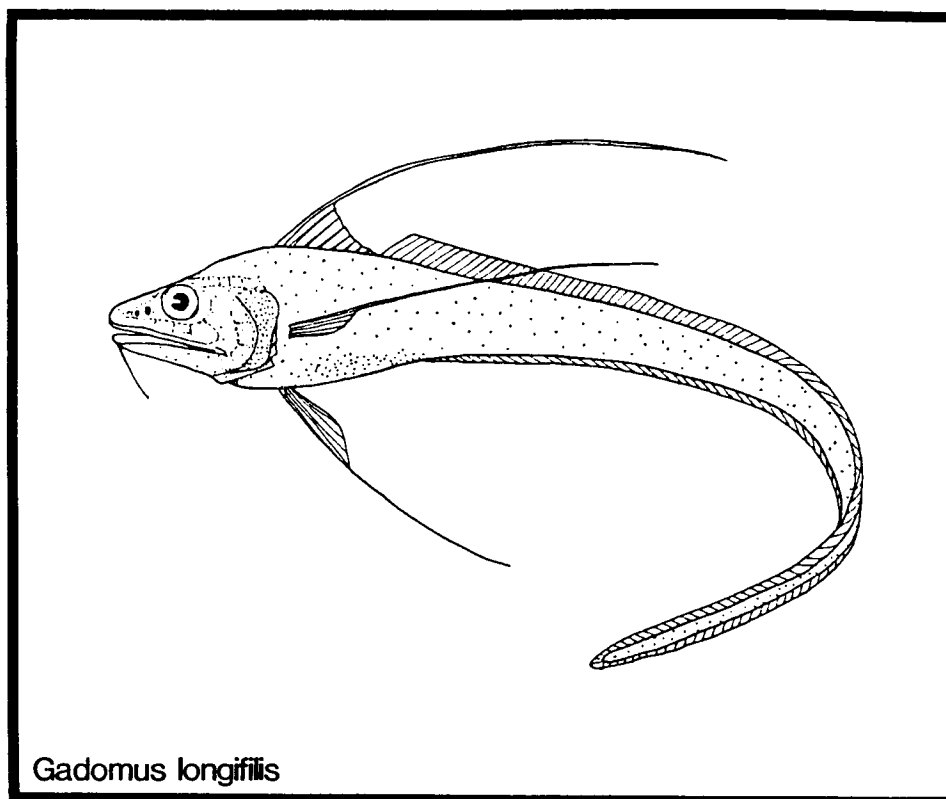


Northern Gulf of Mexico Continental Slope Study Final Report Year 4

Volume I: Executive Summary



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Editor

Benny J. Gallaway

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ACKNOWLEDGEMENTS

In a recent treatise which needs not be identified, a deep-sea biologist of some reputation noted that the history of deep-sea biological studies has been shaped by relatively few persons. Most, if not all, of these persons were characterized by often having an acute sense of personal involvement and some awareness of a personal place in the history of the science. Most deep-sea biologists can easily trace their scientific roots through short personal links to such names as Bigelow, Agassiz and Murray. Strong opinions according to professorial lineage are not unusual and ostensibly our entire Scientific Advisory Committee (Drs. R.S. Carney, F.J. Grassle, R.R. Hessler, W.E. Pequegnat, and R. Rosenblatt) might be expected to fit this characterization. Thus, we, as novice workers entering the field, began this project with great temerity. What we experienced from the above named people was open-minded and insightful encouragement to pursue independent lines of thought, and rigorous, but fair, reviews of the materials submitted for their inspection. We acknowledge all of them and our COTR, Dr. Robert Avent, for their assistance in a most demanding project.

This project also proved almost impossible from a taxonomic standpoint. New species, genera and families became commonplace--even representatives of a phylum not described until 1983 (the first year of our project) was recorded at all but a few of our sampling stations. The taxonomic consultants used in this project, with or without pay, earned their "money". All are listed in our Year 3 Annual Report. We can only hope that their scientific reward will exceed the pay they received from this project.

We gratefully acknowledge our report production staff (notably Ms. Jean Erwin and Jan Fechhelm) who produced the documents comprising the final reports. They did remarkably well with little guidance provided by the editor. Again, we would be amiss not to mention our COTR, Dr. Avent, who conducted a presubmittal review of the document at personal time sacrifice to ensure consistency with the Minerals Management Service's (MMS) editorial standards. Ms. Janice Blake of MMS is also especially thanked for her efforts to shorten and expedite the review process.

Lastly, we thank our Contracting Officer, Mr. Carroll Day. Mr. Day has proven to be a fair and just representative for the Government, and for us. We extend our appreciation.

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INTRODUCTION

Between 1983 and 1987, LGL Ecological Research Associates, Inc. (LGL) in conjunction with Texas A&M University (TAMU) conducted a study of the continental slope of the northern Gulf of Mexico for the Gulf of Mexico Regional Office of the Minerals Management Service (MMS). The objective of the program was to develop a basic knowledge of the deep Gulf fauna and their relationship with their environment.

Prior to initiation of this study, MMS had funded TerEco Corporation Inc. to synthesize all available environmental information for the Gulf slope. The resulting report (Pequegnat, 1983) described and interpreted information available through 1982. It formed the basis for the design of this study.

The specific objectives of the program were to:

- (1) Provide an environmental and biological background characterization of the continental slope of the northern Gulf of Mexico, based upon pre-study information, with emphasis on how the Gulf might be expected to differ from other temperate and subtropical deep-sea regions.
- (2) Describe the environment of the continental slope of the northern Gulf of Mexico in terms of overlying water masses, bottom water conditions, sedimentary character and hydrocarbons with emphasis on identifying spatial (by depth and region) and seasonal discontinuities that might account for observed biological patterns, and to compare findings to observations from other deep-sea systems.
- (3) Describe, over time and space, the composition, distribution and abundance of the meiofauna of the continental slope of the northern Gulf of Mexico. Also to relate any observed trends to environmental features and the macrofauna, comparing results to other deep-sea regions, and to identify any unusual or important meiofaunal resources.

- (4) Describe, over time and space, the composition, distribution and abundance of the macrofauna of the continental slope of the northern Gulf of Mexico. Relate any observed trends to environmental features and compare results to other deep-sea regions. Identify any unusual or important macrofaunal resources.
- (5) Describe, over time and space, the composition, distribution and abundance of the megafauna of the continental slope of the northern Gulf of Mexico. Relate any observed trends to environmental features and compare results to other deep-sea regions. Identify any unusual or important megafaunal resources.
- (6) Describe and synthesize the available information concerning the types of chemosynthetic communities found on the continental slope of the northern Gulf of Mexico, their distribution and their apparent trophic dependencies.
- (7) Provide, based upon program data and other published and unpublished data, a conceptual model of the ecosystems of the continental slope of the northern Gulf of Mexico, comparing this system to other slope systems.

Activities during 1983 and 1985 were dedicated to field sampling and laboratory sample analyses. During 1987 sample analyses were completed and the data were compiled in usable and interactive format. Analysis and reporting has occurred during 1987-1988.

The acquisition of data occurred over the course of five cruises conducted during the first two years of the program. All of contract Years 1-3 (1983-1986) and a time extension into 1987 were required to complete sample analyses.

Three Annual Reports have been submitted, with that of Year 3 being the most comprehensive. The Year 3 Annual Report (Gallaway et al., 1988) provided a detailed description of all the field collection, laboratory

analyses and data management methods that were used, and in addition provided a hard-copy summary of all the data that were collected and that have been submitted to NODC in specified tape report.

In this Executive Summary of the Year Four Final Report, we summarize the overall methods and approaches used to meet program objectives and our findings describing (1) the slope environment and habitats; (2) the meiofaunal, the macroinfaunal, and the megafaunal communities that occur over soft bottom environments; (3) information concerning chemosynthetic communities on the continental slope of the northwestern Gulf of Mexico and the results of specific studies at one of these sites known as Bush Hill; and lastly, present a conceptual model of the slope ecosystem.

APPROACH AND METHODS

The sampling program was structured to test whether the abundance and composition of the biota on the continental slope varied in response to changes in any of several spatial, temporal, or physiochemical variables. Effects of depth were of particular concern because a major focus of the study was to compare the validity of Pequegnat (1983) versus Carney et al. (1983) concepts of depth-related biological zones.

Pequegnat (1983) characterized the continental slope of the northern Gulf of Mexico as having five distinctive faunal zones, based upon megafauna distributions. These included a Shelf-Slope Transition Zone from the shelf edge to a depth of 450 m; an Archibenthal Zone between 450 and 950 m, subdivided into two distinct horizons; an Upper Abyssal Zone (975 to 2,250 m); and a Mesoabyssal Zone (2,275 to 2,700 m).

In contrast, another view (e.g., Carney et al., 1983) is that faunal assemblages change continually with depth such that a distinct shelf fauna penetrates to about 1,000-m depths, a distinct slope is present below 2,000 m, and a broad transition zone occurs between 1,000- and 2,000-m depths. One focus of the program was to determine if biological assemblages on the slope might best be described by five versus three distinct zones.

Other variables of interest that influenced the sampling designs were season, the presence of special topographic features on the bottom, and geographic region. The need for faunal distributions to be tested against

sediment type, water quality, and presence and type of hydrocarbons in sediments influenced the analytical methods used.

Analytical Design

A major component of the analytical design was the location of sampling stations. Sampling stations were located between the 200-m and 2,900-m isobaths on the continental slope of the northern Gulf of Mexico between about 86° and 94° west longitude (Fig. 1). Station locations by depth reflected the need to compare fauna among depths and thus test the depth-zonation concept; locations east and west generally reflected the need to characterize the different OCS planning regions.

Three series of sampling stations, or transects, one in each MMS lease planning area, formed the nucleus of the sampling plan. (Additional areas were eventually sampled, for reasons to be discussed later.) Some characteristics of these three transects and the planning areas they represented are as follows:

1. Central Lease Planning Area - The transect representing this area extended across the slope in the vicinity of the Mississippi Trough, from approximately 28°20'N, 89°40'W to 26°40'N, 89°20'W (Fig. 1-A). The area has extremely active sediment movement, relatively high terrigenous inputs, and few striking topographic features; it is occasionally bathed by the Loop Current.
2. Western Lease Planning Area - The transect in this area extended across the slope just south of the Flower Garden Banks, from 27°25'N, 93°40'W to 25°50'N, 93°30'W (Fig. 1-B). The area has relatively sluggish circulation, a number of pronounced topographic features, and moderate to low declivity compared to the Mississippi Trough Transect.
3. Eastern Lease Planning Area - The sampling transect crossed the Florida Escarpment from 27°40'N, 85°15'W to 27°30'N, 85°40'W (Fig. 1-B). The area has high declivity

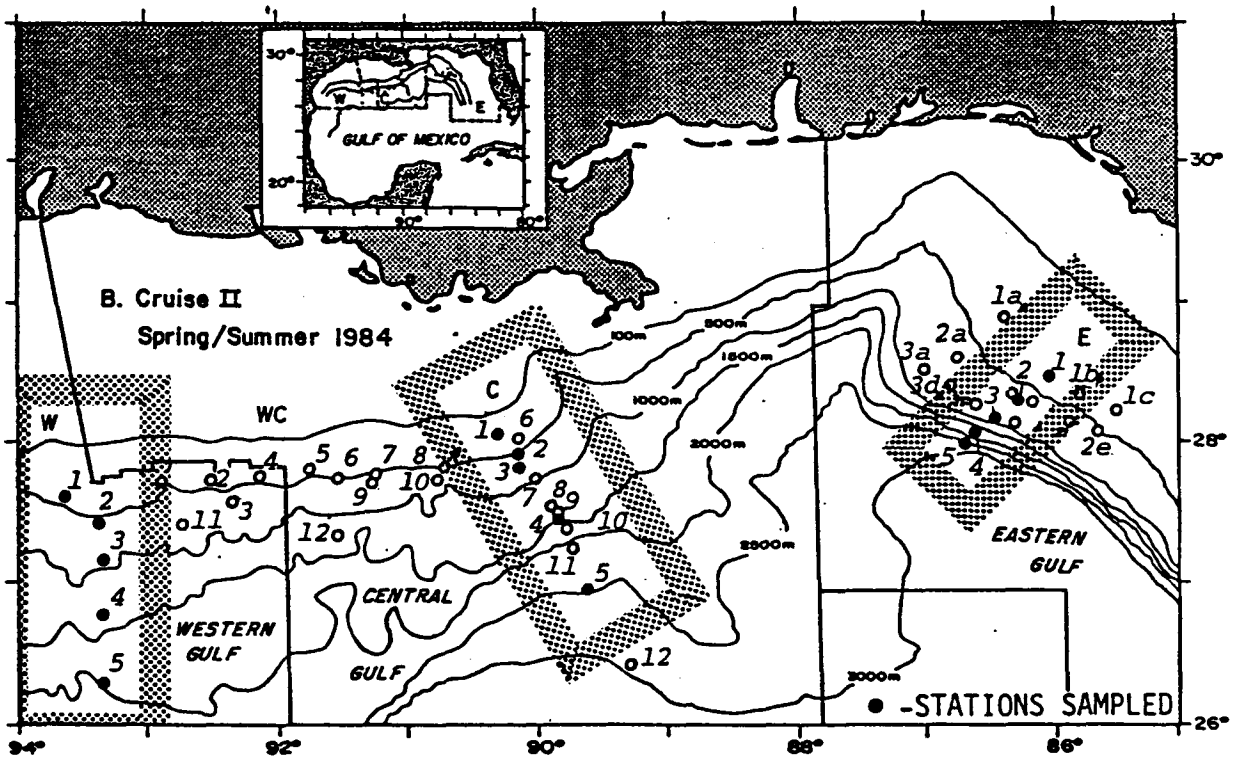
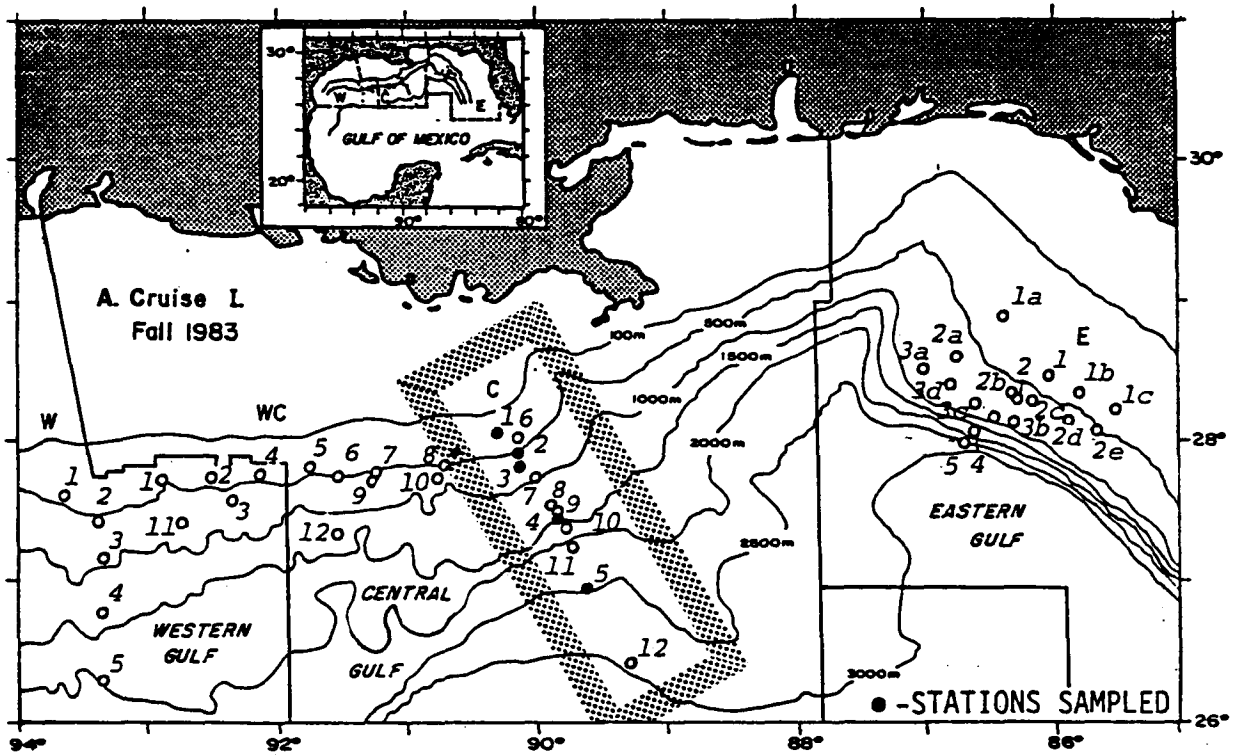


Figure 1. Stations sampled on each cruise.

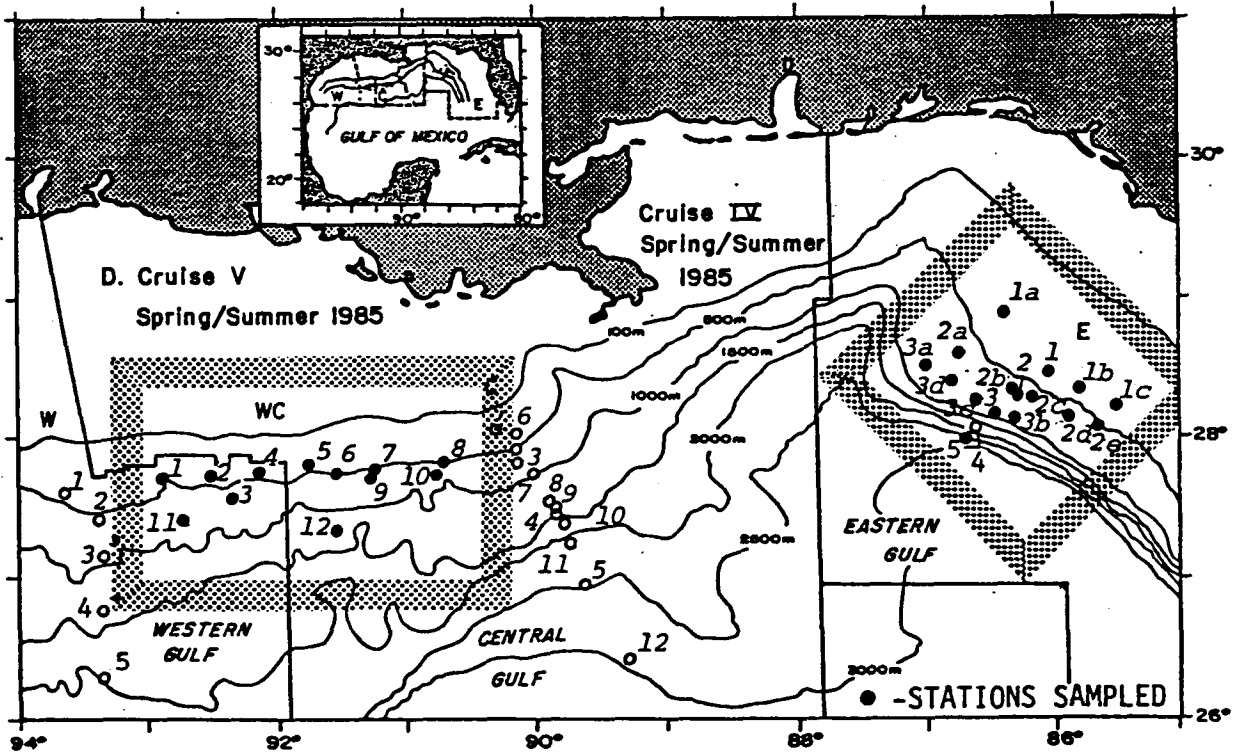
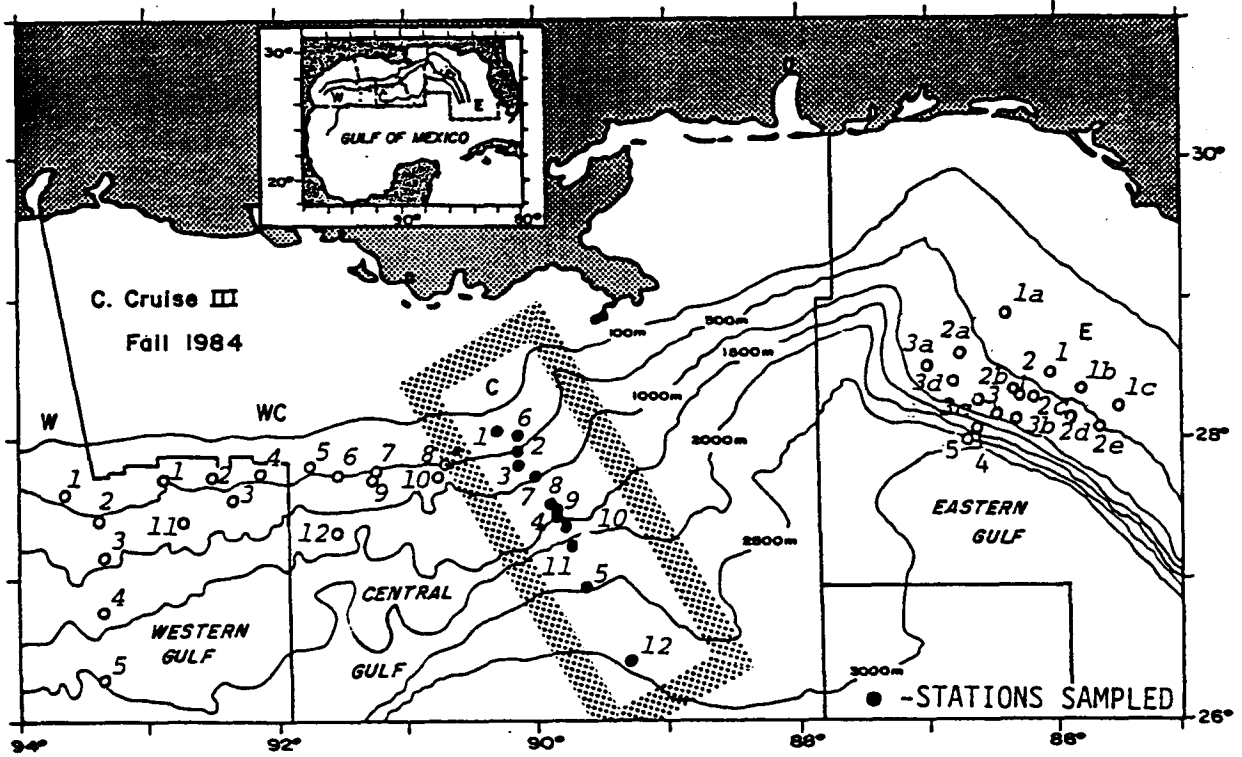


Figure 1 (cont'd).

(especially on the lower slope), a low rate of terrigenous input and sedimentation, and moderate to strong currents along the face of the slope.

Various combinations of these transects were sampled on Cruises I, II, and III. Cruises IV and V sampled additional areas in the eastern and western Gulf, respectively (Fig. 1-C,D). Descriptions of the sampling efforts on each cruise, and the rationale for such efforts, are described below.

On Cruise I (fall 1983), five stations at five different depths were sampled on the central transect (Fig. 1-A). The primary purpose of Cruise I was to collect samples within previously-defined faunal zones over a wide depth range (300 to 2,400 m) as a basis for refining future sampling efforts.

Cruise II (spring/summer 1984) re-sampled the stations occupied on Cruise I and also extended the geographic coverage to the western and eastern regions of the Gulf (Fig. 1-B). Cruise II results provided data for comparisons among planning areas and depths, and for stations on the central transect, between seasons.

During Cruise III (fall 1984), the five original central transect stations were sampled again in fall 1984, along with seven additional stations (Fig. 1-C). The seven new stations were located on the central transect at different depths from the first five stations. The locations for the additional stations were mainly in suspected biological "transition" areas and were based upon the advice of this program's Scientific Advisory Committee. Sampling the five original central transect stations allowed comparisons to be made between the fall cruise of 1983 and that of 1984.

During Cruise IV (spring/summer 1985), 16 stations were sampled near and on the eastern transect, including those previously occupied on the eastern transect on Cruise II (Fig. 1-D). The new stations were grouped by depth at approximately 350 m (four stations), 625 m (six stations), 850 m (five stations), and 2,900 m (one station). The purpose of this grouping design was to test depth-related differences against variability related to distance along these isobaths. Annual variability could also be studied by comparing the data from Stations E1, E2, E3, and E5 on

Cruise IV (Fig. 1-D) to data from Cruise II (Fig. 1-B) from the same stations a year earlier.

Station locations for Cruise V (spring/summer 1985) (Fig. 1-D) were chosen on the basis of two major needs. First, the area of sampling (between the western and central transects) was subject to ongoing and expected future oil and gas exploration and development activities, and many sites were selected along depth contours in this area to document longitudinal variability in sediment and biological characteristics. Second, hydrocarbon seeps had been reported in the area, and the associated biota had not been well documented. Two suspected areas of hydrocarbon seeps (Stations WC6 and WC7) were chosen to compare with probable "control" (non-seep) areas at comparable depths (Stations WC8 and WC2).

The sampling strategy described above permitted project scientists to make the following contrasts:

<u>Contrast</u>	<u>Data Source</u>
Seasonal variation by depth	Central Transect, Cruises I & II
Geographic variation by depth	Western, Central, and Eastern Transects, Cruise II
Annual variation by depth	Central Transect, Cruises I & III
Zonation patterns	Central Transect, Cruise III, plus data from all other cruises
Variation within depths, Western Gulf	West-Central Transect, Cruise V
Variation within depths, Eastern Gulf	Eastern Transect, Cruise IV

These sampling design considerations allowed researchers to analyze faunal distributions and abundance in space and time. Additional relationships of interest were the influences of sediment size, presence and types of hydrocarbons, and water quality on faunal distribution and abundance. Sediments and hydrocarbons were analyzed from the same samples

from which meiofauna and macrofauna were analyzed; this allowed for comparisons among these physical variables and these faunal groups. Water quality was analyzed from samples taken along sampling transects providing data to compare with faunal characteristics of those transects.

Field Methods

Hydrographic Measurements

Continuous and discrete measurements of hydrographic parameters were obtained throughout the water column (surface to bottom) at five stations on each cruise. A Neil-Brown Mark III CTD/Rosette/Transmissometer System was used to obtain continuous data and discrete water samples. Continuous conductivity (salinity), temperature, depth, and transmission records were provided by the Neil-Brown CTD. At each station, a 12-bottle rosette attached to the CTD was used to collect 12 discrete water samples for measurements of temperature, salinity, dissolved oxygen, nutrients, and particulate organic carbon. Bottles were spaced throughout the water column in order to delineate the major water masses at each site. The CTD/Rosette/ Transmissometer system was deployed with a pinger so that the cast could be safely lowered to within a few meters of the bottom. This was done in order to discern whether there were bottom nepheloid layers at each site.

Box Core Sampling

Box core samples were taken at each station to obtain material for macroinfauna and meiofauna identification, sediment grain size, carbonate, total organic carbon, carbon isotopes, and hydrocarbons. Six replicate samples were taken at each station, except on the western and eastern transect stations during Cruise II, when only three replicates were taken per station. The replicates were then subdivided to provide material for the various types of analyses.

Box corers were deployed in yoked pairs, using a TAMU-modified version of the Gray-O'Hara modification of the J&O box corer. On many occasions, only one cast was required to collect two replicates.

The box corer measured 24.5 x 24.5 x 44 cm. It was fitted with a hinged door to prevent washout of samples, and had up to 135 kg of ballast. The door was open until the device had penetrated the substrate, whereupon the jaws and the door closed. The amount of ballast was adjusted to ensure adequate substrate penetration.

The box corer contained six metal coring tubes, 43.5 cm long and 3.5 cm in internal diameter. During Cruise I, these tubes were mounted in three pairs on a wire rack in the center of the box. This design was improved on successive cruises by mounting all six tubes against one wall of the box and securing them behind an aluminum partition that extended the full depth of the box. As each box corer came onboard, the overlying water was carefully siphoned into the macrofauna container, and the remaining subsamples processed according to their intended uses.

Trawl Sampling (Megafauna)

Megafauna sampling was performed with a standard 9-m, semi-balloon otter trawl with 60-cm steel doors, 3.8-cm stretch mesh, and 1.3-cm cod end mesh. Target trawling times were one hour at stations shallower than 1300 m, and two or more hours at deeper stations. The amount of time on the bottom was arbitrarily measured as the time from winch brake application until the winch was started again for trawl retrieval. At a towing speed of one to three knots, a ratio (scope) of 3.5:1 between amount of wire out and the depth produced good samples.

The contents of each retrieved trawl was dumped into metal tubs. Fishes and invertebrates intended for hydrocarbon assays were quickly removed, photographed, and frozen. The remaining organisms were usually rough-sorted into three categories (fish, decapods, and "other"). They were then narcotized with isotonic magnesium sulfate if necessary, and preserved in 10% neutral buffered formalin in sea water.

Benthic Photography

Benthic photographs were taken with the use of a Benthos Model 372 deep-sea camera fitted with a 28-mm lens (angle of view 35° x 48.5°), and equipped with a 200 watt-second (Joule) Benthos strobe. On each visit to

every station, the camera exposed 800 frames of Kodak Ektachrome Professional 5936 film, ISO 200. Photographs were taken every eight seconds.

The photographic gear was mounted inside a protective framework. This framework had a clock and altimeter that recorded the time and altitude above the bottom in the corner of each photograph. The altimeter had a resolution of ± 0.1 m.

The camera system was suspended from the vessel by a hydrographic wire, and allowed to drift near the bottom along transects 1,500 to 5,000 m long. This technique prevented skipping and bouncing on the bottom, thereby minimizing disturbance and reducing the chances of attracting or frightening animals away.

Altitude was maintained by adjusting the vessel's winch in response to an acoustic signal transmitted by a 12 kHz bottom-finding pinger on the framework. The signal was portrayed continuously on a strip chart recorder. Optimum camera altitude was approximately 2 m above the bottom, which produced shots that included 2.27 m² of the bottom. However, acceptable shots were obtained at altitudes from 0.7 m (0.27 m² area) to 4.0 m (9.09 m² area).

Laboratory Methods

Laboratory activities included (1) analyzing sediments and biota for physical, chemical, and hydrocarbon parameters and for carbon isotope ratios; (2) sorting, identifying, enumerating, weighing, and measuring biota and analyzing their gut contents; and (3) analyzing photographs for biota and animal parts. Standard methods were used throughout each analysis and are detailed in Volume II of this report.

ENVIRONMENTAL CHARACTERIZATION

One of the primary objectives of this study was to describe the environment of the continental slope of the northern Gulf of Mexico in terms of overlying water masses, bottom water conditions, sedimentary character and hydrocarbon levels in the sediments. The overall purpose of this physical-chemical characterization was to identify spatial and

temporal variations or discontinuities that might account for or be related to biological features. A major emphasis was placed upon the sources of, and present levels of hydrocarbons in the sediments. Originally, this effort was perceived to be of most importance in that the data would constitute a pre-development baseline which could be used as a standard against which to compare the effects of hydrocarbon development on the continental slope. However, as will be demonstrated in subsequent sections, in this report, including those describing the biological communities around natural petroleum seeps, sediment hydrocarbon levels already influence biological communities of the slope, even when present in only trace amounts.

The primary water column difference between the Gulf of Mexico continental slope and other slope systems is that the shallow sill depth (~1,900 m) at the Yucatan Strait connection between the Gulf and the Atlantic prevents the input of cold (2°C) bottom waters. As a result, slope habitats below 2,000 m remain relatively warm (~4°C). Depth variation in temperature, salinity and dissolved oxygen exhibited classical and expected patterns and there were no, or only minimal, regional differences in these patterns.

Sediment characteristics did exhibit regional differences. The most common sediment type on the slope was silty clay, occurring in all geographic regions. However, in the eastern Gulf this general sediment type had higher percentages of sand than in the western or central areas of the Gulf. In our samples, clay sediments were found in the western and central Gulf but was not present in any of our eastern Gulf samples. In contrast, sand-silt-clay sediments were represented at some eastern Gulf stations but absent from the western Gulf stations. Sandy clay was found at shallow and deep stations in the western Gulf and at deep stations in the eastern Gulf.

Gulf of Mexico slope sediments contain a mixture of terrigenous, petroleum, and planktonic hydrocarbons. The influence of river/land derived material is widespread and is probably delivered to the slope by secondary sediment movement such as slumping and slope failure. Petroleum hydrocarbons were detected at all locations and have a dual source in natural seepage and river associated transport. Other studies have suggested that natural seepage is much more widespread on the Gulf of

Mexico slope than previously thought and probably represents a significant input of petroleum hydrocarbon to Gulf slope sediments (Brooks et al., 1985; 1986; Lacerda et al., 1987; Kennicutt et al., 1987).

In general the concentration of hydrocarbons in slope sediments except in seep areas, was lower than previous reports for shelf and coastal sediments but no consistent decrease with increasing water depth was apparent below 300 m. Hydrocarbon distributions, in general, are patchy on the slope and this may be due in part to the non-uniform distribution of natural seepage on the slope. Variability in hydrocarbon concentrations were as much as 1 to 2 orders of magnitude along an isobath, due to changes in sediment texture and hydrocarbon inputs. Hydrocarbons were preferentially associated with clayey, organic-rich sediments suggesting a linkage with river derived material. Aromatic hydrocarbon concentrations were very low at all locations but their presence was confirmed by fluorescence analysis.

Megafaunal organisms collected from non-seep areas had variable levels of hydrocarbons in their tissues, mainly derived from the sediments either directly or from organisms which had ingested sediments. Hydrocarbons were more prevalent in fishes than in decapod crustaceans. Terrigenous hydrocarbons were common but the majority of the hydrocarbons appeared of plankton origin.

Results of the Principal Component Analyses (PCA) suggested distinct regional differences in slope habitats, with the central Gulf having the highest levels of total organic carbon and petroleum hydrocarbons and the lowest levels of sand in the sediments. The stations in the eastern Gulf had the lowest levels of organic carbon and hydrocarbons in slope sediments and the highest levels of sand. Stations along the western Gulf slope transect were intermediate between these extremes. Data from each regional transect suggested differences along the transect by depth, namely that the proportion of plankton-derived hydrocarbons and the petroleum indicator of high molecular weight hydrocarbons (PE-Hi) increased with depth and distance from shore. There was also an indication of higher organic carbon and petroleum levels associated with topographic irregularities that would enhance sediment accumulation.

Results of the PCA designed to evaluate depth differences suggested distinct differences in habitats by depth on the central transect. Three

general habitats were indicated--shallow (<500-m deep), deep (>2,000 m) and intermediate (500 to 2,000 m deep). This suggests a distinct deep-shelf habitat, connected by a broad transition zone to a distinct abyssal habitat beginning at about 2,000 m. Subsequent PCA's conducted on samples collected along isobaths suggested habitats along depth contours differed more by depth than along a depth contour.

MEIOFAUNA

The meiofaunal collections contained in excess of 230,000 individuals representing 43 major groups of animals. However, representatives of five taxa of permanent meiofauna (Nematoda, Harpacticoida, Polychaeta, Ostracoda and Kinorhyncha) along with naupliar larvae (temporary meiofauna) comprised 98% of the collections. Numerically the collections were dominated by nematodes and harpacticoids, but on a biomass basis polychaetes and ostracods were dominant. This structure was remarkably consistent across all stations, regions, seasons and years (Gallaway et al., 1988).

From inspection of the overall density patterns, meiofaunal abundance appeared somewhat greater in spring than in fall and higher on the central transect than on the eastern and western transects. Also, there was an overall trend of decrease in abundance with depth, but this was not always the case.

A more detailed examination of depth distribution was enabled from the fall 1984 sampling on the central transect. The results of this sampling also suggest a general decline in abundance with depth with notable exceptions to the pattern exhibited at Stations C7 and C4. The former station had anomalously high petroleum hydrocarbon levels and was documented to have had a population of chemosynthetic bivalves (see Chapter 2 of this report and Gallaway et al., 1988).

Relatively little variation was observed along isobaths sampled in the eastern and western Gulf of Mexico, and little across-isobath variation was noted for the depth intervals sampled on these cruises. The samples reflected remarkable constancy.

Mean density of meiofauna across all stations in this study was 700 organisms/10 cm², with individual station values ranging from about 200 to

1,100 organisms/10 cm². In general these counts appear higher than comparable meiofaunal values for the western Atlantic (Wigley and McIntyre, 1964; Tietjen, 1971; and Coull et al., 1977 as shown in Thiel, 1983). There, maximum values were on the order of 100 to 400 individuals/10 cm². Sieve sizes used in the referenced western Atlantic samples ranged from 0.042 to 0.074 mm as compared to the 0.063 mm sieve used in this study. From this comparison we conclude that the Gulf meiofaunal densities are greater than those of the U.S. Atlantic. In fact, review of the data presented in Thiel (1983) suggests that the meiofaunal densities observed in this program are among the highest recorded in any deep-sea habitat.

Both macrofauna and meiofauna numbers and biomass decreased overall with depth. For the macrofauna, numbers declined less rapidly than biomass, suggesting that macrofaunal size decreased with depth. For the meiofauna, numbers also declined less rapidly than biomass but the difference between the two slopes was marginal, suggesting little change in size. In contrast to Thiel's (1983) findings, we observed densities of meiofauna to decline at a more rapid rate than densities of macrofauna (ratio between meio- to macrofaunal slopes was 1.67 to 1 as compared to 0.5 to 1 in Thiel). However, the macrofauna were screened using a 0.300 mm sieve in our program, whereas Rowe (1971) used a screen size of 0.42 mm in his studies. Rowe's (1971) results formed the basis for Thiel's comparison.

Because of the gross level of taxonomy used (and available) for the meiofauna, detailed correlations were considered unwarranted. However, some observations were made. As noted above, significant exceptions to the trend of decreasing density of meiofauna with depth were observed. These included Stations C4 and C7 sampled on the central transect in fall 1984. Station C7 had enriched levels of petroleum hydrocarbons and benthic photographs revealed a dense community of chemosynthetic clams in the surface sediments. This may be indicative that when localized chemical enrichment of sediments provides the basis for a chemosynthetic food web, a general increase in infaunal density and diversity may occur in the larger area.

Some 500 specimens of the phylum Loricifera were collected during this program at depths ranging from 298 to 2,959 m. They were collected

from all but four of the stations sampled. This phylum was only described in 1983 (Kristensen, 1983) based upon specimens collected from near Roscoff, France; the Azores; and near Fort Pierce, Florida at depths ranging from 15 to 480 m. Specimens of this phylum were reported by Kristensen to be generally overlooked since a species shock treatment with freshwater was required to effectively dislodge them from marine sediments. One must wonder how many might have been collected if our samples had been treated accordingly. In any case, the program findings substantially increase both the geographic and depth ranges for the Loricifera.

The meiofauna of the Gulf of Mexico are poorly known and remain so. However, meiofaunal densities on the continental slope of the Gulf are abundant and rival or exceed the macrofauna in biomass, attesting to the small size of Gulf macrofauna. The patterns of abundance as compared to the macrofauna lend credence to the idea that, in comparison to other slope systems, food or energy availability in the Gulf may be low, thereby limiting population density levels.

MACROFAUNA

The macrofauna of the continental slope of the Gulf of Mexico are abundant (average transect densities ranged from 1,500 to 3,000 individuals/m²) and highly diverse. Except in the region of the shelf break, there is little or no tendency towards dominance by any species. For example, only 110 of the 1,121 species that were identified were represented by ten or more individuals and only 60 species were represented by 90 or more individuals. A total of 324 individual benthic samples were taken in the program which contained nearly 50,000 macrofaunal organisms. Only 12 species were represented by as many as 324 specimens, the number of grabs taken. The concept that the slope macrofauna of the Gulf of Mexico is depauperate is clearly in error. The macrofauna, in fact, consists largely of "rare species."

However, as compared to the macrofauna of the U.S. Atlantic slope (Blake et al., 1985; Maciolik et al., 1986) the Gulf of Mexico slope macrofauna are indicated to be neither as abundant nor as diverse. This may be indicative of a higher degree of food limitation on the Gulf slope

than on the Atlantic slope as suggested by Rowe and Menzel (1971). Given that both diversity and density levels are reduced in the Gulf as compared to the Atlantic, we suggest that food limitation is a more likely explanation for the observed differences than a low standing stock due to higher turnover rates in the Gulf (e.g., Rowe and Menzel, 1971).

Most species exhibited highly restricted depth distributions, with variation across isobaths being much greater than variation along isobaths. However, even along isobaths, environmental variables (e.g., sediment hydrocarbon levels) reflected a patchy distribution and there was often a measurable response by at least some of the more common biota. This type of distributional pattern lends itself readily to the definition of faunal zones.

Our sampling depths ranged from approximately 350 to approximately 3,000 m. The shallowest point was clearly beyond the Shelf Zone but began in an area that most likely represents a transition between shelf and slope forms. Our results suggest that this Shelf/Upper Slope zone extended to at least 650 m in all areas of the Gulf sampled. This zone, which was delineated based upon macrofauna, would incorporate both the Shelf/Slope Transition (150-450 m) and most of the Archibenthal Horizon A (475-750 m) Zones of Pequegnat (1983) who made his determinations based upon megafauna. It corresponds well to what Haedrich et al. (1980) coined the Upper Archibenthal Transition Zone (300 to 700 m) based upon megafaunal studies off New England.

Our data also suggested a distinct zone between 800 and 2,000 m having two subzones. One was 800 to 1,200 m, which also agrees well to Haedrich et al.'s (1980) Lower Archibenthal Transition Zone (700 to 1,300 m) and somewhat to Pequegnat's (1983) Archibenthal Horizon B Zone (775 to 950 m). The other subgroup included two stations around 1,450-m deep, and the assemblages at these stations were more similar to those 800- to 1,200-m deep than to stations comprising our fourth zone, the Abyssal Zone, (2,000- to 3,000-m deep). These hypothesized zones correspond well to the Upper Abyssal (1,400 to 2,000 m) and Mesoabyssal Zones of Haedrich et al. (1980). However, in our case, the assemblage at 1,450 m was obviously much more similar to the one at 800 to 1,200 m than to the one at 2,000 to 3,000 m. Therefore we conclude it should be considered as part of the Archibenthal Zone.

We conclude that there are three macrofaunal zones on the continental slope of the Gulf of Mexico, one subdivided:

- (1) Shelf/Slope Transition Zone (300 to 700 m),
- (2) Upper Archibenthal Zone (700 to 1,300 m),
- (3) Lower Archibenthal Zone (1,300 to 1,650 m) and
- (4) Abyssal Zone (2,000 to 3,000 m).

The depth ranges of these zones correspond well to zonation schemes defined by both Haedrich et al. (1980) and Rowe et al. (1982) based upon megafaunal studies in the U.S. Atlantic. It is similar to that proposed by Pequegnat (1983) for the Gulf, except that we consider, based upon macrofauna, that the Shelf/Slope Transition and Archibenthal Zones extend to deeper depths than proposed by Pequegnat (1983) based upon analyses of megafaunal distributions.

The patterns of station similarity based upon macrofaunal collections as described above were remarkably concordant with the patterns of station similarities yielded by Principal Component Analysis (PCA) of environmental data. The key factors to which the biota appeared to respond were hydrocarbon levels, bottom water dissolved oxygen, and sediment grain size. When the abundance of individual species of macrofauna was correlated to environmental factors, 121 significant correlations between macrofauna abundance and habitat variables were obtained out of the 1,342 possible correlations (61 species x 22 variables). Of the significant correlations, 38% (46) involved sediment hydrocarbon levels, 32% (39) involved sediment grain size and sedimentary characteristics other than hydrocarbons and 30% (36) involved water column characteristics. Most of the species responded negatively to sediment hydrocarbon levels, including those of phytoplankton or terrigenous plant origin.

Sediment grain size and levels of calcium carbonate and delta ¹³C appeared to be the most important of the sediment variables based upon the relative numbers of significant contrasts. Within the water column variables, bottom water temperature and dissolved oxygen levels appeared most important on the same basis.

Assuming the observed results are not due to chance alone, we interpret the findings to result largely from a combination of the typical low densities of any one species and their restricted abundance by depth patterns combined with the uniformity of most physical conditions within an isobath, except for hydrocarbons and sediment grain size. Bottom water and temperature, of course, vary markedly with depth and a relatively high number of correlations would be expected to result.

MEGAFUNA

Despite the aforementioned deficiencies, our trawl collections contained over 5,400 vertebrates (fish) and more than 40,600 invertebrates. Some 126 species of fish and 432 species of invertebrates were collected. A complete listing of all taxa by cruise and station is provided in Gallaway et al. (1988).

Abundance and Diversity

In general, megafaunal invertebrate density was four to five times greater than fish density, and the two groups exhibited similar patterns in abundance and diversity. Both groups also showed strong species dominance patterns--i.e., the overall patterns usually reflected the distribution of one or two abundant species. Only 22 of the 126 species of fish exhibited a total abundance of more than one percent of the catch (>54 specimens) and only 14 of the 432 species of megafaunal invertebrates were represented by as many as 400 specimens (one percent of the total, Table 1).

Fish density (no./ha) was markedly higher on the eastern transect than on the central and western transects, with density on the western transect being slightly higher than that observed on the central transect. Based upon data from the central transect, fish density appeared higher in fall than during the spring and there was little difference between collections made in fall 1983 and 1984. Likewise, based upon common stations sampled on the eastern transect, there was little difference in overall fish density between the 1984 and 1985 spring collections.

Table 1. Most abundant species (>1% of the total) of fishes and invertebrates collected during the Gulf of Mexico continental slope study.

<u>Fishes</u>		<u>Invertebrates</u>	
<u>Species</u>	<u>Count</u>	<u>Species</u>	<u>Count</u>
<u>Dibranchius atlanticus</u>	575	<u>Aega Sp. 285</u>	9,911
<u>Urophycis cirratus</u>	380	<u>Nematocarcinus rotundus</u>	3,393
<u>Bembrops gobioides</u>	366	<u>Penaeopsis serrata</u>	2,896
<u>Synaphobranchus oregoni</u>	352	<u>Bathyplox typhla</u>	2,287
<u>Chlorophthalmus agassizi</u>	305	<u>Plesionika holthuisi</u>	1,664
<u>Hymenocephalus italicus</u>	252	<u>Munida valida</u>	1,634
<u>Nezumia aequalis</u>	236	<u>Benthochascon schmitti</u>	1,390
<u>Coelorinchus coelorhyncus</u>	205	<u>Chrysogorgia agassizii</u>	1,283
<u>Gadomus longifilis</u>	191	<u>Ophiernus adpersus</u>	1,087
<u>Coelorinchus caribbaeus</u>	177	<u>Amphilepis ingolfiana?</u>	959
<u>Epigonus pandionis</u>	175	<u>Ophiocamax fasciculata</u>	857
<u>Poecilopsetta beani</u>	155	<u>Stereomastis sculpta</u>	695
<u>Chaunax pictus</u>	150	<u>Polymastia sol</u>	682
<u>Peristedion greyae</u>	128	<u>Trilasmis kaempferi</u>	
<u>Laemonema barbatulum</u>	116	<u>inaequilaterale</u>	561
<u>Malacocephalus occidentalis</u>	111		
<u>Merluccius albidus</u>	107	TOTAL	29,299
<u>Bathygadus macrops</u>	106		
<u>Bathygadus melanobranchus</u>	97		
<u>Setarches guentheri</u>	94		
<u>Ilyophis brunneus</u>	84		
<u>Etmopterus schultzi</u>	62		
TOTAL	4,424		

Density by depth patterns of fishes on the eastern transect during spring 1984 showed two peaks, one at the shallowest station (355 m) and the other at the 1,400-m deep station. Inspection of the distribution by depth data for the central and western transects shows either the same (but markedly less pronounced) pattern or a decline in abundance with depth. The bimodal pattern was confirmed by sampling conducted on the central transect in fall 1984. However, the shallow abundance peak occurred at 474 m and the deeper peak occurred at 1,064 m. Fish were relatively scarce below 1,064 m as compared to all shallower depths.

During spring 1985, a series of samples were taken along the 350-, 650- and 850-m isobaths in the eastern Gulf, between latitudes 28°00' and 29°00'N. More isobathic variation was exhibited along the shallow as opposed to the two deeper isobaths, and abundance appeared greater at sampling sites north of 28°20' than south of this latitude. Some of the differences observed for the shallow transect may have been attributable to differences in sediment type, but the data do not lend themselves for such an analysis.

Similar isobathic sampling was conducted during summer 1985 in the region between our central and western Gulf across-isobath sampling transects. Overall fish density was lower in this region than had been observed in the eastern Gulf. The isobathic sampling in the west-central Gulf included a number of specific contrasts as outlined in Chapter 4 of Volume II of this report. Few of the contrasts exhibited significant differences. One of the significant differences observed was that fish abundance at a topographic high was higher than abundance at a station of the same depth but without relief.

Density patterns of megafaunal invertebrates was similar to density patterns observed for fishes in that density levels in the eastern Gulf of Mexico were far greater than those observed for either the central or western transects. Density observed on the central transect during fall appeared similar to spring levels, and little difference was detected within seasons or between years. Density by depth was also similar to that observed for fish. However, density of invertebrates at the deepest stations on the central transects during fall 1983 was as high as that observed for the shallow stations. While this depth trend was not pronounced on the fall 1984 central transect, there was a peak in

abundance at shallow depths, low density at intermediate depths and a slight increase in density following the mid-depth low.

Invertebrate abundance along isobaths in the eastern Gulf suggested reasonably uniform density along the 350- and 850-m isobaths and at all but one station along the 650-m isobath. The high abundance station was at about 28°10'N latitude. No explanation is readily apparent. Abundance along the 650-m isobath was higher than along either the 350-m or 850-m isobath.

Isobathic sampling in the west-central Gulf along the 550-m and 850-m isobaths yielded invertebrate density patterns similar to that previously described for fish. Invertebrate density at the topographic high (WC11) was higher than density at the same depth at Station WC12.

In contrast to the fish abundance data, diversity levels of fishes differed little among regions, seasons or years, and generally declined with depth in each region, season/year sampled. Comparison of diversity levels by depth on the central transect during fall 1984 showed high and reasonably uniform diversity levels for stations sampled between 350 and 1,200 m. At the five stations sampled below 1,200 m in depth, diversity was uniform at about one-half the level observed at shallower depths. There was virtually no variation in fish diversity along the isobaths in either the eastern or west-central Gulf area. Fish diversity in the gulf appears remarkably similar to fish diversity in the U.S. Atlantic (Musick, 1976).

Decapod crustaceans dominated the megafaunal invertebrate collections, and diversity for this group was used for a direct comparison to fish diversity patterns. As with fish, there were no distinct regional, seasonal or annual differences in decapod diversity and depth trends suggested a decline in abundance with increasing depth. However, maximum diversity was often associated with some of the mid-depth stations as opposed to the shallower sites. With the exception of Station C10 where diversity was 0 (only one decapod species collected) intensive sampling across isobaths on the central transect in fall 1984 showed remarkable homogeneity in diversity. Likewise there was little variation in decapod diversity along or between isobaths in the eastern Gulf.

Isobathic sampling in the west-central Gulf produced few major differences in decapod diversity except for the shallowest and deepest station pairs.

Zonation

Throughout this study, emphasis was placed upon determining the validity of the megafaunal zonation scheme hypothesized by Pequegnat (1983) for Gulf megafauna. The general observation that the fauna of the ocean bottom changes in species composition with increasing depth has been unchallenged since the turn of the century. The debate concerning zonation centers on whether there exists sharply delineated zones having distinct faunal assemblages, or does the fauna simply change continuously with depth. The exercise has practical utility. If the existence of homogeneous zones can be tested and proven, applied research (e.g., monitoring of oil and gas development impacts) and management decisions can be greatly simplified by focusing on depths that include the major biological resources.

Our approach was undertaken in three steps. First, during Cruises I and II, samples were taken at the mid-point of each Pequegnat's (1983) proposed zones with the samples representing three regions and two seasons. The results of our analysis suggested that the faunal differences between depths of 350, 650, 850, 1,350 and 2,550 m were marked and that the observed differences were constant over the two seasons and three regions sampled (LGL Ecological Research Associates, Inc. [LGL] and Texas A&M University [TAMU], 1985). However, the observed degree of dissimilarity between the sample depths was not exactly what would have been predicted based upon Pequegnat (1983). We would have expected to have seen the greatest similarity between the faunal assemblages represented at 650 and 850-m depths (Horizons A and B of the Archibenthal Zone), which would comprise one cluster distinct from three other clusters representing faunal assemblages at 350-, 1,350- and 2,550-m depths (Shelf/Slope Transition, Upper Abyssal, and Mesoabyssal Zones, respectively).

The results of the analysis of megafaunal data gathered during Cruises I and II suggested a higher degree of faunal similarity between

the 850- and 1,350-m deep stations (500 m depth difference) than between the fauna at these two depths and the one at 650 m (200 m depth difference). The most disparate assemblage was observed at the 2,500-m depth, some 1,200 m deeper than the next closest sampling site. The faunal assemblage at 350 m was also suggested to have been markedly dissimilar from those at 650 to 1,350-m depths. From these results one could best defend three major zones, one subdivided:

Shelf/Upper Slope (350 m)
Upper Archibenthal (650 m)
Lower Archibenthal (850-1,350 m)
Abyssal (2,550 m)

The next step was to conduct a more finely-spaced sampling effort to test faunal similarity over smaller segments of the bathymetric range. This effort was made on Cruise III in fall 1984 (LGL and TAMU, 1986). Samples were taken at depths of 346 (C1), 474 (C6), 632 (C2), 802 (C3), 964 (C7), 1,064 (C8), 1,510 (C4), 1,735 (C10), 2,074 (C11) and 2,504 (C5) m. Megafaunal invertebrates dominated the collections made on this cruise (mean density of invertebrates over the transect was 115/ha as compared to 12 fish/ha). Further, the invertebrate collection, although containing a large number of species, was dominated by a small number of species. Examination of these data showed the presence of at least two areas where groups of species having greatly restricted bathymetric distributions co-occurred over a depth interval which was separated by a sharp discontinuity from the next group of co-occurring species. The first group ranged from about 500 to 800-m in depth, with peak abundance occurring between 475 and 650 m in depth. This was not a shelf assemblage (an outer shelf group of penaeids, e.g., Penaeopsis serrata, were present at 350 m but were absent at 475 m), but a group of upper slope forms. Included were Benthochascon schmitti, Bathyplox typhla, and Plesionika holthuisi.

The next group of species was most abundant at about 1,100 m, with the range being from 800 to some undefined depth between 1,500 and 2,000 m. From inspection of the distributions we have placed the boundary at about 1,650 m. The dominant among this group was Nematocarcinus rotundus.

For lack of better terminology we have labeled these two zones as the Upper and Lower Archibenthal Zone. None of the dominant species characteristic of the Upper Archibenthal Zone occurred in the lower part of the zone and only Stereomastis sculpta and Nematocarcinus rotundus from the Lower Archibenthal Zone occurred in the Upper part of the zone. However, several species of the Lower Archibenthal Zone penetrated down slope.

Minor peaks in abundance by one to two species appeared to occur at about 1,500 and 2,100 m, but one species (which also occurred in the Lower Archibenthal Zone) the asteroid, Plutonaster intermedius, contributed to both peaks. The depth zone between 1,650 and 2,250 m appeared to be a broad transitional area characterized by low biomass. The decapod crustaceans which were dominant at shallow depths were absent. We have called this zone the Upper Abyssal Zone.

At 2,500 m biomass began to increase, and the fauna was markedly different than that observed at shallow depths. Representative species included holothuroids, ophiuroids, and gastropods. We have labeled this zone as the Mesoabyssal Zone. Biomass in the Abyssal Zone did not approach the levels characteristic of the Archibenthal Zone.

Results of cluster analyses for Cruise III on the central transect, based upon all invertebrates collected represented by ten or more individuals, supports the above account based upon dominant species. Three major station groups are formed, each with an outlier representing the faunal "breaks" suggested above (Station C1, Shelf Slope Zone; Station C3, boundary between the Upper and Lower Archibenthal Zone; C10, near the boundary between the Lower Archibenthal and Upper Abyssal Zone).

Based upon data from all cruises and regions, there was some variation in the abundance of decapods with depth, leading to uncertainty as to where the boundary between the Lower Archibenthal and the Upper Abyssal Zone should be placed. As evidenced by data from the eastern Gulf, high diversity and biomass of the decapods can extend down to 1,500 m in this region and data from the central transect during Cruises I and II shows the same down to 1,350 m in the central Gulf. Nevertheless there appears marked "breaks" in faunal assemblages at about 400, 800, 1,650 and between 2,000 and 2,500 m. Shallower than 1,650 m, the faunas are characterized by a high biomass of megafauna, dominated by decapod

crustaceans and fishes. Below these depths, the megafauna are sparse, with the invertebrate populations consisting of forms such as holothuroids and ophiuroids as opposed to decapod crustaceans.

The third step in our evaluation of zonation was to sample along selected isobaths at different depths to determine if there would be fewer exchanges of faunal species along as opposed to across isobaths. Based upon results of cluster analyses as well as the constancy in the abundance of individual species, similarity along isobaths was remarkably uniform as compared to similarity across isobaths (Gallaway et al., 1988). Thus, the concept of zones generally holds up (i.e., species composition is predictable among depths).

The questions regarding what constitutes a zone versus a subdivision of a zone, etc., is probably unimportant for practical purposes. Pequegnat (1983) defined five faunal assemblages for the depth intervals sampled during our study. Above, we have presented our results as three zones--Shelf, Archibenthal and Abyssal. Nevertheless the latter two are subdivided such that five "zones" are actually recognized. The only difference between the designations presented here and that originally proposed by Pequegnat (1983) is (1) terminology, (2) we deepen the extent of the Lower Archibenthal Zone and (3) we classify Upper Abyssal Zone as being largely transitional in nature. Overall, the Pequegnat was (1983) zonation scheme was documented to have predictive value.

In Chapter 2 of Volume II of this report, PCA was applied to the environmental data collected at central transect stations. The results (see Fig. 2-16 in Chapter 2) indicated three clusters of stations shallow (C1, C6), mid-depth (C2, C3, C4, C7, C8, C9) and deep (C11, C12, C5). The mid-depth and deep stations were subdivided into two groups, respectively. Within the mid-depth set of stations, C3 and C7 clustered apart and this environmental classification corresponds to the area we have delineated as a boundary between the Upper and Lower Archibenthal Zones. In the deep stations, the environment at Station C5 (biologically distinct as the Mesoabyssal zone) was markedly different from Stations C11 and C12. A biological collection was not obtained at C12, but Station C11 and C5 were considered biologically distinct--one in the Upper Abyssal and the other constituting what we have called the Mesoabyssal Zone.

Hydrocarbon levels and sediment grain size were the important environmental components for classifying the sampling sites. By implication these may be important factors in determining biological differences. An important observation, we think, is that the depth zone constituting the Upper Archibenthal Zone (between 500 and 800 m) where megafaunal biomass is highest corresponds to the zone where petroleum seep communities are prevalent (14 of 19 documented petroleum seep sites have occurred within a depth range of 500 to 700 m) and where dissolved oxygen levels are relatively low.

Life History Observations

Life history data were taken for macrofauna trawled at the 60 sampling stations. The specimens were first measured and weighed, and invertebrates were sexed and examined externally to determine the number of ovigerous females. Fish were dissected to determine food habits and state of maturity. As noted earlier, over 5,400 fish were collected, representing 126 species. However, 104 species were represented by fewer specimens than the number of trawls taken (60). Only five species were represented by more than 300 specimens, or on average as many as five specimens per trawl. Thus, while the data are of value because there is very little life history information concerning any of the species, they were not adequate to delineate trends or differences among regions, seasons, years and depth.

For the invertebrates, 364 (84%) of the total 432 species collected were represented by fewer than 60 specimens, but 19 species were represented by more than 300 specimens. However, among this group were four species that represent incidental species (e.g., small isopods and barnacles) contained in the tows. Although the numbers appear large, at least compared to the fish, even these data were not adequate to determine trends among regions, seasons, years and depths. For the most part, a few large trawl catches comprise most of the data for each of the abundant species.

Nevertheless, some useful information was obtained from the macrofauna collections. The complete data and detailed life history

accounts can be found in Gallaway et al. (1988). These data are synthesized below.

Length-Weight Information

The length-weight data represent the largest of the life history data sets (Gallaway et al., 1988). The relationships, even when pooled, all exhibited very tight fits to a linear regression, indicating low variability across seasons, years and regions. These relationships can therefore be used as a predevelopment, baseline measure of megafaunal health or condition. The relationships also enable one to estimate biomass levels of megafauna given numbers and size distribution.

The length data showed ovigerous females of a number of invertebrates to have been significantly larger than males and non-ovigerous females--not a surprising result. Our data were not adequate to determine any seasonal or spatial patterns in the distribution of decapod crustaceans in a given reproductive state.

Although the size frequency data were often bi- or multimodal, indicating the possibility of multiple age groups, the sampling schedule was not frequent enough to delineate growth patterns. More frequent sampling at fixed locations than was planned for this program would be required. The data suggest, however, that with adequate sampling (e.g., monthly) size groups or cohorts could be followed through time, yielding growth information.

Fish Food Habits

We were able to obtain reasonably good trophic information from a limited number of specimens representing eight species of fish (Table 2). Poor success in obtaining trophic information from fish raised from great depths is not unusual. Complete data for all fish, although fragmentary, is found in Gallaway et al. (1988). Of the eight species, four were generally distributed at depths of about 500 m or less, members of the Shelf Faunal Zone. Two (Coelorinchus caribbaeus and Poecilopsetta beani) fed mainly on polychaetes and amphipods, respectively. The other two

Table 2. Food habits for eight species of fishes collected on the Gulf of Mexico continental slope, 1983-1984.

<u>Species</u>	<u>Number Caught</u>	<u>Number Stomachs</u>	<u>Depth Distribution (m)</u>	<u>Dominant Prey (% Wt.)</u>
<u>Dibranchius atlanticus</u>	575	33	500-871	Pagurids (41%), polychaetes (19%)
<u>Bembrops gobiodes</u>	366	30	<555	Natantia (87%)
<u>Synaphobranchus oregoni</u>	352	24	1,000-1,500	Fish (47%), Natantia (28%)
<u>Chloropthalmus agassizi</u>	305	21	<500	Fish (47%), calanoid copepods (21%)
<u>Nezumia aequalis</u>	236	13	500-871	Natantia (82%)
<u>Gadomus longifilllis</u>	191	23	1,100-1,200	Natantia (44%), calanoid copepods (21%)
<u>Coelorinchus caribbaeus</u>	177	15	<500	Polychaetes (55%), Natantia (26%)
<u>Poecilopsetta beani</u>	155	21	<500	Amphipods (77%)

(Chlorophthalmus agassizi and Bembrops gobiodes) were predatory on larger forms, feeding mainly on fish and natantia, respectively.

Dibranchus atlanticus occurred over a wide depth range, but were most abundant at depths of 400 to 870 m, suggesting an affinity with the Upper Archibenthal Zone as described above. While the biomass data would indicate that this small predator fed largely on small hermit crabs (pagurids) and polychaetes, these data are misleading since pagurids actually occurred in only two of 33 stomachs. The primary food of this species consisted of amphipods and polychaetes. Nezumia aequalis had a depth distribution similar to Dibranchus atlanticus but fed almost exclusively on natantia (82%), based upon the contents of 13 somtachs.

Specimens of Gadomus longifilllis and Synaphobranchus oregoni from which we were able to obtain stomachs in good condition were largely associated with the Lower Archibenthal Zone. The diet of Synaphobranchus oregoni consisted of fish and natantia, whereas Gadomus longifilllis fed mainly on natantia and copepods.

The biochemistry work on this project, conducted to compliment the food habits investigation, showed that the megafauna of the continental slope of the northern Gulf of Mexico reflect the signatures of planktonic as well as terrestrial biogenic and petroleum hydrocarbons. Biogenic hydrocarbons of planktonic origin were the most prevalent, especially in the eastern Gulf. The biomass of megafauna in the eastern Gulf was markedly higher than biomass observed in the western Gulf, however, the macrofauna did not reflect this pattern.

CHEMOSYNTHETIC COMMUNITY OVERVIEW

Discovery and History of Study

The sequence of discoveries relating to chemosynthetic communities on the Gulf of Mexico continental slope began with the first successful retrieval of thermogenic gas hydrates in deep ocean sediments in Green Canyon lease block 184 (GC-184, see Fig. 6-1 in Volume II of this report) in 1983 (Brooks et al., 1984). Gas hydrates are solid, ice-like clathrate structures in which gases are occluded in a crystalline water lattice under appropriate conditions of high pressure and low temperature. The

stability zone of gas hydrates in marine sediments is generally found in areas where water depths are greater than 500 m and bottom water temperature is low (Kvenvolden and Barnard, 1983; Kvenvolden et al., 1983). Although a wide range of gases can form hydrates, methane and possibly CO₂ are the only gases found in sufficient quantities in deep-sea sediments for hydrate formation. The few previous reports of deep-sea, gas hydrates were of biogenic hydrates obtained primarily at subbottom depths of several hundred meters [all but one were recovered at Deep Sea Drilling Project (DSDP) sites on the Blake-Bahama Outer Ridge of the Atlantic Ocean and the Middle America Trench region of the Pacific Ocean (Brooks et al., 1985)]. Under conditions of temperature and pressure appropriate for hydrate stability, gas concentrations must exceed solubility before hydrates can form. Therefore, hydrates can be found only in regions where there is significant biogenic methane production or where there is seepage (migration) of thermogenic gases from deeper horizons.

Since the initial Gulf of Mexico hydrate discovery, seven other areas on the Louisiana slope have been identified which contain hydrates. These sites range from 530 to 2,400 m water depth and span an area of more than 10,000 sq mi. All sites were sampled by conventional piston coring except for the hydrates obtained from the Orca Basin (20-40 m subbottom) as part of DSDP Leg 96. Of these nine sites, five contained biogenic hydrates composed predominantly of methane and four contained thermogenic hydrates. All thermogenic hydrates were associated with oil-stained cores containing up to 15% by weight of hexane-extractable oil. The associated oil in these cores has undergone extensive biodegradation after reaching the surficial sediments. The thermogenic hydrate cores are often associated with carbonate-cemented rubble, which may result from the biodegradation of the seeping oil. In addition, there is a flux of oil out of some of these sediments into the overlying water as indicated by high molecular weight hydrocarbon gradients above the sediment/water interface. The gradients have been detected by sensitive fluorescence and high pressure liquid chromatographic/UV/VIS diode array techniques.

In Brooks et al. (1984) report of thermogenic hydrates, it was stated that the effect of oil-stained sediments and solid hydrates on the benthic ecology of the area was unknown and needed further study. Therefore, on

Dr. Brooks' NSF-sponsored R/V Gyre Cruise 84-G-12 (November-December 1984) two trawls were taken in two separate seep locations on the Louisiana slope. The trawls sampled populations of hydrothermal vent-type organisms including bivalves, gastropods, and tube worms. The trawls were taken through regions characterized by 3.5 kHz seismic records as "wipe-out" zones. Piston coring in and out of these "wipe-out" zones indicated that the sediments in these regions contained oil, hydrate and/or gas.

Carbon isotopic analyses were performed on the bivalves, gastropods and tube worms that were collected in order to identify nutritional strategies of these organisms. Stable carbon isotopes are useful in delineating the flow of carbon through ecosystems since there is considerable evidence that minimal carbon isotopic fractionation occurs as carbon is transferred through marine food webs. Marine, photosynthetically-derived carbon generally has carbon isotopic ($\delta^{13}\text{C}$) values from -6 to -24 ppt (vs. PDB). Bivalves and vestimentiferans sampled from these areas had carbon isotopic values between -27 and -35 ppt. These values are similar to those reported for Pacific vent animals (clams and mussels) whose nutrition is based on chemoautotrophic bacteria that derives energy from hydrogen sulfide oxidation (Childress et al., 1986). The Louisiana slope, seep ecosystems also gain chemoautotrophic energy from hydrogen sulfide produced by sulfate reduction or from seeping gas/oil that contains hydrogen sulfide. Hydrogen sulfide is present at all oil seep areas. It has now been shown that methane can also be used as a reduced substrate in these chemoautotrophic systems (Childress et al., 1986).

On a subsequent cruise (May 1985, R/V Gyre Cruise 85-G-5), 12 additional trawls were undertaken in the vicinity of the two areas previously sampled. These trawls also recovered large numbers of chemosynthetic organisms. GERG undertook cruises in 1986 (86-G-1/2) to (1) test the hypothesis that communities based on chemosynthesis are broadly distributed on the Gulf of Mexico continental slope in oil seep areas that can be identified by either seismic "wipe-out" zones or bubble plumes and (2) study the nature of the hydrocarbon seepage (gas and/or oil) in these "wipe-out" areas. Earlier investigations had shown that chemosynthetic communities were present at two restricted sites on the continental slope (Fig. 2).

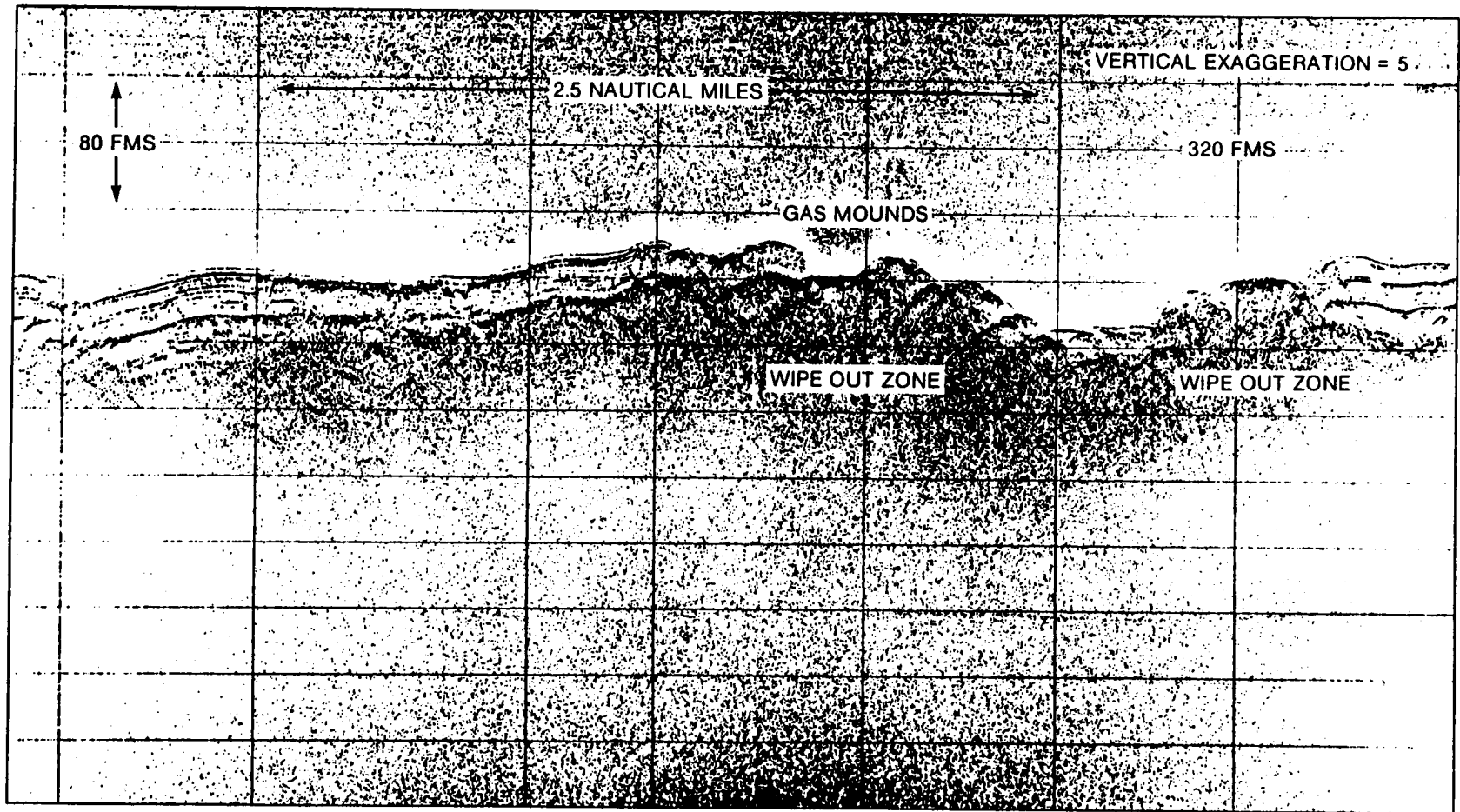


Figure 2. Typical seismic "wipe-out" zone in the Gulf of Mexico. These areas are characterized by oil seepage, gas hydrates and/or gas-charged sediments.

The Offshore Operators Committee, in conjunction with the Minerals Management Service, supplied GERG with 33 locations on the continental slope where shallow seismic profiles from hazard surveys indicate "wipe-out" zones. GERG took 39 trawls and piston cores in these areas.

The results of the latter field study demonstrated that chemosynthetic organisms (either their remains or living tube worms, mussels and/or clams) were present in the Green Canyon (GC) (13 sites), Garden Banks (six sites), Ewing Bank (1 site) and East Breaks (1 site) lease areas. This significantly expanded the geographic area where these organisms occur. Chemosynthetic tube worms, clams and mussels were found in 18, 12 and 5 trawls, respectively. The higher occurrence of tube worms in the trawls may have been related to the higher catch efficiency (although probably still low) of the otter trawl for this type of chemosynthetic organism.

The above studies were followed in late 1986 and 1987 by a series of three submersible operations whose primary objective was to visually examine these ecosystems. Six dives with the submersible Johnson Sea-Link-I (four dives on "Bush Hill" in Green Canyon blocks 184/185 and two dives in GC-233/234) from the R/V Edwin Link during September 1986 were funded by MMS. These dives examined the community on "Bush Hill". The site contained a dense chemosynthetic community consisting of: (1) large tube worm clusters (up to 2 m in length), consisting of hundreds of individuals; (2) mussel beds (containing thousands of individuals), generally associated with active gas bubble seepage; (3) bacterial mats, often containing a separate phase oil lying beneath them; and (4) a variety of associated macrofauna (Brooks et al., 1987a).

In March/April 1987 GERG received support from the Office of Naval Research for 23 dive days aboard the U.S. Navy nuclear-powered submersible NR-1 to study chemosynthetic sites. Additional dense communities of chemosynthetic tube worms and mussels were directly observed in GC blocks 272, 185, 234, and 29, among others. These dives photographically documented large communities of chemosynthetic clams.

These operations were followed by an additional 26 dives (Dives 2053-2077; June 1987) aboard the Harbor Branch Oceanographic Institution's Johnson Sea-Link-I from the R/V Seward Johnson. This dive series was funded by the NOAA Undersea Research Program (NURP) with research support

provided by the Texas A&M Sea Grant program. A multidisciplinary dive team headed by Dr. James M. Brooks (GERG) undertook ecological, physiological, chemical and taxonomic studies at "Bush Hill" in GC-184, and sites in GC-234 and GC-272.

Community Types

The oil seep community has been subdivided into five basic assemblage types including (1) mussel beds, (2) tube worm clumps, (3) clam beds, (4) epifaunal brachiopod-solitary coral assemblages, and (5) gorgonian fields (Brooks et al., 1988). The mussel and tube worm clumps often form distinct assemblages which are exploited by surrounding soft-bottom browsers and predators. Due to the relative ease of sampling the mussel assemblages, they are the most completely described (Fig. 3). Both sessile suspension feeders (gorgonians), epifaunal browsers (urchins) and predators (gastropods) derive carbon from chemosynthetically-based production. A comparison of what is known about hard-bottom communities on the slope in areas with and without seeps is shown in Figure 4.

Energy Sources

Taxonomic, enzymatic, and isotopic analyses confirm that the Gulf of Mexico seep chemosynthetic communities are similar to those at hydrothermal vents in the Pacific and that the primary mode of nutrition is chemosynthesis based on endosymbiotic bacteria (Kennicutt et al., 1985; Childress et al., 1986; Brooks et al., 1987). The majority of the bivalves (Calyptogena ponderosa, Vesicomys cordata, and Psuedomiltha sp.), vestimentiferans (Lamellibrachia sp. and an Escarpia-like unidentified species), and pogonophorans are primarily if not exclusively deriving their energy from bacterial conversion of H_2S to elemental sulfur and sulfate. In contrast to this, laboratory incubations with ^{14}C labeled substrates, enzymatic analyses, and carbon isotopic compositions confirmed that a mussel (*Bivalvia*, Mytilidae) at these sites derives its carbon, energy and nutritional needs from a symbiotic relationship with methane oxidizing bacteria in its gills (Childress et al., 1986; Brooks et al.,

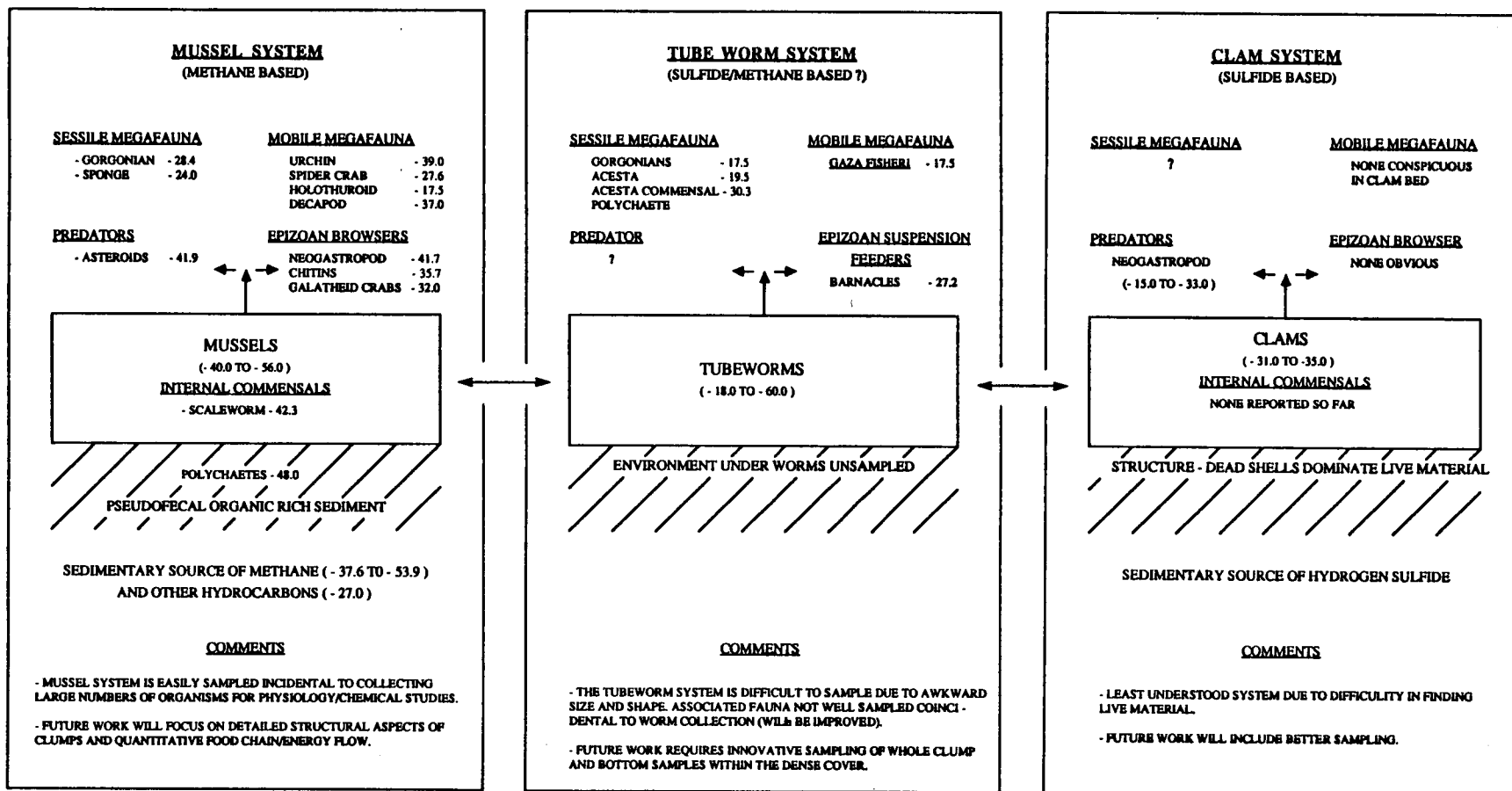


Figure 3. Relationships between chemosynthetic assemblage types, carbonate rock system, and the associated epifaunal browsers, sessile suspension feeders and predators. Initial isotopic measurements on the 1987 Sea-Link cruise samples show relationship between system components.

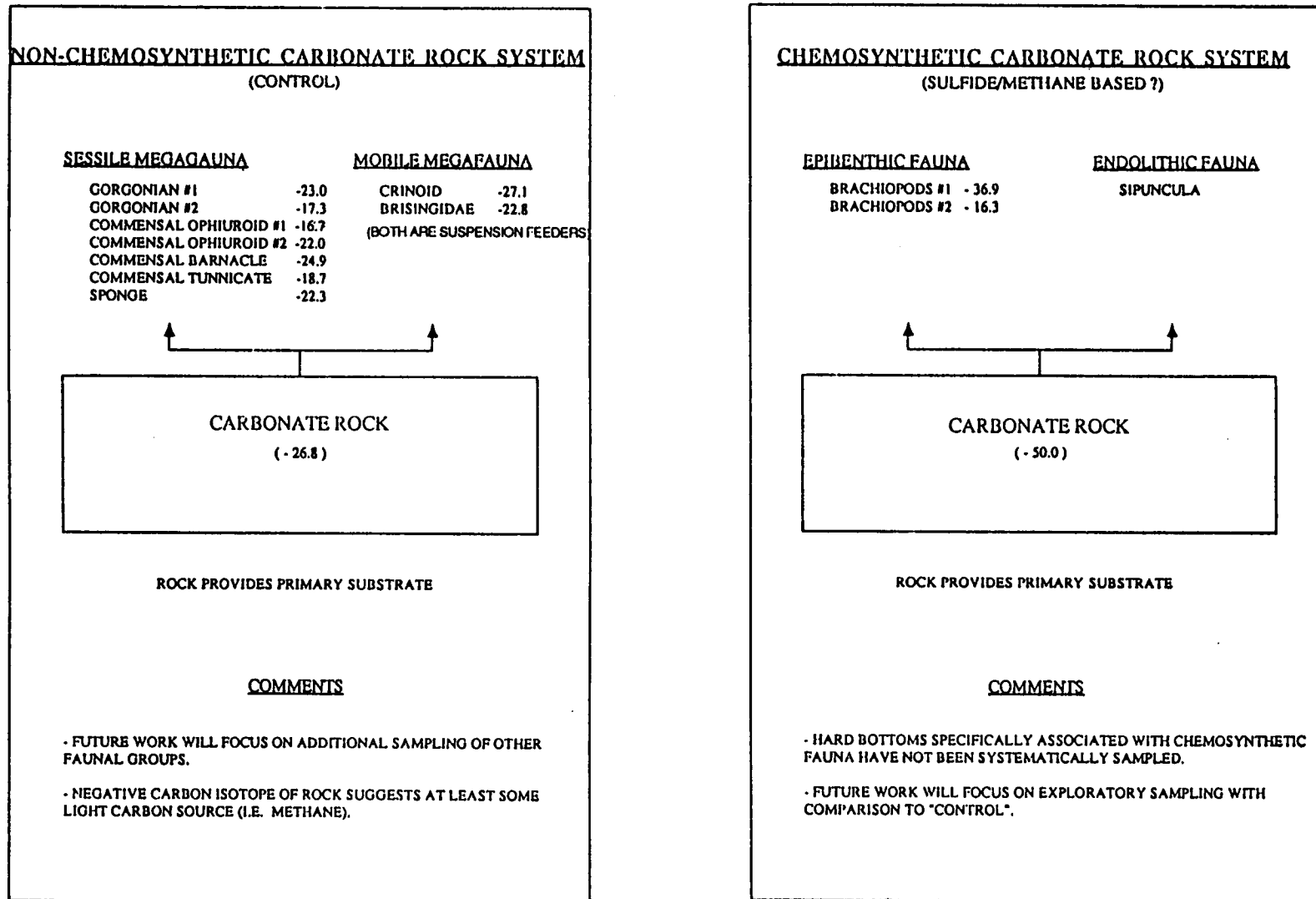


Figure 4. Relationships between chemosynthetic and non-chemosynthetic carbonate rock assemblage types and the associated browsers and sessile suspension feeders. Initial isotopic measurements on the 1987 Sea-Link cruise samples show relationship between system components.

1987). This was the first confirmed report of a molluscan symbiosis based on methane.

A variety of tests are used to determine the nature (and presence) of endosymbionts in seep fauna. The mussel is the only animal with confirmed methanotrophic symbionts and is the only seep species which possesses methanol dehydrogenase, a diagnostic enzyme for methylotrophy (Childress et al., 1986). The mussel is also the only animal tested whose bacterial symbionts contain stacked internal membranes (typical of Type I methanotrophs). Mussel gills lack the enzymes diagnostic of sulfur oxidation (ATP sulfurylase and APS reductase), lack elemental sulfur, and have only trace activities of RuBP carboxylase (an enzyme diagnostic of autotrophic carbon fixation); indicating that their symbionts are not sulfur oxidizing chemoautotrophs.

Three bivalves and two vestimentiferans recovered at these sites appear to harbor sulfur-oxidizing chemoautotrophic symbionts. The enzyme activities, presence of elemental sulfur in the symbion-containing tissue and electron microscopy provide convincing evidence that both vestimentiferans and the lucinid clam, Pseudomiltha sp., contain chemoautotrophic, sulfur bacterial symbionts. The evidence for the vesicomyid clams is not as conclusive since no tissue from Calypptogena ponderosa was frozen in liquid nitrogen for enzymatic analysis and the one Vecicomya cordata collected died before dissection. The absence of specific enzyme activities is therefore of questionable significance. Nonetheless, the high level of elemental sulfur in the gills of C. ponderosa and the high levels of ATP sulfurylase in V. cordata gills suggest that sulfur oxidizing symbionts are present. The sulfide oxidase activities in all animals assayed are at the level expected for invertebrates exposed to a sulfide environment (Powell et al., 1986).

These seep fauna contain mostly 'dead' carbon. Several sources of dietary carbon are possible for the seep animals. First, carbon can be derived from particular detritus fixed photosynthetically in the upper water column. Second, carbon can be derived from bacterial organic carbon synthesized chemoautotrophically from dissolved inorganic carbon (DIOC). DIOC can be derived either from ambient bottom water or from 'dead' CO₂. 'Dead' DIOC can be derived from (1) seeping oil/gas, (2) bacterial degradation of the seeping oil/gas, (3) dissolution of ancient carbonate,

and/or (4) degradation of sedimentary organic matter. 'Dead' carbon can also be derived from the direct utilization of methane by symbiotic bacteria. 'Dead' carbon is most likely the result of direct utilization of methane by the mussels and extensive biodegradation of the oil/gas by bacteria. Methanotrophic bacteria are believed to be carbon isotopically light due to the isotopic compositions of their source carbon. Relatively little fractionation has been observed in converting methane to cellular carbon. Large amounts of isotopically light, authigenic carbonate and extensively biodegraded oil in sediments from the seep sites indicate active CO_2 production (Brooks et al., 1984; 1986). Although most reservoired gases in the Gulf of Mexico contain small amounts of CO_2 , this source of 'dead' carbon is hypothesized to be minor relative to other CO_2 sources. In order to determine the isotopic fractionation between an inorganic carbon source and tissue carbon it is necessary to know the form of the carbon source (CO_2 or HCO_3^-). The species of inorganic carbon used by invertebrates with chemoautotrophic symbionts has not been determined and may well vary between species (C. Fisher, pers. comm., unpubl. data).

At the hydrothermal vent sites, the principal source of dietary carbon for mussels and tube worms is DIOC (Williams et al., 1981). At the Florida Escarpment where methane is apparently the major energy source for the mussel, the radiocarbon content of three tube worms and the mussels was older, although not predominantly 'dead'. In contrast to the hydrothermal vent and Florida Escarpment sites, many of the mussels, tube worms and clams reported from the Gulf seeps contain nearly 'dead' carbon. The 'dead' carbon in the mussels support the metabolic and physiological studies that indicate that there is a bacterial symbioses between the mussel and methanotrophic bacteria (Childress et al. 1986). In contrast, the sulfur-based tube worms and clams have to be utilizing 'dead' DIOC derived from bacterial degradation of hydrocarbons. Thus, much of their dietary carbon is derived ultimately from the sediments, not the more recent DIOC of seawater. These observations are consistent with the hypothesis that these seep taxa are fueled by oil and gas (Childress et al., 1986).

Importance

These previous studies confirm that the northern Gulf of Mexico continental slope is the site of a number of unusual habitats. Visible oil seepage to the sea surface has been observed at the Green Canyon-184 and 190/234 areas. At one of these areas, extensive molecular and isotopic analyses have demonstrated that near surface sediment bitumens and surface slicks are derived from reservoirs 1,800-2,700 m below the surface (Kennicutt et al., 1988a). Nine locations on the Louisiana slope (530 to 2,400 m water depth) have currently been identified that contain either biogenic or thermogenic gas hydrates in shallow sediments (<6 m). Analyses of bitumens from several thousands of cores taken on the continental slope suggest that oil and gas seepage is a widespread phenomena on the Gulf of Mexico continental slope. This seepage supports widespread populations of chemosynthetic organisms in this area of the deep-sea. A number of new species of tube worms (Meredith Jones, Smithsonian Institution) and bivalves (Ruth Turner, Harvard University) are being described from the trawl collections at these sites. The physiology that allows animals to thrive in these high hydrocarbon environments must be unique (Kennicutt et al., 1988b).

These discoveries significantly expand the geographic area of the deep ocean where (1) hydrates are known; (2) oil seepage has been documented; and (3) one would expect to encounter dense assemblages of vent-type taxa. These discoveries are significantly different from the Pacific hydrothermal vents and the Florida Escarpment brine outflow since they are associated with natural, mature oil seepage. Since oil and gas seepage is common on the Louisiana/Texas continental slope as well as other oil producing regions of the ocean, it is probable that chemosynthetic communities are more widely distributed on the sea floor than previously believed. In fact, GERG has recently discovered such communities offshore northern California.

THE BUSH HILL CHEMOSYNTHETIC COMMUNITY

As part of this study, manned submersibles were used to study one of the sites that had been identified to have chemosynthetic organisms.

This site has been named the Bush Hill chemosynthetic community. This effort represented the first attempt to make extensive in-situ observations of such a community in the northwestern Gulf of Mexico and to relate the distribution of biota to environmental levels of hydrocarbons. Below we summarize the findings.

The sediments of the depauperate periphery of Bush Hill were pale ochre in color, with an easily-disturbed flocculent layer. Although the bottom in this region showed extensive lebensspuren including burrows, shallow depressions and mounds, very few organisms were seen or photographed. Generally, as the JSL proceeded up the slope of the diapir, the color of the sediment changed to a slate-grey, and the lebensspuren appeared to become less frequent. Carbonate outcroppings were observed, ranging in form from low rubble to prominent boulders. Along the western side of the diapir, the carbonate outcroppings formed an escarpment, which rose about 15 m at its steepest point. The larger boulders were topped by gorgonians, which were in turn frequently inhabited by large ophiuroids. Colonies of the scleractinian coral Lophelia sp. were also seen attached to the exposed portions of the boulders. White, filigreed patches of bacteria were observed on the sediments (Fig. 5A). Continuing toward regions of greater community density, the bacteria patches increased in area and were interspersed with slender (3.5 mm) black tubes of a pogonophoran Galathealinum n. sp., family Polybranchiidae (E.C. Southward, pers. comm.). The most prominent features of the dense area of the community were tube worm bushes, which occurred both among the carbonate outcroppings and on soft sediments away from surficial rubble.

Two species of vestimentiferan tube worms were identified as Lamellibrachia sp., family Lamellibrachidae and Escarpiid-like species, family Escarpiidae (M.L. Jones, pers. comm.). The escarpiid, which could be distinguished in the 35 mm photographs by its distinctive flaring of the tube opening (Fig. 5B), was fewer in number and generally formed sparse clusters of recumbent individuals. The Lamellibrachia sp. formed bush-like clusters in numbers ranging from a few tens to many thousands of individuals. Although Lamellibrachia sp. were clearly dominant, mixed clusters of Lamellibrachia sp. and the escarpiid did occur.

Numerous clusters of tube worms were observed in the video records. Morphology, both of the individual tubes and of the clusters, changed as

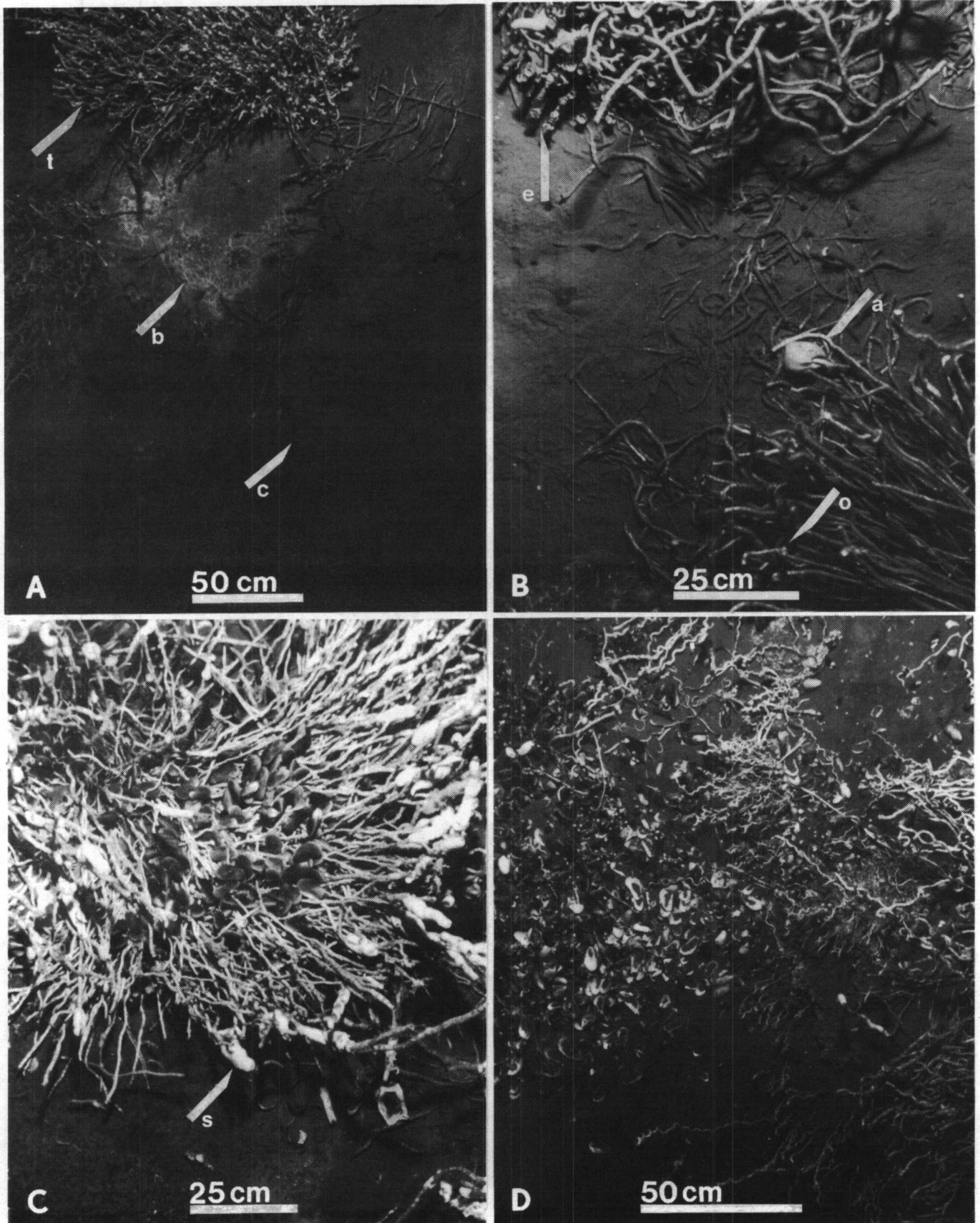


Figure 5. Bush Hill biota. A: Lamellibrachia sp. (t), carbonate boulder (c) and bacterial mat (b). B: Lamellibrachia sp. with attached Acesta bullisi (a) obturacular plume (o) and an escarpiid vestimentiferan (e), C: Lamellibrachia sp. with seep mussels in center, epifaunal sponge (s). D: Seep mussels and Lamellibrachia sp.

the number of tube worms in a cluster increased. Low tangles, 30 to 40 cm in diameter, consisted of individuals with twisted and curled tubes (Fig. 5D). Larger clusters, up to 1 m in diameter, had a collapsed, basket-like center and consisted of longer, less convoluted individuals (Fig. 5C). The larger bushes were dome-shaped, 2 m or greater in diameter and 1.5 m in height; they consisted of long, relatively straight individuals (Fig. 5A). Obturacular plumes were clearly visible on the individuals that formed the outer surface of the bushes. On several occasions, individual Lamellibrachia sp. were observed to retract their plumes in a single, rapid movement upon the close approach of the submersible. The largest formation observed was a continuous cluster over which the JSL transited for a distance of 9.3 m.

Attempts to collect both species demonstrated that their tubes were often burrowed below the soft sediments for a greater length than they protruded. One individual, which protruded approximately 50 cm, measured 168 cm when fully extracted. On this basis, the largest individuals may have been 250 cm or more in length. The opisthosomes (Jones, 1985) always broke away from the posterior ends of the tubes and were never collected.

An undescribed mussel (Mytilidae), which is similar to members of the genus Bathymodiolus (R.D. Turner, pers. comm.), formed discrete beds on both soft sediments and among carbonate outcroppings. Mussels and tube worms were observed together (Fig. 5C); however, the larger mussel beds contained only small tube worms, if any (Fig. 5D). The beds were irregular in shape, often in close proximity to each other, and ranged in area from less than 1 m² to approximately 20 m². Within the densest portions of the beds, mussels of a range of sizes were packed on end with umbos down. Elsewhere, they lay on their sides or in a horizontal position with hinges up. Where it could be observed, the periostracum on the umbos was often deeply pitted, revealing shell nacre. Several beds, consisting of disarticulated and broken shells were also observed. Living mussels were sometimes surrounded by a scatter of dead shells, both articulated and disarticulated and in various states of preservation (Fig. 5D).

Streams of methane bubbles were observed escaping from the substrate, both within the mussel beds and in their immediate vicinity. Some of these bubble streams were intermittent releases; others continued

throughout the period of observation. When the JSL first approached one such area to collect samples, its bow gently nosed the bottom. This disturbance released several large oil globules, which drifted upward. Such releases of oil were subsequently observed in several other locations, usually as a result of some disturbance of the bottom. A dense orange-colored mat of bacteria, apparently different from the bacteria patches described above, often covered the oily sediments.

A diverse assemblage of common slope fauna was recorded in the still photographs and the video tapes. Bathypelagic organisms included tunicates, squid and trichiurid fishes. The fish Hoplostethus sp. was frequently seen hovering over the tube worm bushes. Other fishes (including Chaunax pictus, Urophycis cirratus and Peristedion greyae) were frequently observed swimming near or resting on the bottom. Crustaceans included decapod crabs (Geryon sp., Bathyplox typhla and Rochinia crassa) and shrimp and the giant isopod Bathynomus giganteus.

Epifaunal organisms were observed living on the tube worms and mussels. The bivalve Acesta bullisi (R. Turner, pers. comm.; Boland 1986) was commonly attached to the ends of Lamellibrachia sp. tubes. Examination of photographs and collected specimens showed that the tubes were inserted through a concavity in the posterior margin of the A. bullisi shells, and that the Lamellibrachia sp. plumes were extended within the mantle cavity of the bivalves (Fig. 5B). Several photographs showed a galetheid crab, Munidopsis n. sp. (L. Pequegnat, pers. comm.), clinging to the ends of escarpiid tubes. Other tubes of both species were encrusted with hydroids and sponges. Epifauna on the mussels included nerite gastropods (E.N. Powell, pers. comm.), an undescribed caridian shrimp, Alvinocaris n. sp. (A. Williams, pers. comm.) and the crab Benthochascon schmitti. The hag fish, Eptatretus sp., was observed at rest in several mussel beds.

Distribution of Seep Organisms and Correlation to Hydrocarbons

The locations of individual mussel beds and tube worm bushes observed in the video record were plotted on the map of the sampling area. The distribution of both types of features was distinctly non-uniform (Fig. 6A and Fig. 6B). Mussel beds were sighted only in the center of the surveyed

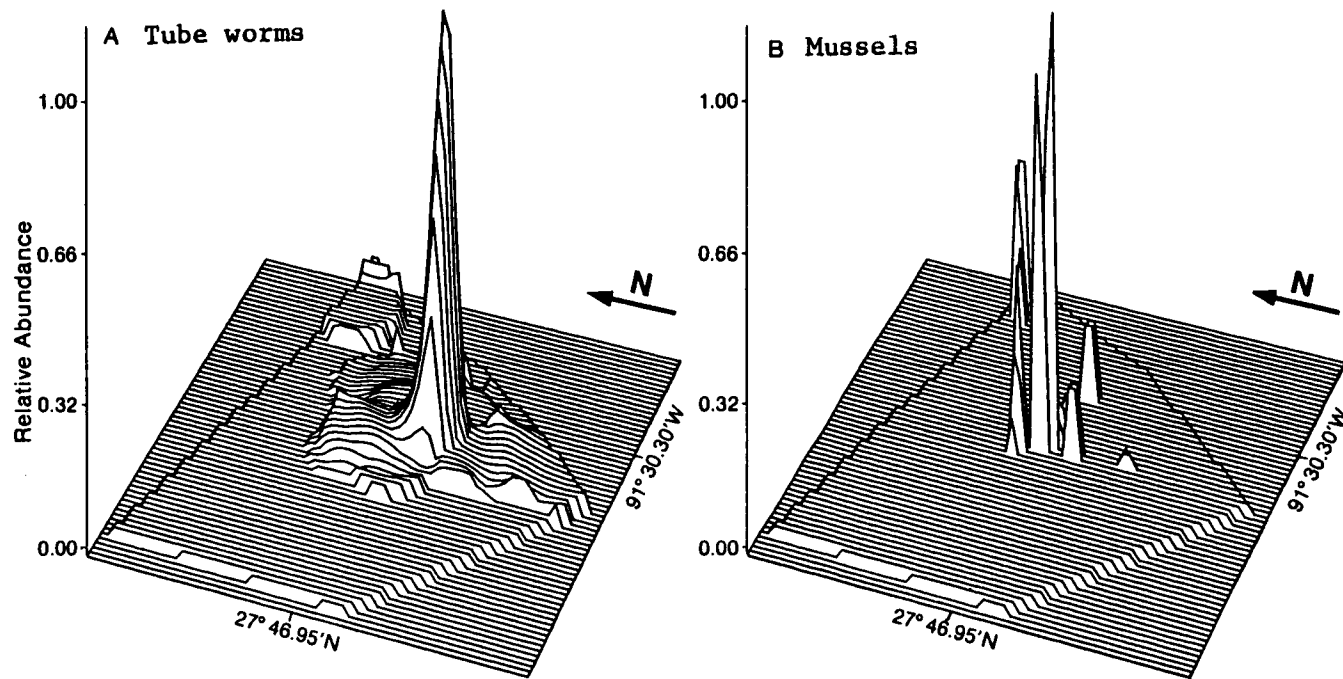


Figure 6. Estimated relative abundance of chemosynthetic organisms within the area of video sampling at Bush Hill. The projection was rotated counter clockwise and tilted toward the viewer. Raised edges show outer extent of video coverage (see Figs. 7-2A and 7-5, Chapter 7 in Volume II of this report). A: Relative abundance of tube worms (Lamellibrachia sp. and escaipiids). B: Relative abundance of seep mussels.

area and in its northeastern corner. Significant positive correlation ($p < 0.05$) was observed between the concentration of methane in the water column directly above the bottom and the area of the bottom that was covered with beds of living mussels.

Tube worm bushes were much more widespread. The data did, however, show two nodes of higher abundance: one in the center and one in the northeastern corner. These nodes were separated by areas in which the bottom often had a mottled appearance and was overlain with white bacterial mats. Solitary tube worm bushes were seen in places; these tended to be smaller than those in the areas of higher abundance and were often occupied by the epifaunal A. bullisi described above. Significant positive correlation ($p < 0.05$) was also observed between the concentration of EOM in the sediment and the area covered by tube worm bushes.

GENERAL CONCEPTUAL MODEL

One of the objectives of the program was to integrate the findings into a conceptual model(s) that would have management utility to Minerals Management Service (MMS), and enable a comparison of the Gulf slope system to other, similar systems. One problem with this approach is that conceptual models which can be defended with certainty are usually too simplistic to be of comparative value (i.e., all deep-sea ecosystems are poorly known from a functional standpoint). If, on the other hand, one builds more complex models, they rapidly delve into a level of speculation that renders their comparative value dubious at best.

We do believe, however, that the program has yielded some useful information about the continental slope ecosystem of the Gulf of Mexico that has not been observed or highlighted in any studies we have seen. Below, we first discuss a generalized conceptual model that would be valid for any slope ecosystem and outline how the Gulf system differs from others. We next discuss the standing stock structure of the Gulf of Mexico slope benthic community, which is followed by a discussion of zonal patterns. From this point, we proceed to identify some of the environmental factors that appear to account for, or at least correspond to, our biological observations in some coherent fashion.

Lastly, we will point out some of the deficiencies of our program, and make recommendations concerning improvements that could be made if future programs were conducted. Notable among these were our lebensspuren studies (see Gallaway et al., 1988) the results of which, although of interest, yielded little usable information.

Smith and Hinga (1983) characterize the deep ocean as an open ecosystem with energy exchanges across both the air-sea interface and sediment water interface. In vertical profile this ecosystem can be divided into layers defined by depth, salinity, pressure, temperature and light. Except for chemosynthetic communities in residence around petroleum seeps (discussed separately, see Chapters 6 and 7 in Volume II), the solar energy that primarily drives this system is fixed into chemical energy by the phytoplankton in the euphotic zone (Fig. 7). Much of this production is consumed by euphotic zone zooplankton who, in turn, support a pelagic food web. However, this energy is ultimately disseminated throughout the water column by passive sinking (the "organic rain" of Fig. 7) or active dispersion mediated by organisms. Detrital rain of pelagic biological origin is supplemented by sinking terrigenous carbon in areas affected by significant river discharge. Ultimately, the chemical energy passes downward to the benthic boundary layer. In addition to this sedimentation of organic materials, slumping and erosion down the slope can be a significant means of energy transport from shallow to deeper areas of the benthic boundary layer (Fig. 7).

Rates of average productivity for the open Gulf of Mexico ($55 \text{ g C/m}^2/\text{yr}$) show the Gulf is not very productive as compared to other oceanic areas (Pequegnat, 1983). Therefore, the standing stocks of deep-sea benthic communities in the Gulf would be predicted to be lower than in many systems. Rowe and Menzel (1971), Rowe et al. (1974), and Smith and Hinga (1983) among others, have provided evidence supporting this view. Results from this program do not invalidate the hypothesis that the standing stocks of the Gulf benthic community are relatively low.

The benthic boundary layer (Benthic Zone in Fig. 7) in the deep ocean has been defined biologically as the sediment community and the assemblages of organisms in the overlying water column associated with the bottom (Smith and Hinga, 1983). The sediment community consists of bacteria and invertebrates, above which, at the sediment water interface,

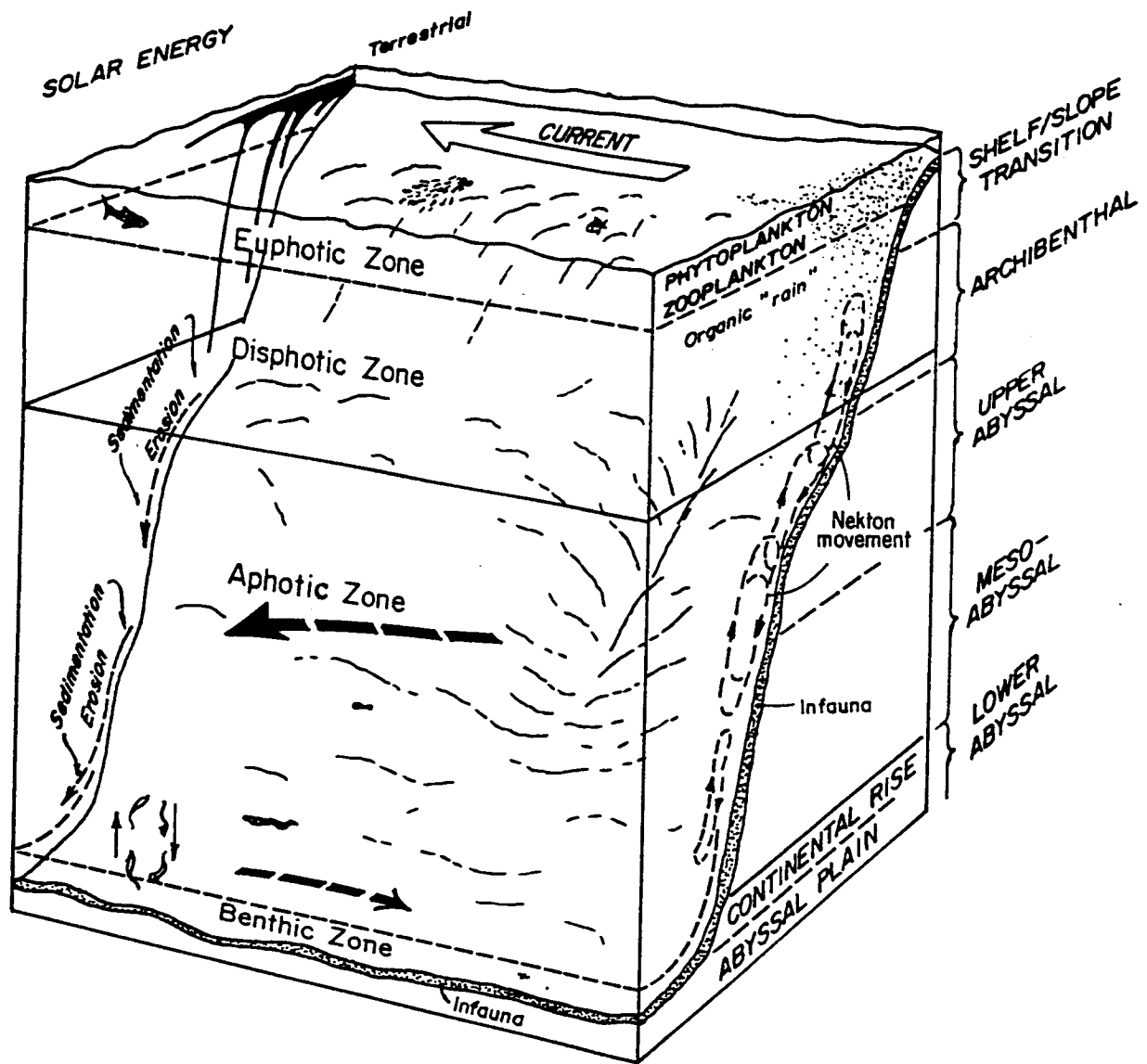


Figure 7. Conceptual model of the continental slope ecosystem, petroleum seep communities excepted.

larger animals ingest both the sediments and their biota for energy. In the water column above the sediment-water interface, pelagic fish and invertebrates feed both in the water column and on the bottom. Many of these benthopelagic animals move up- and down-slope to feed (Nekton Movement in Fig. 7), as well as communicate directly with higher mid-water animals above the boundary layer (Fig. 7). Sediment dwelling animals also make forays into the water column. An active exchange of food throughout the water column is suggested; i.e., a continuum of communities (Fig. 7; Smith and Hinga, 1983).

Overall, the deep-sea benthic community is an energy-poor environment, with the energy constraints becoming more and more severe with increasing depth and distance from land (petroleum seep communities in the Gulf provide the exception demonstrating the rule; Rex, 1983). The quality, rate, and pattern of energy input is generally considered to exert one of the most powerful selective forces acting on the deep-sea fauna.

DEPTH PATTERNS OF STANDING STOCKS

According to Rex (1983), and others, the best indication of food availability, whatever its origin and nature, is the actual standing stock of various components of the benthos. The generally accepted pattern of standing stock of slope benthos with depth is that density declines in an exponential fashion (e.g., Rowe, 1983; Thiel, 1983). Based upon results of this study, meiofaunal, macrofaunal and megafaunal standing stocks in the Gulf will also fit such a pattern overall. However, at shallow depths, considerable variation occurs, and a uniform decline with depth is not exactly the case (Fig. 8).

A consistent decrease in the standing stocks of meiofauna and macrofauna of an exponential nature was observed to occur between depths of about 1,500 to 3,000 m. Above this level, both of these groups exhibited density peaks at depths of about 500 and 1,000 m with lower densities at the intervening depths (Fig. 8). At the 1,000 m depths, the samples were taken in an area demonstrated to have been in proximity to a petroleum seep. For the megafauna, density levels at depths from about 1,500 m and deeper dropped abruptly in a marked step-fashion, when

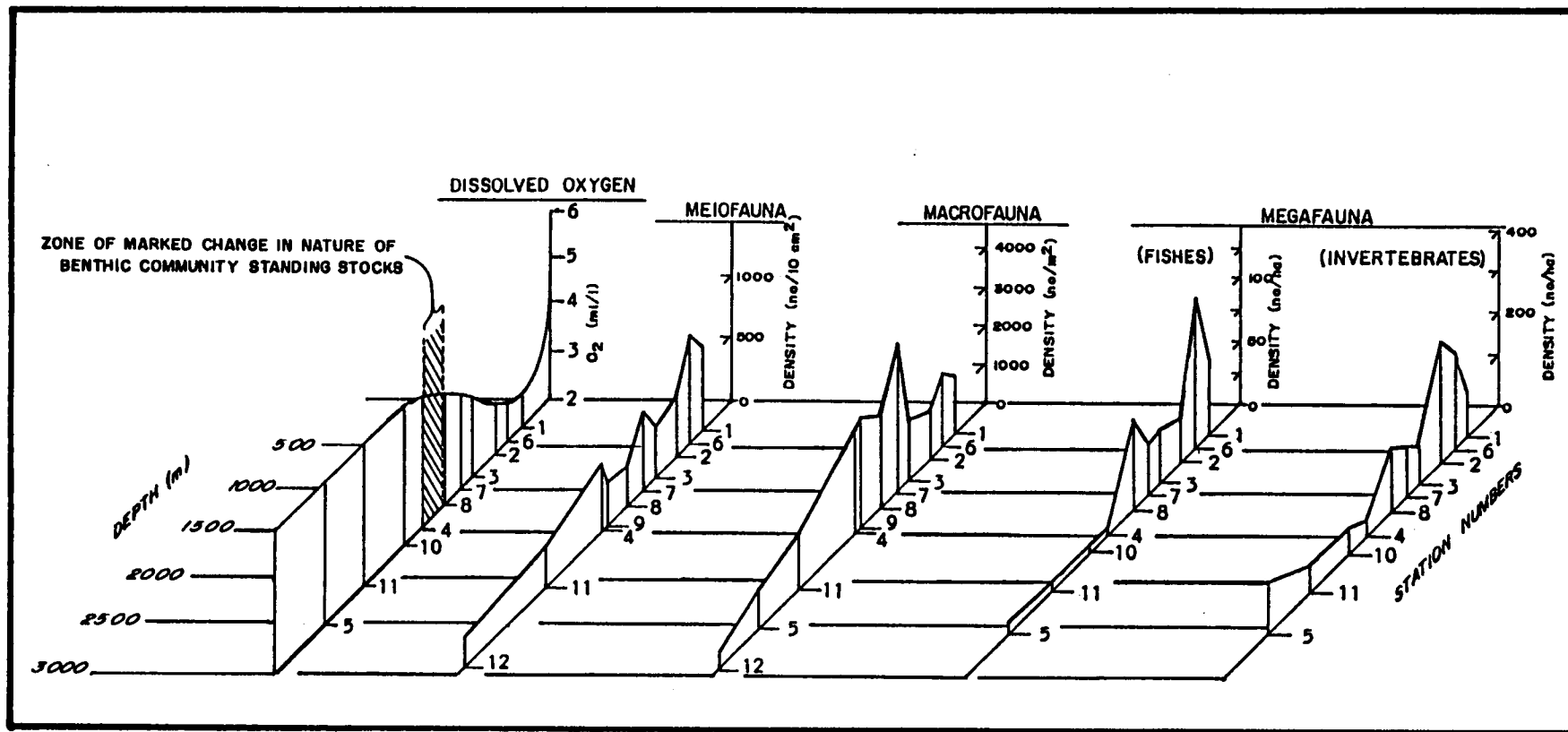


Figure 8. Dissolved oxygen levels as compared to the standing stocks of meiofauna, macrofauna and megafauna (fishes and invertebrates) on the central transect, fall 1984.

densities at these depths are compared to density levels characteristic of depths between 350 and about 1,100 m. Within the shallower depth range, peaks in megafauna standing stocks were observed at about 500 and 1,100 m with depressed density levels at the intervening depths. Fourteen (74%) of the 19 documented petroleum seep communities occur within a depth range of 500 to 700 m of which seven (50%) have occurred at depths between 500 and 550 m.

The standing stock data for each component of the benthic community evaluated appear to indicate that a marked change in the community biomass structure occurs between 1,100 and 1,500 m. The depths where high standing stocks prevail (350-1,100 m) generally corresponds to a number of environmental features, the most notable of which is that it occurs within the oxygen minimum layer (Fig. 8). The meiofaunal and macrofaunal data suggest enhanced standing stocks for samples known to have been taken in the vicinity of petroleum seeps and the zone of highest megafauna abundance corresponds to the depth range where petroleum seep communities are most prevalent, between 500 and 700 m. Other environmental factors that appear correlated to a general break in standing stock biomass patterns between 1,000 and 1,500 m include that (1) it is at or near these depths that light from the surface is completely attenuated (Fig. 8) and (2) at about these depths bottom water temperature drops below 5°C in the Gulf.

For the megafauna, standing stocks on the continental slope in the eastern Gulf appeared higher than standing stocks in the western Gulf. Further there was a trend for high densities to have been characteristically deeper in the eastern than in the western Gulf. This suggests, possibly, that productivity is higher in the eastern Gulf, but this was not indicated by either the macrofaunal or the meiofaunal data from our study.

Smith and Hinga (1983) observed that sediment community respiration in the eastern Gulf of Mexico was significantly higher than respiration at a station of comparable depth in the northwestern Atlantic. He noted that primary production and macrofaunal biomass did appear to support this premise. He suggested that the complex pattern associated with the convergence of the Loop Current and the southeasterly current flowing along the Florida continental margin might serve as a concentrating

mechanism for organic matter. He also reported that, for a station in the Straits of Florida region, that the organic carbon flux was not sufficient to fulfill the food energy requirements of the sediment community as estimated from respiration rates. Macroscopic plants such as turtle grass and sargassum along with vertically migrating animals were suggested as possible sources of the required organic carbon (Smith and Hinga, 1983).

FAUNAL ASSEMBLAGES AND ZONATION

Above we have suggested that from a biomass standpoint the continental slope of the Gulf might be divided into two zones--a zone of high standing stocks extending from the shelf edge to about 1,100 m and a zone of low standing stocks extending down the slope to the abyssal plain where biomass once more increases, but moderately so. We have also noted that standing stocks of benthic biota do not uniformly decline with depth but exhibit variable patterns that correspond to major environmental features.

In Chapter 4 (macrofauna) and Chapter 5 (megafauna) of Volume II of this report, we have provided data suggesting that recognizable and different assemblages were associated with each of the abundance peaks from the shelf edge to about 1,500 m. A comparison of the zonation patterns yielded by the macrofauna and megafauna is provided:

Macrofauna	Megafauna
Shelf/Slope (300-700 m)	Shelf/Slope (350 m)
Upper Archibenthal (700-1,300 m)	Upper Archibenthal (350-800 m)
Lower Archibenthal (1,300-1,650 m)	Lower Archibenthal (800-1,650 m)
Abyssal Zone (2,000-3,000 m)	Upper Abyssal (1,650-2,250 m)
	Mesoabyssal (2,250-3,000 m)

While several appreciable differences exist between the two schemes, they are similar in that both suggest a faunal break at about 1,650 m. Both data sets reflect a basic three zone array, but the subdivisions we have

recognized are distinctive, and do not appear attributable to a sampling artifact--at least in the Archibenthal Zone.

Key Environmental Factors

Findings of the present study indicate that four factors can account for many of the faunal changes observed on both axes of the continental slope. Two of these operate on a massive scale, viz., the huge East Gulf Loop Current, which flows into the Gulf's eastern half via the Yucatan Channel, and the Mississippi River System, whose waters pour into the Gulf a little east of the middle of the northern boundary and then spread westward over the continental shelf. This is not to say that the Gulf east of the Mississippi does not receive river waters, for it does, e.g., the Pearl, Pascagoula, Apalachicola, and Tombigbee rivers, to mention but a few. But their influence is dwarfed by the input of the Mississippi-Atchafalaya complex, which is among a dozen of the great rivers of the world and delivers about one million cubic yards of sediment (Pequegnat, 1983) to the Gulf each day. This huge volume of sediment accounts for prograding of the delta and the continental shelf to the west. These accumulations of sediment may from time to time slump down the slope devastating the bottom fauna, but at the same time delivering volumes of terrigenous sediments and organic matter to lower reaches of the slope. Both the normal sedimentation processes from the river and these slumps explain the relatively larger terrigenous than pelagic component in the sediments on the central and western transects as compared with the eastern transect. Both of these phenomena can contribute to the existing patchy distribution of sand, silts, and clays on the slope.

The Loop Current, which contributes to the waters of the Gulf Stream, enters the Gulf at speeds in excess of four knots. This current and its branches drive the major surface circulation of the Gulf and account for some of its biological features. It brings pelagic larvae and fishes, plant material and heat into the eastern Gulf in particular, but it does influence the western Gulf as well by spinning off anticyclonic eddies that drift slowly westward. The flow path of the Loop may be one important factor that explains why the somewhat isolated western Gulf has a higher degree of benthic endemism than the east.

A third factor that influences the distribution of the slope fauna is the presence of vertical layers in the water column that intersect the seabed at various depths and create changes in the physics and chemistry of the slope and near-bottom waters. These physico-chemical factors may have direct, indirect, or both, effects upon the benthic fauna. For instance, where the oxygen minimum layer bathes the slope, there is a zone of high biological standing stocks. The depressed dissolved oxygen concentration may impact some species but not others. The key point may be that the oxygen levels may not be sufficient to oxidize organic matter as rapidly as elsewhere.

The fourth major factor that appears to shape the distributional patterns of the bottom fauna on the central and western parts of the northern slope is the presence of oil and gas seeps where the concentrations of organic matter and living biomass are high. Various chemoautotrophic bacteria are the primary producers in the seep food web, which is otherwise characterized by the presence of rich biological communities composed of large tube worm thickets and associated fishes, crustaceans, and mollusks. The high biomass of these "biological cases", which are scattered randomly within the matrix of a far less productive seabed, leaves little doubt that food availability is probably the most important single factor accounting for the local distribution of faunal assemblages in a given range of depth on this, as well as other, continental slopes.

Some evidence was provided that the high productivity associated with petroleum seep communities may be exported into the surrounding region. This evidence included enhanced standing stocks of meiofauna and macrofauna outside of but in the general area of such communities, and the correlation between the depth distribution of petroleum seeps and the highest levels of megafaunal biomass (500-800 m). Our speculation that Gulf of Mexico petroleum seep community production may be exported into adjacent environments and result in an enhancement of productivity is not without precedent. A number of published papers (e.g., Spies and Davis, 1979; Davis and Spies, 1980; Spies et al., 1980; Spies and DesMarais, 1983; and Montagna et al., 1987) have demonstrated such an effect on communities associated with shallow-water petroleum seep communities in the Santa Barbara channel.

As presented in Chapters 2, 4, and 5 of Volume II of this report, environmental classification of station groups were remarkably concordant with classification schemes yielded by analysis of biological data. For example, classification of stations sampled on Cruise III were independently prepared using biological data (cluster analysis) and environmental data (Principal Component Analysis, PCA) as noted in Chapters 4 and 5 of Volume II of this report. The results were remarkably concordant. For example, the macrofauna dendrogram for Cruise III yielded five discrete clusters that were arrayed into three depth categories: shallow with a range of 350 to 650 m, a mid-depth cluster with depths ranging from about 880 to 1,465 m, and a deep cluster of depths over 2,000 m. When the environmental parameters of Cruise III were subjected to principal component analysis, an almost similar set of five clusters arrayed into the above three depth categories were obtained. Furthermore, about 40% of the variance among stations was accounted for by sediment hydrocarbon concentrations, clay content and temperature. The hydrocarbon component was clearly derived from terrestrial and in situ petroleum sources. The fact that the clay content sorted out the shallow station from mid-depth and deep stations is explained by the influence of the sediment input of the Mississippi River which is rich in clay (the subject stations were along a transect in the path of the Mississippi's sedimentary plume).

Sediments on the continental slope of the Gulf contain a mixture of terrestrial, petrogenic, and planktonic hydrocarbons. The quantitative importance of these sources varies with location. Accordingly the highest average concentrations of extractable organic matter is found in the western and central Gulf while very low values are found on the eastern transect. In view of this, it is not surprising that principal component analysis of macrofaunal data derived from the eastern transect showed that only 15% of the variance was explained by concentrations of alkanes of which most were of planktonic origin. Here some 45% of the variance was related to percentages of silt and clay, bottom temperature and bottom dissolved oxygen.

CONCLUSIONS

Our study might be viewed as a series of tests designed to evaluate certain hypotheses. Below we list these hypotheses and the basis for their tentative acceptance or rejection.

Hypothesis 1: There is no significant regional variation in the continental slope ecosystem of the Gulf of Mexico.

This hypothesis was rejected. First, the eastern Gulf of Mexico continental slope region appears characterized by a higher biomass of megafauna and a lesser degree of endemism than the western Gulf of Mexico. Circulation differences between the two regions provide a likely explanation.

Second, the western Gulf of Mexico continental slope region is characterized by a prevalence of shallow petroleum seep communities which enhance local productivity. Such may or may not be present in the eastern Gulf but they were not encountered in our study.

Hypothesis 2: There is no significant annual variation in the continental slope ecosystem of the Gulf of Mexico.

This hypothesis was not rejected since little annual variation was observed.

Hypothesis 3: There is no significant seasonal variation in the continental slope ecosystem of the Gulf of Mexico.

This hypothesis was rejected. Spring levels of productivity appeared higher than levels observed during fall, likely in response to increased energy input to the benthic system from increased plankton production and from increased Mississippi River discharge.

Hypothesis 4: There is no significant depth variation in the continental slope ecosystem of the Gulf of Mexico.

This hypothesis was rejected. Standing stocks and faunal assemblages differed markedly by depth. Depths between the shelf break at about 1,650 m were characterized by high biomass as compared to deeper depths.

Hypothesis 5: There is no significant variation within depth zones at least as compared to variation across depth zones.

All other key factors equal, this hypothesis was not rejected. However, environmental factors were not typically equal and significant isobathic variation was observed in response to petroleum levels, other hydrocarbon levels, and sediment grain size.

Hypothesis 6: The continental slope ecosystem of the Gulf of Mexico is less productive than other slope ecosystems.

This hypothesis was not rejected based upon comparisons of meiofaunal and macrofaunal population biomasses.

Hypothesis 7: There are no unusual slope resources associated with the Gulf of Mexico continental slope ecosystem.

This hypothesis was rejected based upon the presence of petroleum seep communities in the western Gulf. Such communities may ultimately prove to be characteristic of slope ecosystems as opposed to unusual occurrences.

SAMPLING DEFICIENCIES AND RECOMMENDATIONS

Within the scope of what was attempted in this program, the greatest deficiencies in the continental slope study were mainly related to sampling adequacy and the fact that the voluminous lebensspuren data obtained were of little interpretative value.

With regard to sampling, a much higher degree of replication of box core samples would be required if quantitative differences with a reasonable level of accuracy and precision are needed. Likewise, if trawl tows are to be incorporated into a deep-sea program, the nets should be larger than 9-m wide, towed for more than one to two hours bottom time, and be replicated.

Benthic photography and the use of submersibles provided the best means of studying special features such as seep communities. The features cannot be adequately studied remotely from the surface using conventional sampling gears (box cores, trawls, etc.). For survey work to determine presence or absence of seep communities in an area, benthic still photography provides an adequate approach. However, if information about seep community dynamics and processes is needed, the use of manned or unmanned submersibles is dictated.

The level of effort required for sample and data analysis was greatly underestimated--on the order of a third too low. This was mainly due to the taxonomic complexity of the biota. The plans for any future programs should bear this in mind if budgets and schedules are to be met.

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