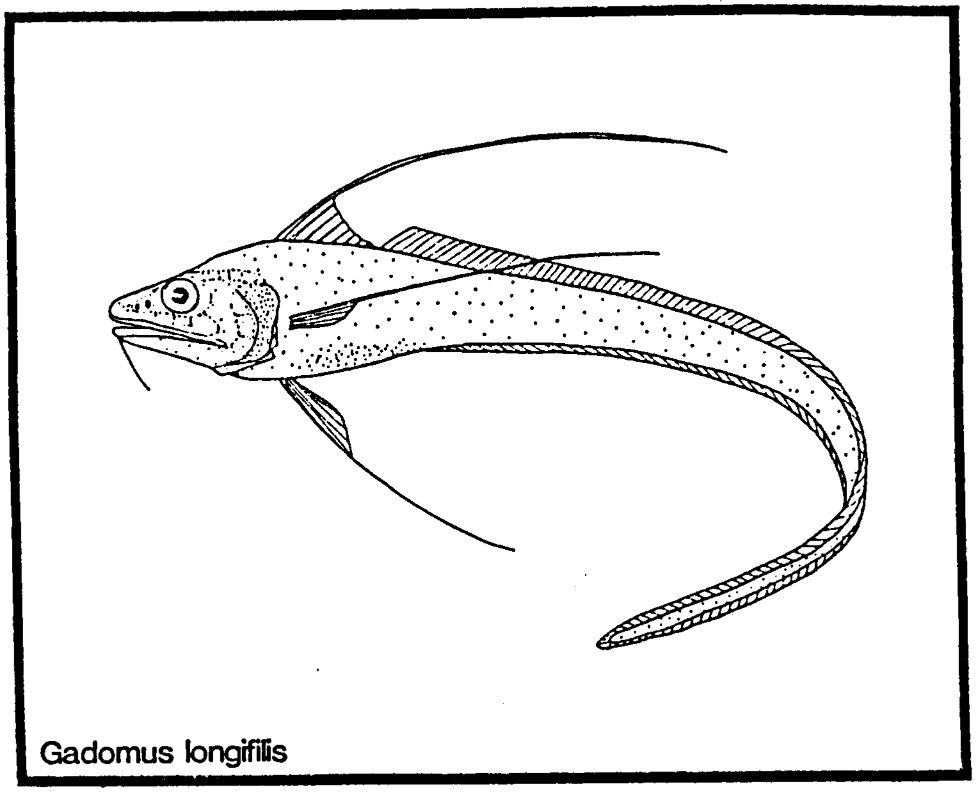
OCS Study
MMS 88-0053

Northern Gulf of Mexico Continental Slope Study Final Report Year 4

Volume II: Synthesis Report



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U.S. Department of the Interior
Minerals Management Service
Gulf of Mexico OCS Region

OCS Study
MMS 88-0053

Northern Gulf of Mexico Continental Slope Study Final Report
Year 4

Volume II: Synthesis Report

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 encouragment 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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CHAPTER 1. THE GULF OF MEXICO CONTINENTAL SLOPE STUDY--OBJECTIVES, BACKGROUND AND APPROACH

B.J. Gallaway

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 chapter we provide an environmental and biological background as a context for the study findings, and summarize the overall methods and approaches used to meet program objectives. In subsequent chapters we will present our findings describing the slope environment and habitats, and the meiofaunal, the macroinfaunal, and the megafaunal (Chapters 2, 3,4, and 5) communities that occur over soft bottom environments. Chapters 6 and 7 are related chapters, the first presenting an overview of the information concerning chemosynthetic communities on the continental slope of the northwestern Gulf of Mexico and the second deals with project specific studies at one of these sites known as Bush Hill. Chapter 8 presents a conceptual model of the slope ecosystem, noting deficiencies in our knowledge of the system and the types of studies that might be considered in future efforts to improve our understanding.

ENVIRONMENTAL SETTING AND BACKGROUND

General Physiography

The Gulf of Mexico covers an area of more than 1.5 million square miles, has a maximum water depth of about 12,140 feet, and consists broadly of the Continental Margin (composed of the Continental Shelf, Slope, and Rise) and the abyssal plain. The width of the Continental Shelf varies from about 174 miles off southern Florida to a minimum of 6 miles at the Mississippi Delta.

Physiographically, the northern Gulf of Mexico is divided into nine distinct provinces. Figure 1-1 shows these provinces, in the context of the three MMS lease planning areas. They are roughly from east to west, the West Florida Shelf, the West Florida Slope and Scarp, the DeSoto Canyon, the Mississippi Fan, the Texas-Louisiana Shelf, and the Texas-Louisiana Slope (Bergantino, 1971).

The continental slope is a region of relatively steeply sloping seafloor that extends from the shelf edge to the upper limit of the continental rise, or locally to the abyssal plain (Bergantino, 1971). It

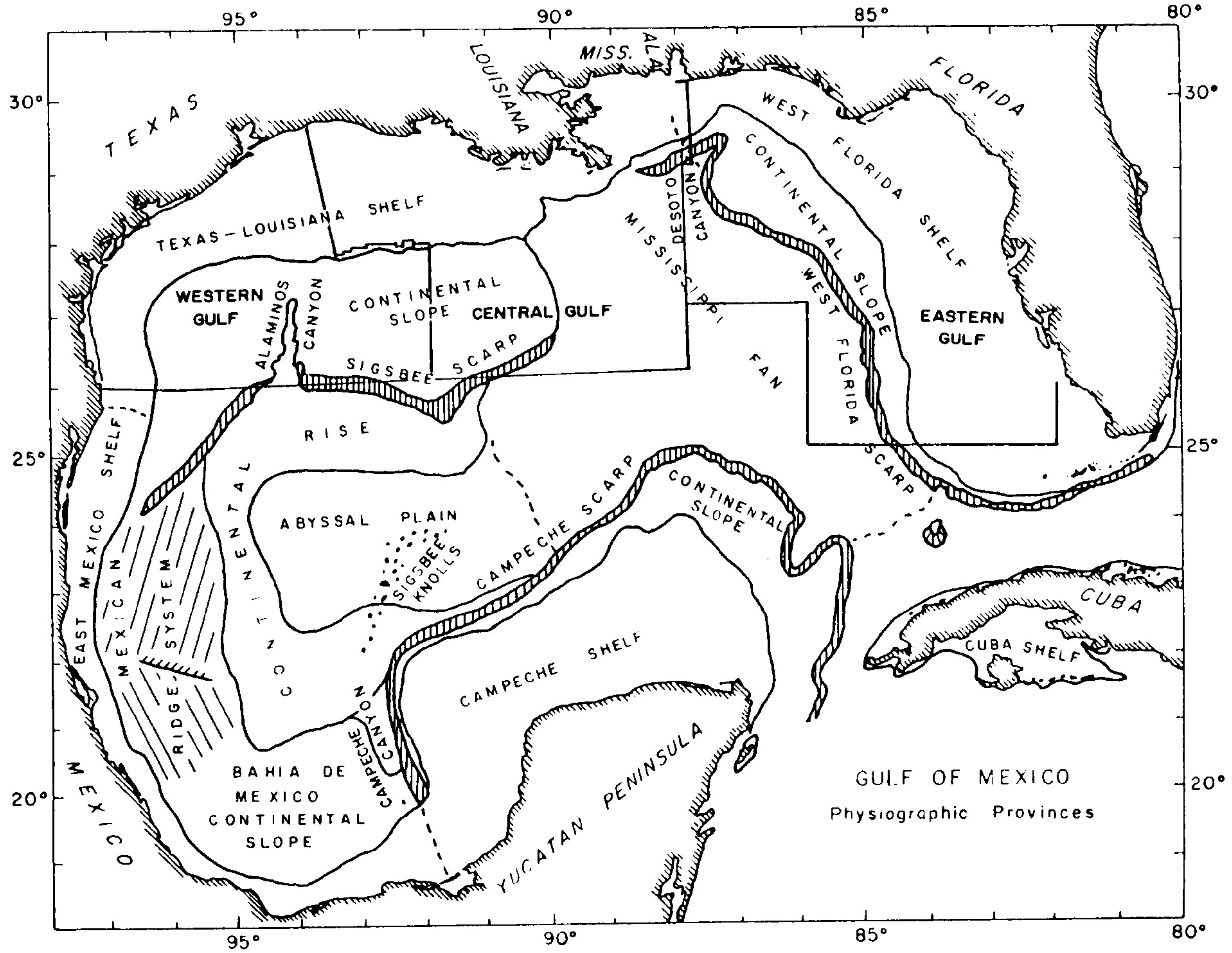


Figure 1-1. Physiographic provinces of the Gulf of Mexico, and MMS planning areas of the northern part.

contains a variety of submarine landforms and generally possesses steep, irregular topography but can sometimes have rather large, smooth areas. In the northern Gulf, the continental slope is believed to be the southern and growing edge of the Gulf Coast geosyncline (Uchupi, 1975), the primary structural element within that region (Wilhelm and Ewing, 1972; Antoine et al., 1974).

Depths of the continental slope range about 150 m at the shelf edge to nearly 3,000 m where it meets the abyssal plain. West of the Mississippi Fan, the slope has a hummocky topography of various-sized hills and depressions underlaid by structures such as diapirs (salt and shale), slides, slumps, and growth faults. The Mississippi Fan dominates the topography of the central Gulf slope, covering an estimated 160,000 to 300,000 km^2. The Mississippi Fan is bounded on the east by the DeSoto Canyon and beyond is the steep Florida escarpment and slope (Pequegnat, 1983).

The Gulf is often described as a Mediterranean-type sea, but it is much smaller (1.6 vs 2.8 million km^2), shallower (3,850 vs 5,090 m), and has a much more typical deep-sea fauna than the Mediterranean Sea. In fact, the Mediteranean does not have an abyssal habitat in spite of its depth. The temperatures of its deepest waters range between 12.7 and 14.5°C at salinities between 38.4 and 39 ppt, whereas the abyssal bottom waters in the Gulf reach 4.35°C and a salinity of 34.97 ppt. Moreover, nutrient levels in the deep waters and sediments of the Mediterranean are very low, resulting in a very impoverished fauna (Riedl, 1983). The nutrient depletion results from the fact that the only natural source of ocean water of the Mediterranean comes from the Atlantic over the Gibraltar Sill which has a depth of 300 m or less (Fairbridge, 1966). Because these shallow waters have already supported phytoplankton growth in the Atlantic, they are depleted of much of their nitrate, phosphate, and silicate. Yucatan Strait is the Gulf's principal connection with the Atlantic (via the Caribbean Sea) but the sill here has a depth of 1,500 to 1,900 m (McLellan and Nowlin, 1963), which does not block the input of nutrients but does prevent the input of the Caribbean's 2°C bottom waters.

Geological History

During a period approximately 220 to 160 million years (my) ago (the Triassic and Jurassic Periods), crustal thinning and eventual rifting took place in the area of the present Gulf of Mexico, initiating the transformation of a continental region into an oceanic one. New oceanic plates formed in the central area. However, the ridge system failed, and instead of oceanic pelagic sediments accumulating in the flanking basins, uplift followed and halite-rich evaporites were formed. One of these formations, the Louann and equivalent salts of Upper Jurassic Age (160 my), is disposed in a northwest-southeast trending belt, northwest of the ridge system, beneath the present and earlier sites of the continental slope of Texas and Louisiana. These salt deposits, now buried by thicknesses of up to 18,000 m of tertiary sediments (younger than 60 my), have flowed because of their plastic nature, forming stocks, domes, ridges and tongues in the sediments above. Such features are of major importance in determining the topography of the continental slope.

The history of the present continental shelf-slope system in the U.S. Gulf of Mexico can be traced to a specific event, although one which took place over a substantial span of geological time. This was the Laramide Orogeny, 60 to 40 my ago, involving the collision of Pacific and American crustal plates and the formation of the Cordilleran mountain chains. Prior to this event, during the period between 160 and 60 my ago, the Gulf of Mexico again became a deepwater basin accumulating principally pelagic sediments. The basin was rimmed by shallow waters where limestones were deposited. The margins were reefal, made up of algal, coral and rudistid banks. These carbonate shelf margins were exceptionally linear, following a line 80 to 100 miles inward of the present Texas-Louisiana coastline, then turning southeast, ultimately determining the position of the present-day Florida Escarpment. A conceptual model for the cretaceous shelf margins is found today in the Bahama Banks, where conditions are little altered from those of Cretaceous times. The Cretaceous carbonate shelf margin did not possess a continental slope analogous to the present one. Waters deepened precipitously at the reef edge, dropping to oceanic depths at slopes of up to 20°.

The Laramide Orogeny, resulting in the uplift and immediate erosion of the Cordillera of the western United States, initiated a new epoch in the evolution of the Gulf. Immense volumes of river-borne sediments: sand, silt, and clay, were deposited at the western Gulf margins. These sediments, first laid down during the Eocene (50 my ago) are deltaic, whether they are terrestrial (distributary channel, levee, or lagoonal), neritic (beach, barrier/distributary mouth bar, or deltaic forest beds) or slope-bathyal (bottommost mudstones, or turbidite sands and silts). Strata of these types built the past and present continental shelves and slopes. They were deposited on, across, and in front of the cretaceous carbonate banks, so that the latter, for example the Lower Cretaceous Edwards and Sligo formations of South Texas, now occur at subsurface depths of some 3,000 m. The shelves have continually prograded seawards, so that the present shelf break is approximately 150 miles seaward of the Cretaceous shelf edge in south Texas.

The positions of maximum shelf advance have changed progressively during post-Cretaceous time. Broad Eocene and Oligocene shelves were constructed in south Texas, while development in the Louisiana area did not take place until Miocene to Recent times. The shifting depocenters represent the locations of the mouths of the principal contemporary rivers, latterly the Mississippi. Each depocenter accumulated 3,000 to 6,000 m of sediments.

The history of sedimentation at any given point on the shelves, past or present, is one of progressive reduction of water depth as sediment accumulated. The record in a well drilled to 7,000 m on the inner shelf off the western Louisiana coast was described by Strude (1984). Waters shallowed from 900 m in the Late Miocene to some 90 m in the Pleistocene. The same sequence of events has taken place at all points in front of the carbonate shelf edge described above. As a result, sand-rich, shallow water sediments occur above mixed shale-sand sequences which were deposited in waters of intermediate depths (90 to >300 m), and these lie above deep water mudstones. Beneath all, and intruding the Tertiary sediments, are the mobile salt bodies which significantly modify the topography of the slope.

The location of past and present depocenters and present-day rates of sedimentation, are responsible for the present topographic details of the continental slope, whether smooth, hummocky, incised by canyons or channels, marked by craters or escarpments, or other topographic forms. This comes about because of the linkage between type and amount of sediment deposited and the tectonic stability of a slope region. Sediments deposited rapidly on a sloping surface are prone to slump. This may occur on a small scale or on the extraordinary scale of the "growth" faults of the Gulf of Mexico shelf and slope. In the latter, the height of the fault surface, with a steep dip, may exceed 3,000 m, before the slope of the surface diminishes to near zero, becoming bedding-parallel.

Because the circulation patterns over geologic time have carried Mississippi River discharges mostly to the west (Pequegnat, 1983; Lynch, 1954; Lynch and Rudolph, 1984), the Texas and Louisiana shelf and slope as well as the Mississippi Fan have had rapid sedimentation rates and a massive accumulation of silts, sands, and clays. Scattered throughout these central and western regions are thousands of small diparic structures of Middle Jurassic salt that have influenced the stratigraphy (and consequently the petroleum potential) of the region (Lynch and Rudolph, 1984).

The Eastern Gulf of Mexico Continental Margin (West Florida Shelf) is dominated by a thick accumulation of southeasterly trending carbonate rocks and evaporite deposits of the Mesozoic and Cenozoic eras. This area has been subsiding since Cretaceous time (Pequegnat, 1983) but has not been influenced by the massive terrigenous regime to the extent that other parts of the Gulf have. Hence, the hydrocarbon potential of the Eastern Gulf is not believed to be great (Lynch and Rudolph, 1984).

One of the principal features at slope depths of the northeastern Gulf is DeSoto Canyon east of the Mississippi Fan. There are many salt diapirs in the canyon but they scarcely reach the sediment surface. Antoine (1972) found it difficult to account for the continuing presence of the canyon with the encroachment onto its western edge of prograding sediments from the Mississippi. It seems likely that the canyon owes its origin and its persistence to the action of oceanic currents (Pequegnat, 1983).

In the northwestern Gulf is a complex submarine canyon-fan valley located about 200 km south of Galveston, Texas. It begins at the 80-m isobath and terminates after receiving other systems in the abyssal plain.

Bouma (1972) believes this complex (Alaminos Canyon) was very likely connected with the Rio Grande and Brazos-Trinity Rivers (Pequegnat, 1983).

The sediments of the Mississippi Fan are detrital and come from the Mississippi Delta (Bouma, 1972). On the fan and abyssal plain turbidity currents were important agents of transport and deposition. Also, it is now known that bottom currents strong enough to scour the bottom and winnow out sands exist on the fan and extend up into DeSoto Canyon. In areas where sediment is actively accumulating from Mississippi River deposition, the bottom becomes structurally unstable, slumping is common, and it may occur on the upper slope in the western Gulf as a result of the seaward prograding of the shelf break as the sediment overload causes the deep salt beds to flow under steady pressure (Pequegnat, 1983).

Sediments

As noted above the major source of sediment for the northern Gulf of Mexico is Mississippi River discharge. Lesser amounts of weathered products are supplied to the northwestern shelf by the Rio Grande and the many rivers and streams positioned between these two. The northeastern sector receives little sedimentation.

During transport to and within the Gulf basin, sedimentary materials were mixed and sorted by a variety of agents before deposition. Sediments are deposited on the inner continental shelf and Phleger (1967) speculates that some detritus from land is also being deposited on the continental slope and in the basin. Sediment being supplied to the Gulf may not reach the outer shelf, or if it does, it may be deposited seaward of the shelf (Pequegnat, 1983). Sea level fluctuations strongly determine the amount and type of sediment being transported to the continental slope (Bouma et al., 1980). During the period of lowest sea-level stand, sediments from all rivers were carried directly across the exposed continental shelf where currents and longshore drift dispersed them throughout the present deeper portions of the Gulf. Near the break, these sands collected in submarine canyons; however, further transport by sliding, gravity flow, and turbidity current mechanisms resulted in ultimate deposition on the lower slope or deeper water submarine fans.

Pequegnat (1983) constructed a Gulf of Mexico sediment distribution map based heavily on the work of Grady (1970) (Fig. 1-2). This map indicated fine-grained sediments to dominate in the central and western portions of the northern Gulf continental slope, but coarser-grained sediments to intrude in the eastern portion. This trend agrees with what is known about sediment sources for these regions.

Hydrocarbon Seepage in the Gulf of Mexico

Petroleum hydrocarbons can enter the environment by natural processes (seepage) as well as by man-related activities. Marine and terrestrial organisms synthesize normal alkanes, branched alkanes, and sometimes small quantities of specific aromatic compounds. Biowaxes in recent sediments with a predominance of odd number, normal carbon chain lengths from 23 to 33 have a terrestrial biogenic plant origin. Petroleum products represent the second major source of hydrocarbons to the environment. Hydrocarbons generated from thermogenic processes can be distinguished from <u>in situ</u>, biologically produced hydrocarbons by their molecular composition (Farrington et al., 1973; Wakeham and Carpenter, 1976; Farrington and Tripp, 1977; Meyers et al., 1984). Petroleum-related hydrocarbons are a complex mixture of alkanes, cycloalkanes, branched alkanes, aromatic compounds, polar compounds, and large macromolecular structures (i.e., Wakeham and Farrington, 1980; NAS, 1975). This is in contrast to hydrocarbons derived from biological sources which are relatively simple mixtures dominated by a few specific hydrocarbons (Giger et al., 1980). Unaltered petroleum hydrocarbons generally contain a complete suite of normal alkanes with little or no carbon-number preference (Wakeham and Carpenter, 1976; Farrington and Tripp, 1977). Petroleum hydrocarbons can also contain a gas chromatographically unresolved complex mixture noted as UCM (Farrington et al., 1973; Farrington and Tripp, 1977). Two- to five-ring aromatic compounds are assumed to principally originate from petroleum.

As other regions of the world oceans, the major inputs of hydrocarbons (HMWHC, C_{15}+) to the Gulf of Mexico include biological production, natural seepage, offshore petroleum production and drilling operations, transportation activities, coastal and riverine additions, and

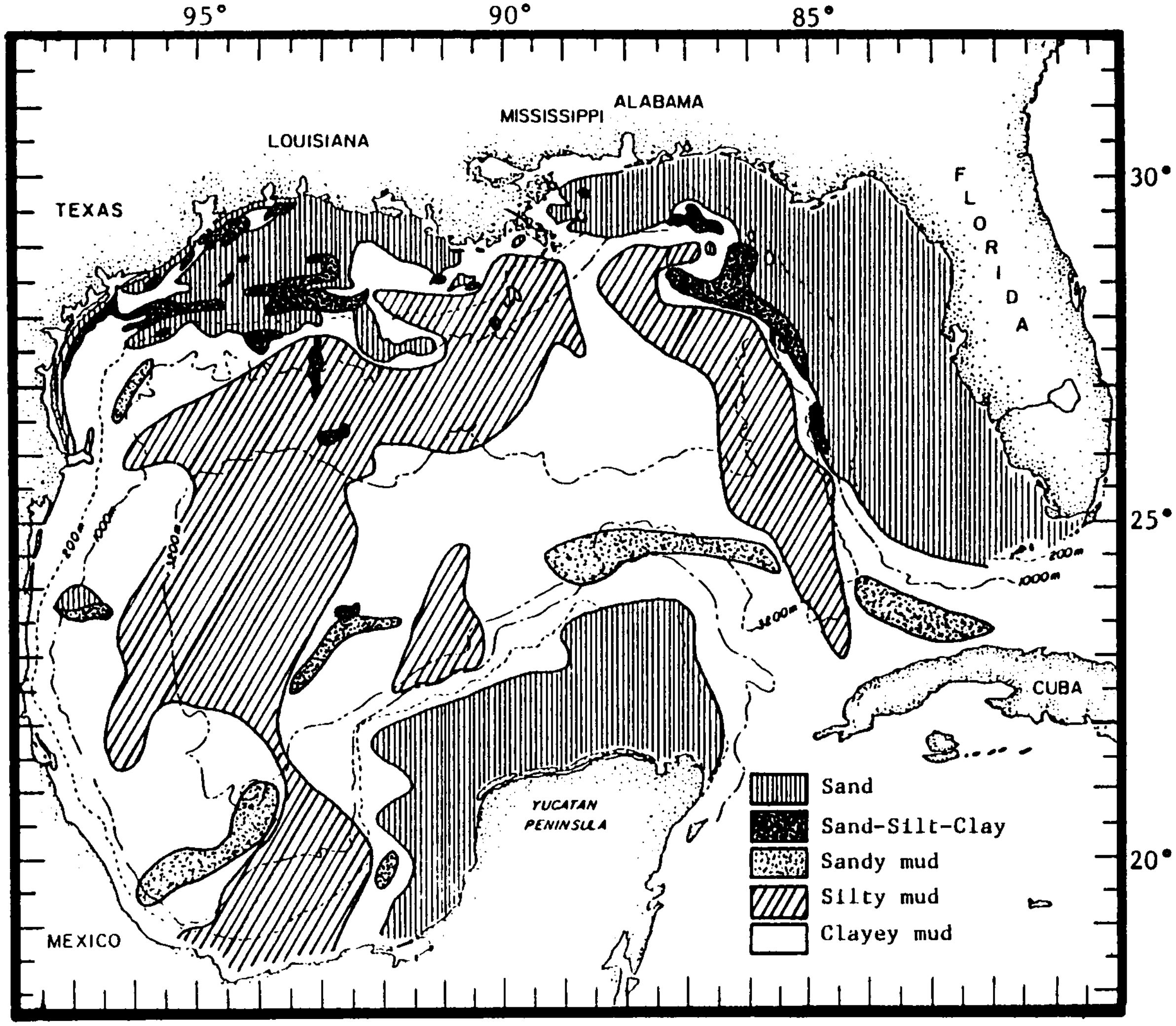


Figure 1-2. Predominant sediment types in the Gulf of Mexico (from Pequegnat, 1983).

atmospheric exchange or fallout. Prior to the industrial revolution and the extensive usage of petroleum and related products both onshore and offshore petroleum seeps were known around the world (Geyer and Giammona, 1980). In fact most of the major oil-producing regions of the world were originally found based on the presence of surface oil and gas seeps (Wilson et al., 1973). The magnitude, occurrence, and significance of natural seepage to the marine environment is difficult to assess. One such assessment estimates that 2 to 30% of the hydrocarbons in the environment may be the result of natural seepage with a best estimate of ~8% (NAS, 1985). Gas seepage has been widely documented in the ocean (Dunlap et al., 1960; Bernard et al., 1976; Sackett, 1977) but reports of liquid hydrocarbon seepage are few (Wilson et al., 1973; Geyer, 1980; Jeffrey, 1980). Recent discoveries in the Gulf of Mexico suggest that natural, liquid hydrocarbon seepage occurs frequently on the Gulf of Mexico continental slope (Anderson et al., 1983; Brooks et al., 1984; 1985; 1986a; b). In these areas, the sediment can be as much as 15% by weight petroleum. These reports suggest that chronic, massive oil seepage is a process that occurs on the Texas-Louisiana Gulf of Mexico slope and may constitute a significant input of hydrocarbons to this region of the deep sea.

Seepage into shallow sediments on the Gulf of Mexico slope appears to be predominantly controlled by fault systems created by salt tectonics that provide a nearly direct, vertical conduit (Martin and Case, 1975). Based on extensive chemical analyses, Kennicutt et al. (1988) concludes that oil and gas reservoired in at 1,800 to 2,700 m in the subsurface has migrated upwards along faults to near surface sediments. The amount of oil in the sediment is sufficient for globules to form and leave the sediment, rise to the seawater surface and form slicks and tar balls. Gas concentrations in the sediments are sufficiently high for gas hydrates to form. This and other studies suggest that the natural seepage of liquid and gaseous hydrocarbons is a common phenomena in oil generating basins throughout the world and represent a significant natural input of hydrocarbons to the worlds's ocean.

Hydrography

The Gulf of Mexico is warm-temperate in its northern parts. The quality of Gulf waters depends partly on their source--inflow through the nearly 2,000-m depths of Yucatan Strait to the south. Hydrographic measurements taken at a station in the west-central Gulf (Fig. 1-3) illustrate the five vertically-layered water masses that are generally recognized in the Gulf. These masses are as follows (Pequegnat, 1983):

(1) Surface Mixed Layer - This is the upper isothermal layer, variable in thickness but averaging about 75 m. Temperature and salinity are highly dependent on interactions with the overlying atmosphere. Temperature depends on the heat budget and salinity distribution depends on evaporation minus precipitation, runoff from land, and the horizontal advection of currents.

(2) Subtropical Underwater - This layer is characterized by an intermediate maximum of salinity in 50-200 m depths. This water mass is present as well throughout the Caribbean. Its source in the Caribbean and Gulf is probably from the tropical North Atlantic at 20-25^{o} N, 30-50^{o} W.

(3) Oxygen Minimum Layer - This layer has minimum oxygen values within depths of approximatly 300-600 m. It is not associated with salinity or temperature extremes, and is clearly continuous with the oxygen minimum layer of the Caribbean. In the eastern Gulf a secondary oxygen minimum layer is present throughout the water bounded by the Loop Current (see following section), but is almost completely suppressed in the western Gulf.

(4) Subantarctic Intermediate Water - In the Gulf this layer has a salinity minimum of 34.86-34.89 ppt at depths between 550-900 m. This water mass has its origin at the Antarctic Convergence where cold, low salinity water sinks

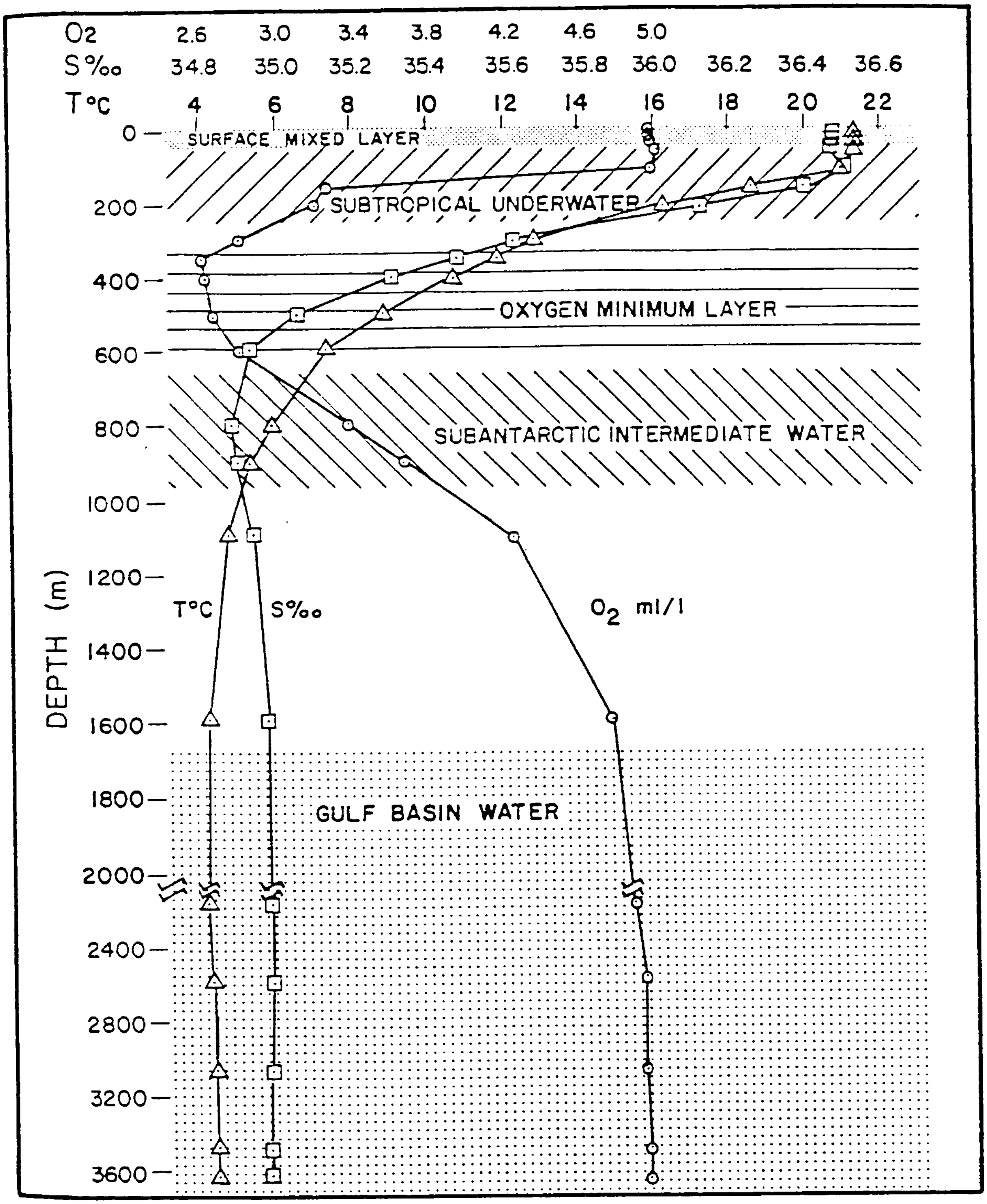


Figure 1-3. Physical characteristics and water mass designation from a west-central Gulf hydrographic station (25°09'N, 94°11'W; 15 March 1968). Deepest sample taken four meters above the bottom. (From Pequegnat, 1983).

and spreads to the north. The core of minimum salinity enters the Caribbean with salinities of slightly less than 34.7 ppt, but mixing that accompanies horizontal spreading raises the salinity to approximately 34.8 ppt by the time it reaches the Yucatan Strait and to 34.88-34.89 ppt in the western Gulf. The percentage composition of Subantarctic water in the core is less than 5% at the Yucatan Strait and only some 1-2% in the western Gulf.

(5) Gulf Basin Water - Gulf Basin Water is defined as waters below 1,650-1,900 m (estimate of Yucatan sill depth). At approximately 2,000 m the mean temperature and salinity are 4.23°C and 34.97 ppt respectively. Below 2,000 m in situ temperature increases approximately 0.1°C per 1,000 m (adiabatic warming) and salinity increases approximately 0.002 ppt per 1,000 m.

Temperature and salinity measurements made near the bottom of the northern Gulf at 45 stations (Fig. 1-4) show the same general changes with depth as found at a single station (Fig. 1-3). Most of these stations were on the continental slope (Pequegnat, 1983), suggesting that slope bottom temperatures and salinities follow the same trend with depth as would be predicted by the "model" of water mass layering described above.

Circulation

Pequegnat et al. (1976) and Pequegnat (1983) summarized the state of knowledge about circulation in the Gulf of Mexico. In this section we draw heavily on these synopsis.

Two major circulatory provinces, East and West, exist in upper water-layers in the Gulf. Water enters via the Yucatan Channel and leaves via the Florida Straits (Fig. 1-5). The dominant flow pattern in the east is the Loop Current, which flows in a clockwise direction; that in the west appears to be a series of gyres of alternating rotation flow (clockwise, counterclockwise). Currents in the west are thought to be influenced predominantly by wind and those in the east by the Loop Current and

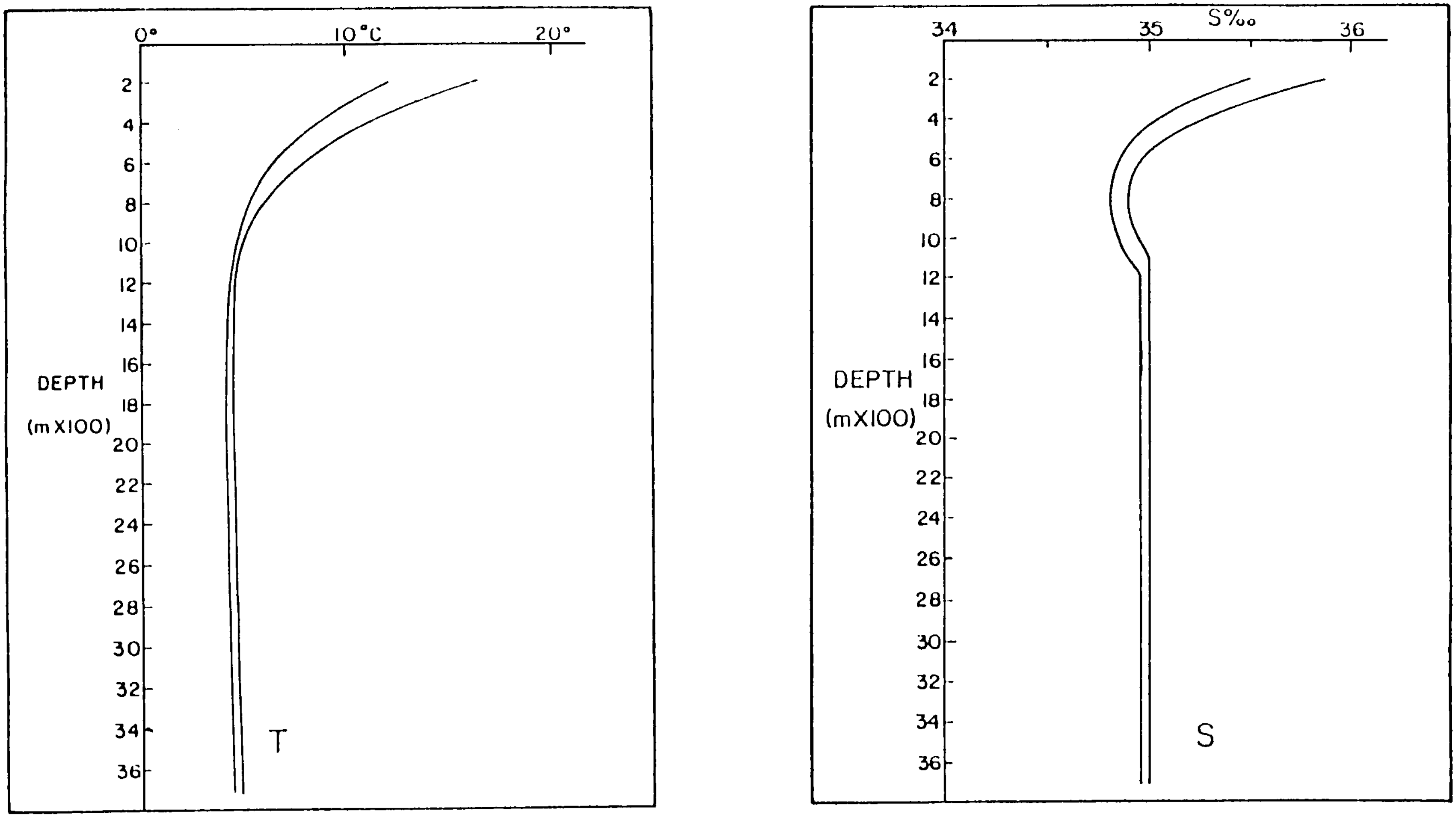


Figure 1-4. Isobathic temperature and salinity "envelopes" of composite data from 45 near-bottom sampling locations in the northern Gulf of Mexico (from Pequegnat, 1983).

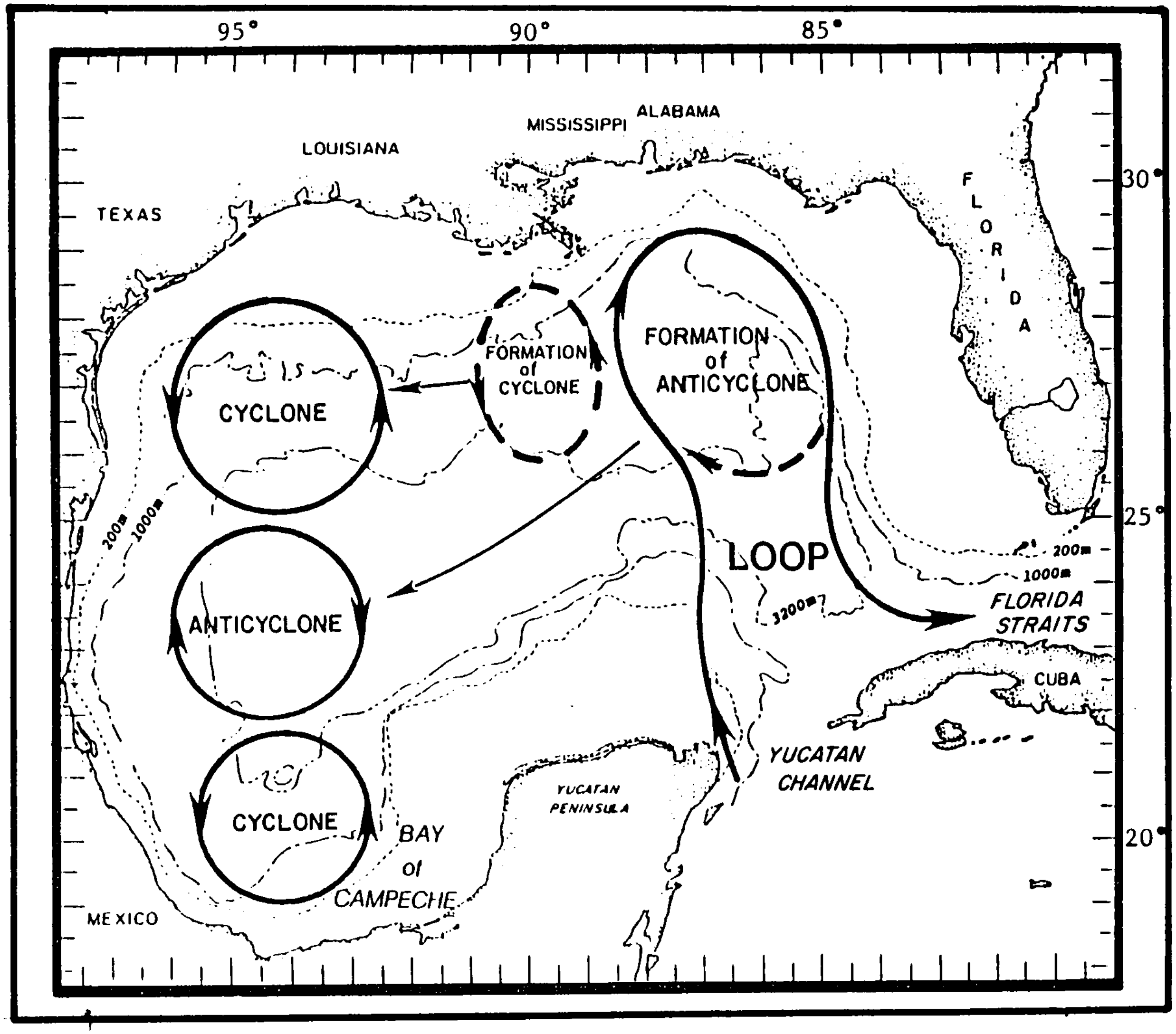


Figure 1-5. Diagrammatic representation of the large scale circulation processes of the Gulf of Mexico (from Pequegnat, 1983).

density differences (Beckert and Brashier, 1981). The positions and strengths of gyres in both the east and west seems highly variable, and may depart appreciably from the pattern shown in Figure 1-5 (Pequegnat, 1983).

Two features of variability in upper-layer flow patterns may be important to the slope environment. First, only rarely does the Loop Current seem to penetrate as far north as illustrated by Figure 1-5. Second, the flow along the western flank of the DeSoto Canyon (east of the Mississippi Fan) is frequently to the north (Molinari et al., 1979). Variations in currents in the western portions of the Gulf are relatively unexplored compared with those of the eastern parts (Pequegnat, 1983).

Little is known about near-bottom currents in the Gulf. Several studies have documented that near-bottom currents exist, sometimes at speeds of up to nearly 30 cm/s, but normally perhaps at a third or less of this speed (Pequegnat, 1983).

Biology

The northern Gulf of Mexico continental slope as habitat for biota is a transitional environment, influenced by both continental shelf and abyssal Gulf processes. The lower boundary of the euphotic zone is about 50-60 m, thus the entire slope is below the level of photosynthetic activity of phytoplankton (Beckert and Brashier, 1981), though twilight conditions, ever darker with depth, persist down to about 1,000-m depths. This zone, between 60 and 1,000 m, has been called the disphotic zone (e.g., Carney et al., 1983). As noted above, temperatures decline from the surface to around 4°C at 1,000 m and remain uniformly cold thereafter. Dissolved oxygen content peaks at the surface and again below 1,500 m; with lower levels occurring from about 300-800 m. Hydrostatic presence increases nearly linearly with depth. The general nature of Gulf circulation probably influences the abundance and richness of endemic biota. Based upon circulation, the eastern Gulf might represent a shallow extension of the Atlantic/Caribbean deep sea, whereas the western Gulf might be analogous to the European Mediterranean Sea; i.e., having a single inlet/outlet but receiving discharge from world class rivers.

Pequegnat (1983) found the faunal assemblages of the western Gulf to have a high degree of endemism, whereas little endemism was noted for assemblages in the eastern Gulf. These apparent differences were related to the presence and frequency of gyres, the loop current, nutrient and detrital (terrestrial vegetation) inputs from rivers, and depth and substrate characteristics, all of which vary markedly between the eastern and western Gulf. Based upon the historical data, however, the fauna of the continental slope of the Gulf of Mexico was similar to that of the U.S. Atlantic continental slope.

Overall, the continental slope fauna of the Gulf of Mexico would be expected to be highly similar to that of other slope systems. Deep sea faunas from depths below 4,000 m tend to be distinctly different among geographic areas and comprise the basis for several zoogeographic classification schemes for the deep oceans (e.g., see Menzies et al., 1973). In contrast, the distribution of faunas along continental margins beyond the shelf is characterized by a high proportion of species that are found on both sides of an ocean and often in all oceans. Menzies et al. (1973) provide an overview of the evidence leading them to conclude that many, if not most, species in the archibenthal zone of transition either are the same from place to place, or are very close relatives to one another. On this basis, the fauna of the continental slope of the Gulf of Mexico would be expected to be highly similar to that of other slope systems. A major objective of this program was to either refute or confirm this hypothesis.

Typically, biomass and production of the deep sea decrease exponentially with depth when levels are compared along a depth gradient of a single continental margin (Menzies et al., 1973). As zooplankton biomass also decreases in a similar fashion, it has been suggested that the deep-sea benthos and zooplankton have the same food source, namely surface derived organic matter (Rowe et al., 1974). The greater the utilization of the organic matter as it sinks to the bottom, the less is available to the benthos.

The simple semilogarithmic linear relationship between biomass and depth is an oversimplification since many exceptions occur. However, most exceptions result from topographic anomalies that trap detrital materials. These include trenches (Belyaev, 1966; Vinogradova et al., 1978), submarine canyons (Rowe et al., 1982; Griggs et al., 1969) and physiographic boundaries where the bottom slope changes sharply (Carey, 1981).

Rowe and Menzel (1971) and Rowe et al. (1974) have provided evidence that biomass and production in the continental slope and deep basin of the Gulf of Mexico were unexpectedly low. Two potential explanations were provided, one suggesting that the observation might be a function of low surface production or an efficient utilization of energy by the pelagic biota. The other idea was that since the deep Gulf basin habitat had a higher temperature (4°C) than other areas of comparable depths (because of the shallow sill depths of the Gulf) this feature could increase the rate at which organic matter is turned over, thereby resulting in lower standing stocks. A major objective of this program was to document biomass levels on the Gulf of Mexico continental slope and compare these levels to other slope systems.

Carbon and particle fluxes in the deep sea region of the continental slope of the Gulf are poorly understood. Pequegnat (1983) reported that unless assimilation of bacteria and meiofauna are unusually high, there are five sources of carbon to the deep slope: dissolved organic matter, deadfalls of carcasses, fallout of shallow marine and terrestrial macrophytes, transport of organic matter by slumps and turbidity flows, and by active foraging into upper water layers by demersal fish and large benthic crustaceans who gather this material and return to the bottom. There is no evidence that dissolved organic matter is used as an energy source by the bacteria and meiofauna. More recently, as will be outlined in Chapter 6, petroleum seeps have now been documented to be a significant source of energy to the Gulf of Mexico continental slope ecosystem.

Two interpretations of faunal zonation with depth on continental slopes have been proposed. The coarser-scaled zonation pattern proposed (Carney et al., 1983) has a "distinct shelf" fauna down to about 1,000 m, a "distinct slope" fauna from 2,000-3,000 m, and a zone in between with both shelf and slope taxa. The finer-scaled scheme (Pequegnat, 1983), based largely on abundances of megafauna and macroepifauna, has five major zones as follows (see Fig. 1-6 for diagrammatic representation):

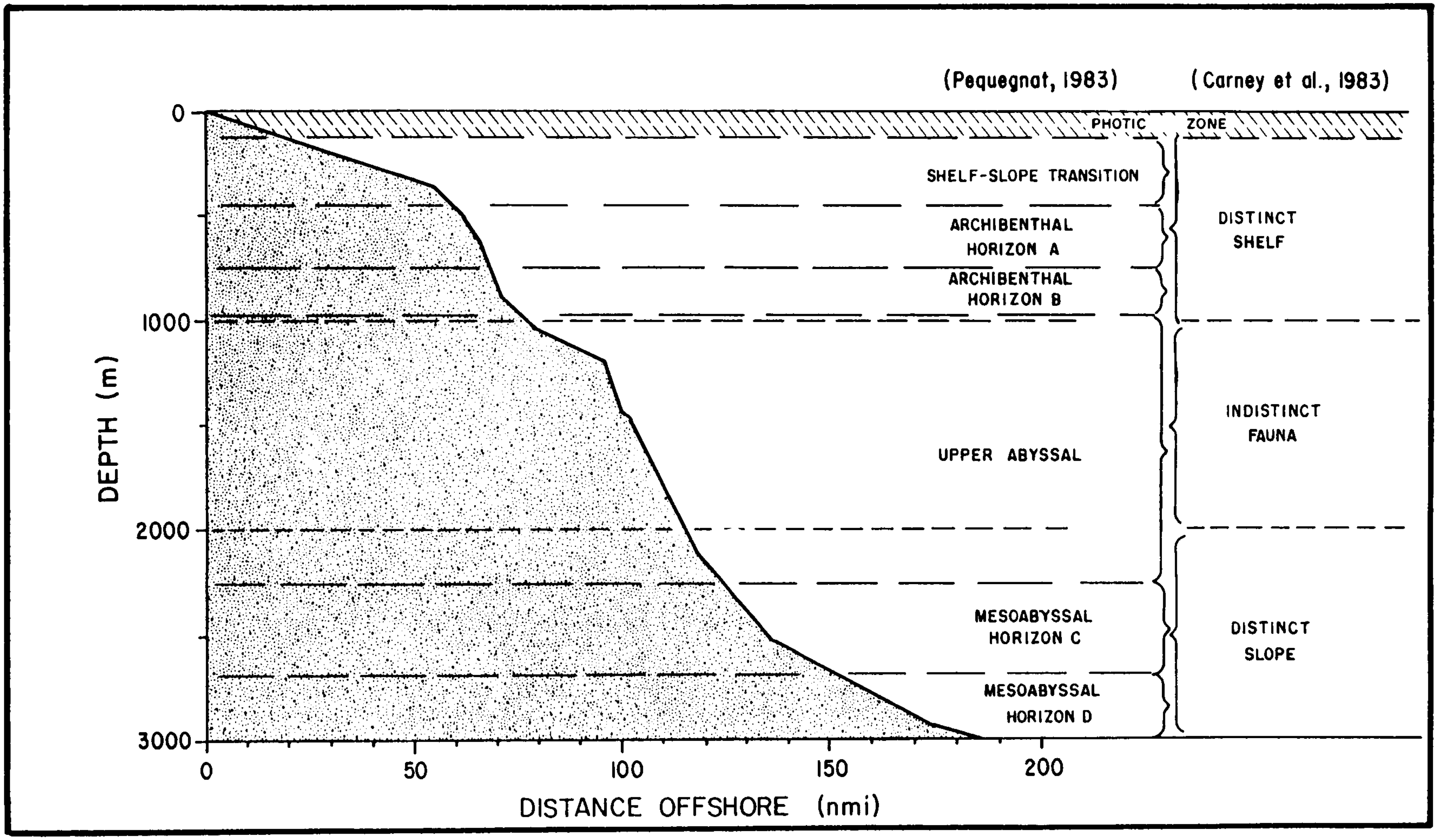


Figure 1-6. Two contrasting views of the expected faunal changes with depth that might be observed on the continental slope of the northern Gulf of Mexico.

1. Shelf/Slope Transition Zone
   - depth range 150-450 m; median depth 300 m
   - demersal fish predominate, as do predatory asteroids and brachyurans
   - very productive with approximately 90 species of demersal fish
   - 66 spp. of demersal fish reach maximum populations in this zone
   - gastropods and polychaetes also prevalent
   - *Brissopsis* urchins extremely aundant
   - very few sea cucumbers

2. Archibenthal Zone - Horizon A
   - depth range 475-750 m; median depth 612 m
   - demersal fish abundant but represented by only 79 species
   - demersal fish species reaching maximum populations in this zone reduced to 45
   - asteroids abundant
   - sea cucumbers doubled in number
   - caridian shrimps also doubled in number
   - *Brissopsis* urchins are almost absent being replaced by *Phormosa placenta* and *Plesiodiadema antillarum*

3. Archibenthal Zone - Horizon B
   - depth range 775-950 m; median depth 862 m
   - demersal fish numbers reduced slightly but numbers reaching maximum populations less than 1/2 of those in Horizon A
   - drastic reduction in number of Brachyuran crabs
   - gastropods and polychaetes still well represented

4. Upper Abyssal Zone
   - depth zone 975-2,250 m; median depth of 1,612 m
   - number of demersal fish reduced to half of that in Archibenthal zone

- number of demersal fish attaining maximum populations is over two times that of Horizon B
- major increase in number of species of large sea cucumbers
- number of brachyurans continue to drop (four as compared to 35 in Shelf/Slope Transition Zone)
- gastropod and sponge species reach a peak
- polychaetes still abundant

5. <u>Mesoabyssal - Horizon C</u>
    - depth range 2,275-2,700 m, median depth 2,488 m
    - very sharp break in fauna of Upper Abyssal and Horizon C of Mesoabyssal
    - number of demersal fish with maximum population drops from 49 to 3; with only two more species in Horizon D (next depth zone)
    - similar reduction in maximum populations noted for other species as well

A major objective of the program was to evaluate faunal zonation patterns, not only for the megafauna but also for the macrofauna.

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, as noted earlier, 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. This focus strongly influenced the spatial distribution of sampling stations.

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. 1-7). 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. 1-7A). 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. 1-7B). 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. 1-7B). The area has high declivity

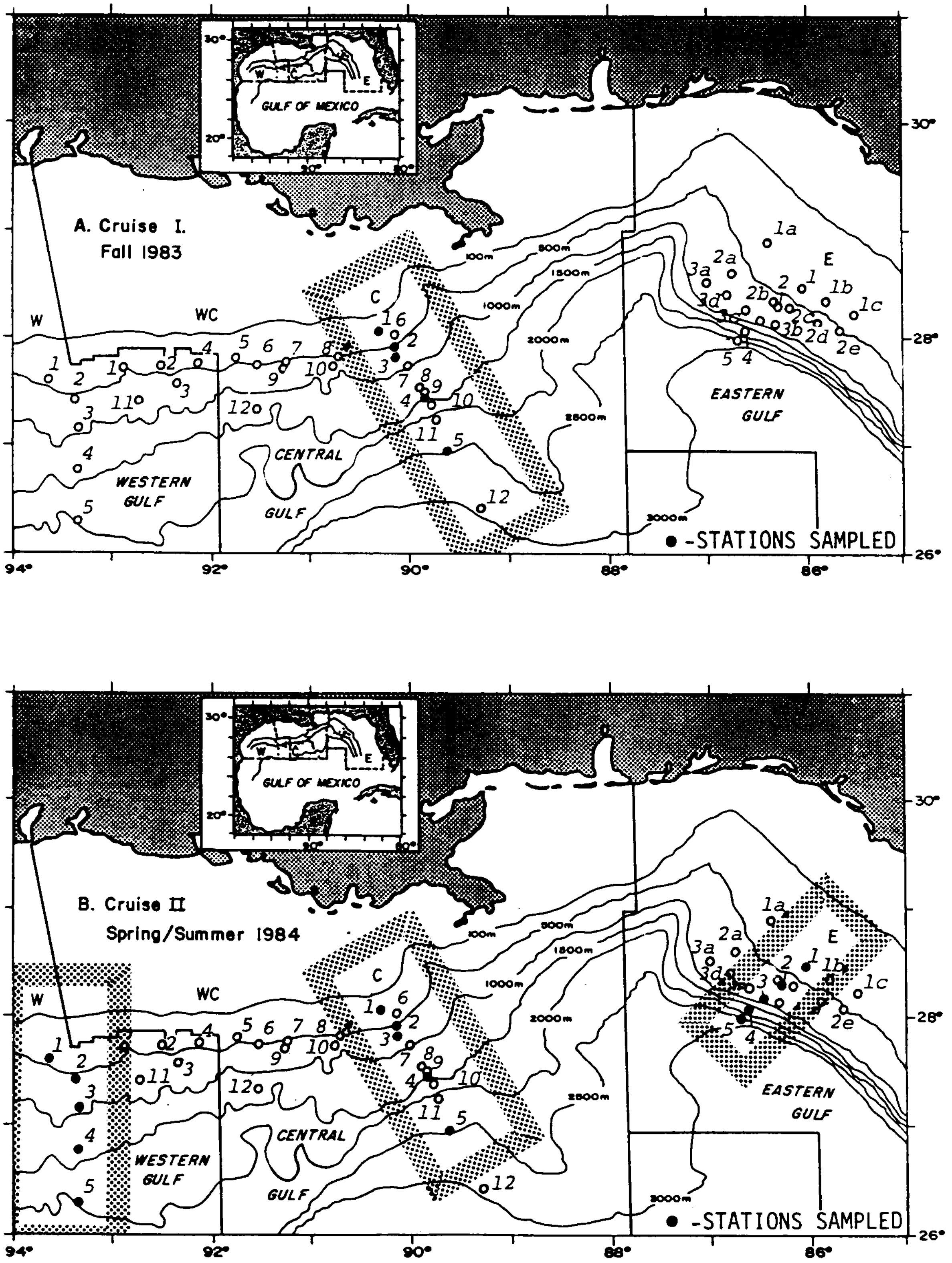
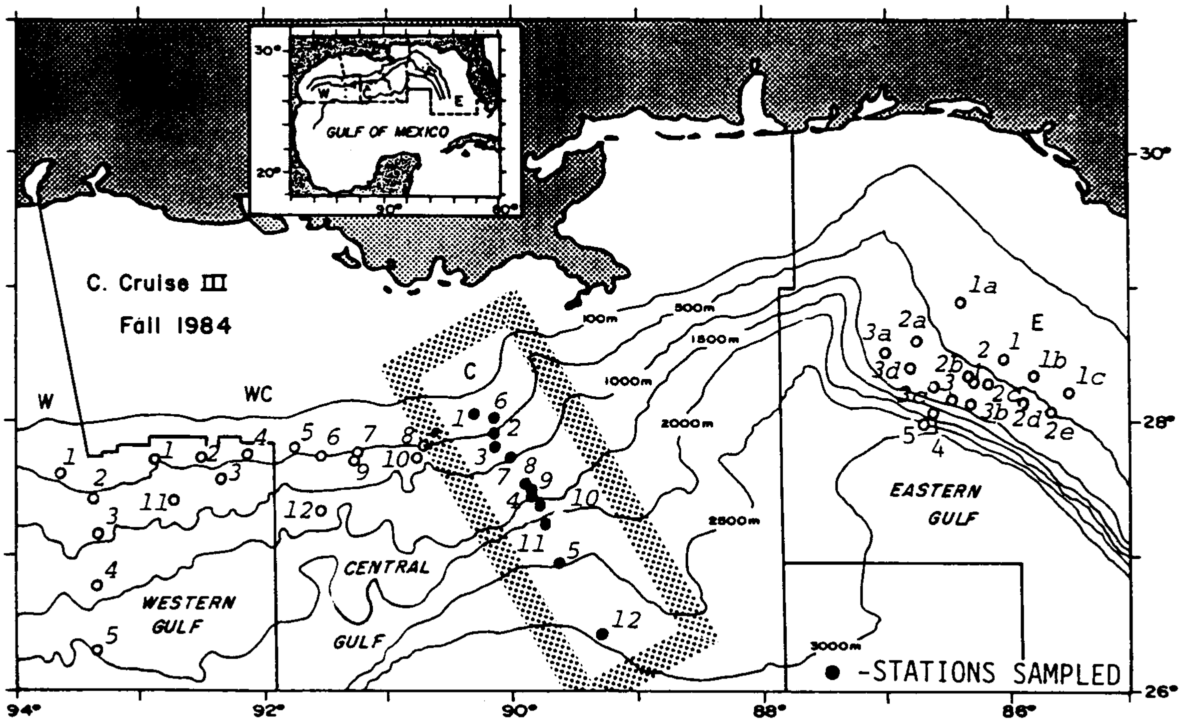


Figure 1-7. Stations sampled on each cruise.



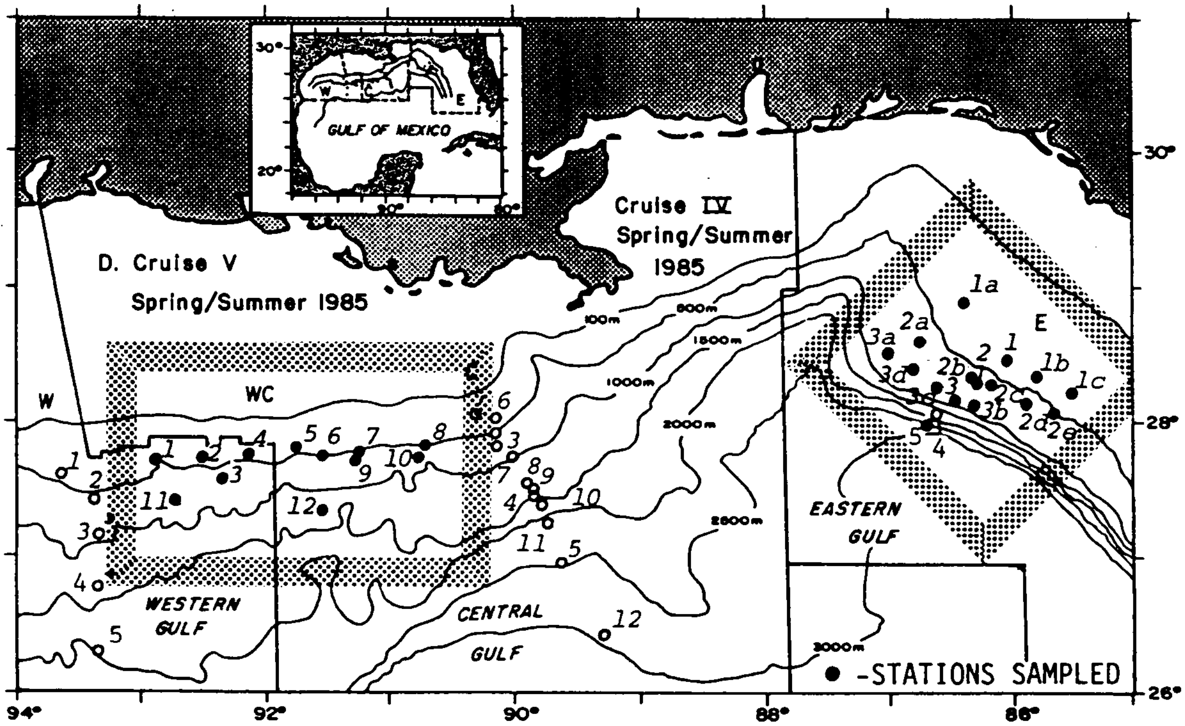


Figure 1-7 (cont'd).

(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. 1-7C,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. 1-7A). 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. 1-7B). 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. 1-7C). 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. 1-7D). 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 to data from Cruise II (Fig. 1-7B) from the same stations a year earlier (Fig. 1-7D).

Station locations for Cruise V (spring/summer 1985) (Fig. 1-7D) 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:

Contrast	Data Source
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 comparions 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 (Fig. 1-8) 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

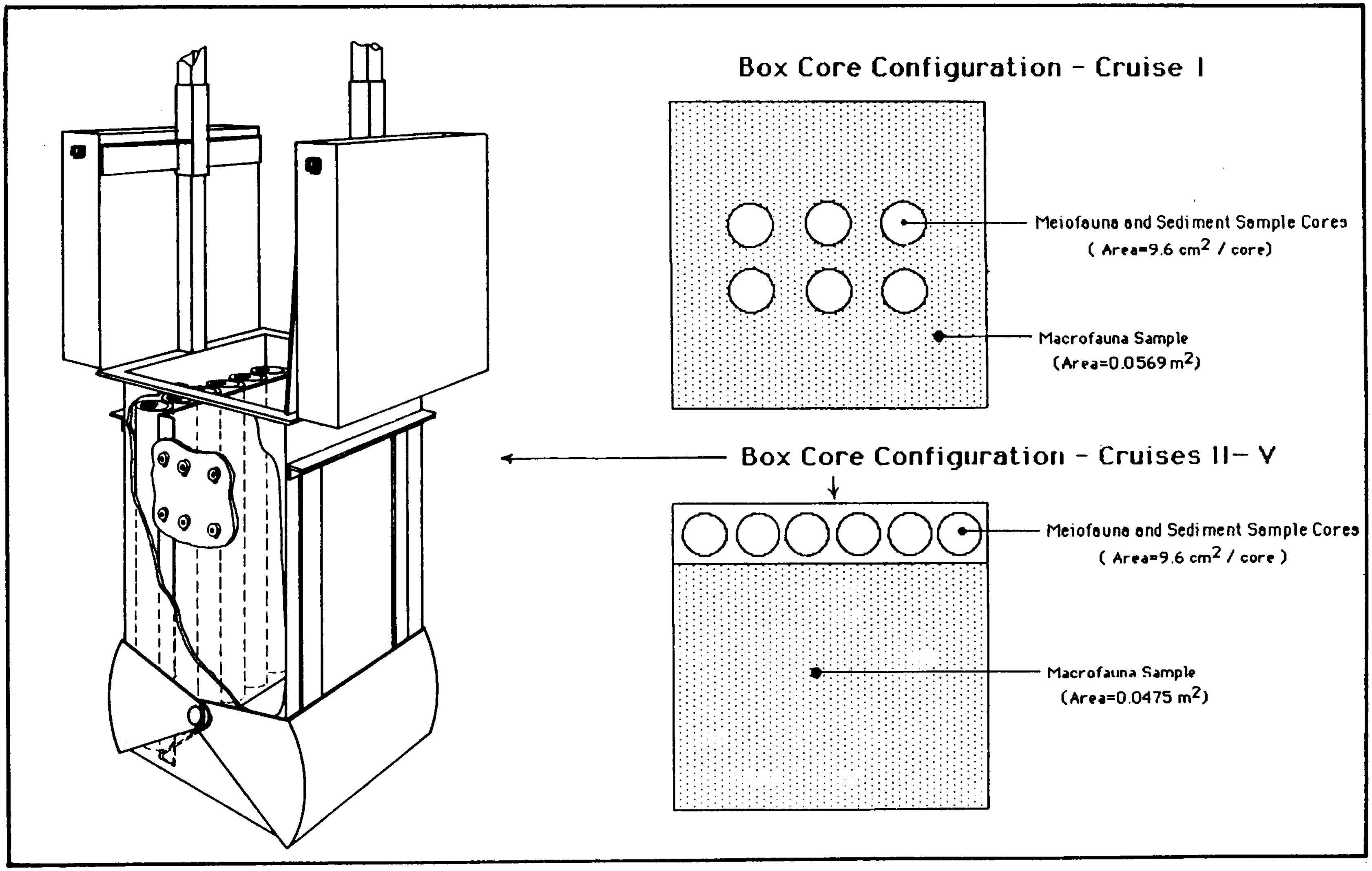


Figure 1-8. Box core and configuration of *in situ* subsampling tubes in the box corer.

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 m^2 of the bottom. However, acceptable shots were obtained at altitudes from 0.7 m (0.27 m^2 area) to 4.0 m (9.09 m^2 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.

Sediment Samples from Box Cores

Grain Size. Sediment grain size was determined as described below. Samples were homogenized and treated with an aliquot of 30% hydrogen peroxide (H_2O_2) to oxidize organic matter, then washed with distilled water to remove soluble salts. Sodium hexametaphosphate was added to deflocculate each sample. The samples were then wet-sieved using a 62.5

micron (4.0 0) sieve to separate the gravel and sand from the silt-clay fraction.

The total gravel and sand fraction was oven dried (40°C) weighed, and sieved at half-phi intervals (-1.5, -1.0, -0.5, 0.0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, and 4.0). Each collected fraction was examined for aggregates, disaggregated if necessary, and reweighed by fraction to three significant figures.

The silt-clay fraction was analyzed for particle size distribution by the pipette (settling rate) method at 4.5, 5.0, 5.5, 6.0, 7.0, 8.0, 9.0, and 10.0 phi intervals.

Organic Carbon. Organic carbon determinations were made using a Leco WR-12 Total Carbon System. Sediment subsamples (0.2-0.5 g) were weighed into disposable 5-ml polystyrene beakers and treated with concentrated HCl to remove inorganic carbon (carbonate). Acid was added dropwise until no degassing was observed. The treated samples were then dried at 50°C in a recirculating oven for 24-36 hours to remove excess acid and moisture. After drying, the sample was quantitatively transferred to a sintered crucible. Iron accelerator and tin-coated copper catalyst were added and analyzed by total combustion on the Leco instrument. Organic carbon was converted to CO_2 and analyzed with a non-dispersive infrared spectrophotometer. Blanks and standards were run on a daily basis. All samples were analyzed in duplicate and averaged. Periodically samples were combusted at >800°C in a high vacuum, Craig-type combustion system as a check on the combustion efficiency of the Leco system.

Carbonate Carbon. Carbonate carbon was determined for the same freeze-dried, homogenized sediment samples that were used for organic carbon and hydrocarbon determinations. Carbonate carbon in Cruise I samples was determined by difference between total carbon and carbonate-free (organic) carbon, using the Leco WR-12 Total Carbon System. For samples from Cruise II, carbonate carbon was determined directly by acidification in a carrier stream, followed by infrared detection.

Carbon Isotope Analyses. Carbon isotope analyses were performed on sediments and selected organisms to determine their food source. Stable carbon isotopes have been shown to be useful in delineating the flow of carbon through ecosystems since there is considerable evidence for minimal carbon isotopic fractionation along marine food chains (Parker, 1964; DeNiro and Epstein, 1978). Fractionation is expressed as delta ^{13}C:

$$\text{delta } ^{13}C = [(^{13}C/^{12}C) \text{ sample} - (^{13}C/^{12}C) \text{ std}/(^{13}C/^{12}C) \text{ std}] \times 1000$$

Plants preferentially assimilate ^{12}C over ^{13}C during photosynthesis, and the degree of ^{13}C fractionation in plants is dependent on the biochemical pathway used for carbon fixation. Photosynthetically derived carbon from plankton and marine algae generally has isotopic values ranging from -19 to -21 ppt. Carbon from terrestrial sources is generally at least 7 ppt lighter (more negative) due to the uptake of CO_2 as opposed to bicarbonate in the sea.

Stable carbon isotopes (delta ^{13}C values) were determined on freeze-dried sediment organic carbon and tissue samples. The stable carbon isotopic CO_2 composition derived from combustion of the organic matter was determined on a Nuclide Corporation six inch, 60° sector, isotope ratio mass spectrometer. The carbon isotope values are reported as per mil deviations from the Pee Dee Belemnite (PDB) standard:

High Molecular-Weight Hydrocarbons. This study involved the measurement of high molecular weight (HMW) hydrocarbons in megafauna (fishes and invertebrates) and sediments in samples collected on the Gulf of Mexico slope. Sediment samples were screened for aromatic hydrocarbon contamination using total scanning fluorescence, but primary detection and quantification of petroleum contamination was based on high resolution capillary gas chromatography and GC/MS/DS analysis. Protocols for analyzing both the sediment and benthic organisms were very similar.

Biological Samples From Box Cores

Meiofauna. Meiofaunal samples were gently rinsed through a 0.300 mm sieve to remove larger organisms, and then through a 0.063 mm sieve. The material on the 0.063 mm sieve was then placed carefully--small amounts at a time--into a sorting dish partially filled with water. Individuals were sorted by major taxon under a dissecting scope, using an Irwin loop to transfer specimens to vials containing 70% ethanol. The vials were uniquely labeled according to collection date, location, replicate number, taxon, and the number of individuals contained in the vial. Biomass was estimated based upon published literature values for the size ranges of organisms in the samples (Fauble, 1982; Rowe et al., 1974).

Macrofauna. Macrofaunal samples were gently rinsed with water to remove preservative, placed in a Petri dish--small amounts at a time--and examined under a dissecting microscope. Specimens were removed and sorted by major taxonomic group into labeled vials containing 70% ethanol. Wet-weight biomass was estimated for each taxonomic group based upon values reported in various published literature (Fauble, 1982; Rowe et al., 1974)

All major taxonomic groups except Nematoda, Harpacticoida, Aplacophora, Scyphozoa (strobilas), Priapulida, and Acarina were given either to in-house or consulting taxonomic specialists for identification to the species level, if possible.

Trawl Sampling (Megafauna)

Megafauna from the trawl samples were removed from the storage containers, rinsed to remove formalin, sorted, identified, and counted to major taxonomic group.

Specimens of fish and selected decapod species were weighed to the nearest 0.1 g (drained wet weight) and measured using the standard method for the taxonomic group in question. Where possible, sex and state of maturity were determined externally or internally if the specimen was examined for gut contents.

Guts of selected representatives of common fishes were dissected and examined for assessment of food habits. Stomach contents were examined for (1) percentage fullness by volume, (2) percentage composition by food item group by volume, (3) wet weight of each food item group, and (4) number of individuals in each food item group.

All utensils were pre-cleaned using procedures described in the sediment section. The target sample weight was 15 g wet weight. The method of digestion of tissues was identical to that used for sediment. The methods used in column separation, gas chromatography (GC), and gas chromatography/mass spectrometry (GC/MS) were also identical to those used in the sediment analytical scheme. No fluorescence screening was performed. Since organisms do not generally contain large amounts of sulfur, desulfurization with copper was not necessaary. Three tissue types (liver, gonad, and muscle) were analyzed in fish specimens. Only muscle tissue was analyzed in other benthic fauna (shrimp, crabs, etc.).

Carbon isotope methods were identical to those used for sediments.

Benthic Photography

A procedure for detailed evaluation of benthic photographs was developed specifically for this project. Benthic photography samples obtained from photographic transects were processed on a digitizing pad driven by a microcomputer. The sizes of objects seen in the photographs were calculated from their distance from the camera (i.e. camera altitude, recorded in the corner of each shot) and the acceptance angles of the camera lens. Knowledge of the scale of the photographs made it possible to calculate the area shown in each photograph, and to measure the sizes of various features and biota. Each photo thus served as a quantitative quadrat sample of the survey site (Grassle et al., 1975).

Processed film was projected through a modified bulk film projector and a front-silvered mirror mounted at a 45° angle. The mirror reflected the photographic image onto a Houston Instruments Hi-Pad DT-11VA digitizing pad connected to an Apple IIe microcomputer. The software for the computer was developed by LGL.

A subsample of either 100 frames (Cruise II) or 200 frames (Cruises III-IV) was selected from an entire roll from each station, using a systematic sampling technique described by Cochran (1977). The digitizer's cursor was then used to count and measure the subjects in the photograph. The operator had the ability to select any of three means to measure objects seen, depending on his judgement of the best representation of the object. He could determine whether the object was most appropriate to measure as a point, a straight line, or a closed figure. Each procedure utilized a different software routine, which could be activated with a cursor command.

Data Management

The sequence of data management and analysis procedures used by LGL is shown in Figure 1-9. Most of the project data comes to the data management group on coding forms which were designed by the data manager and key project personnel at the outset of the program before any data were collected. Field and laboratory data were coded onto these data forms by laboratory personnel and then processed. Once validated, data were submitted to NODC.

CLOSING COMMENTS

In subsequent chapters, descriptions of the Gulf of Mexico environment and biota are presented and potential interactions are discussed. The results of this study provide a more precise description of the slope environment and biota than was previously available, and considerably expands the data base necessary for making environmental assessments as hydrocarbon development proceeds in the deep Gulf of Mexico.

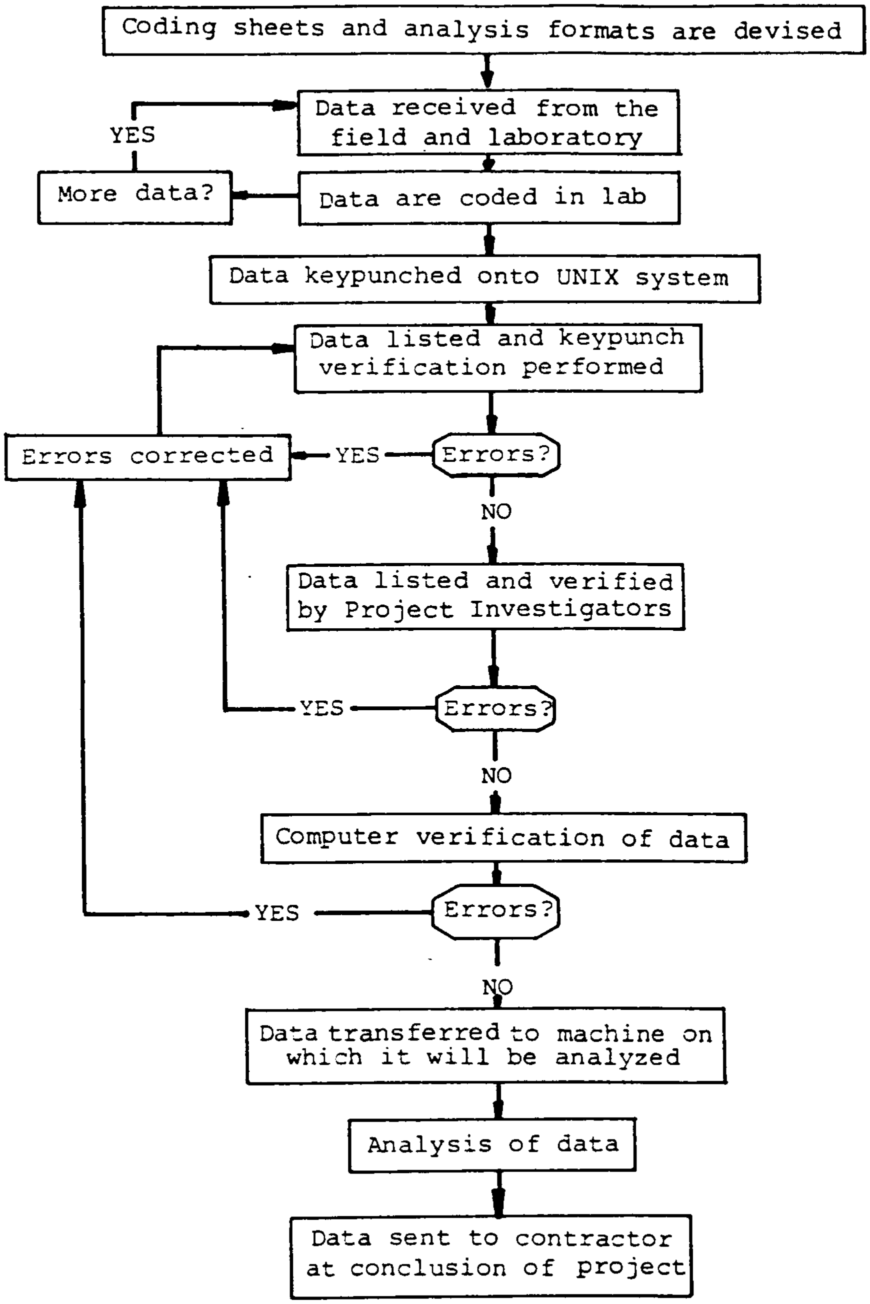


Figure 1-9. Data flow sequence for continental slope study.

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CHAPTER 2. CHARACTERIZATION OF BENTHIC HABITATS OF THE NORTHERN GULF OF MEXICO CONTINENTAL SLOPE

B.J. Gallaway and M.C. Kennicutt, II

INTRODUCTION

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, we demonstrate in subsequent pages in this report, including those describing the biological communities around natural petroleum seeps, that sediment hydrocarbon levels influence biological communities of the slope, even when present in only trace amounts.

In this chapter, we first provide a summary of bottom water characteristics, by depth, over time and space. This is followed by summary descriptions of the non-hydrocarbon characteristics of the bottom sediments and next by sediment hydrocarbon characterizations. Lastly, we describe the observed types and levels of hydrocarbons in selected biota. These are summary accounts but full accounts and listings of all the data collected can be found in the Year 3 Annual Report (Gallaway et al., 1988).

In the final section of this chapter, we provide an environmental classification of the various stations sampled, using Principle Component Analysis (PCA). In subsequent papers, biological classifications of these stations are overlain on the environmental classification to evaluate the relationship between the environment and biota.

STUDY AREA AND METHODS

The study area, sampling methods, and sample analysis methods used are summarized in Chapter 1 and detailed in Gallaway et al. (1988). The area involved was the northern Gulf of Mexico continental slope region (200-m to 2,900-m depths) between about 85° and 96° west longitude. Methods involved (1) measurements of temperature, salinity, and dissolved oxygen levels in waters along sampling transects and (2) measurements of sediment grain size, calcium carbonate levels, and various parameters of organic compounds in sediment samples. Transect sampling stations and sediment samples used were the same as those used to characterize the biota.

Nearly 40 physical/chemical habitat variables were measured as potential factors affecting biota. PCA enables one to transform a large original set of variables such as this into a smaller set of combinations that account for most of the variance of the larger, original set. The purpose is to explain as much of the total variation in the data as possible, with as few factors as possible. The PCA was run on the Texas A&M University computer, using SAS.

The outputs of the PCA enables one to group entities (in our case, stations by depth, seasons and years) in terms of their physical/chemical attributes. This, in effect, provides an environmental classification against which we can compare results of various biological classifications oF the same stations.

Four PCA's were run. The first compared habitats, by depth, among regions, seasons and years. This analysis used data collected for Stations E1-E5 (east transect), C1-C5 (central transect) and W1-W5 (west transect) during the spring (1984) and fall (1983, 1984) seasons (see Fig. 1-7). The second PCA used data from 11 stations, all on the central transect, to address depth differences during fall 1984. The third and fourth PCA's had similar objectives, one to compare latitudinal differences along depth contours in the eastern Gulf and the other to compare longitudinal differences along depth contours in areas between our central and western transects.

BOTTOM WATER CHARACTERISTICS

The three qualities of bottom water (other than hydrostatic pressure) presumed to have important effects on biota were temperature, salinity, and dissolved oxygen. (Descriptions of other water quality variables that were measured can be found in Gallaway et al., 1988.) Levels of all these were strongly and predictably related to depth, irrespective of distance off the bottom. Ranges of variability of these three parameters among all samples were so low that responses of biota to the variation would not be expected.

Temperature

From the surface (upper 25 m) to approximately 1,300-1,400 m depths temperature dropped from near 20° (19.01-25.08°C) to about 4.22-4.35°C at 1,300-1,400 m depth (Fig. 2-1). Below 1400 m temperatures remained constant within this low range.

Between 300 and 1,400 m, temperature variation over time was low. On the central transect, Stations C1, C2, C3, C4 and C5 were each occupied three times--fall 1983, spring 1984, fall 1984. The maximum variations over the three cruises at representative depths of 300, 600, 900, and 1,400 m were 2.59°, 0.78°, 0.29°, and 0.10°C, respectively.

Temperature-depth relationships held regardless of total depth of the water column. In the eastern Gulf, profiles were measured in spring 1985 at stations with bottom depths of 380, 665, 885, 915, and 2,920 m. Temperature variations by depth along the transect were low; ranges were 1.93° (18.35-20.28°C) at 100 m; 1.72° (9.31-11.03°C) at 400 m; 0.68° (7.05-7.73°C) at 600 m and 0.16° (5.10-5.26°C) at 900 m.

On a large horizontal scale, temperature differences from the western to the eastern Gulf also showed only minor changes. From the western to the eastern Gulf the most temperature variation observed by depth was only 0.49°C at 275-m depth.

Salinity

Salinity profiles exhibited the characteristic pattern previously observed for the Gulf of Mexico (Fig. 2-1). Surface salinity ranged from about 35 to about 36.5 ppt and increased with depth to about 100-200 m where the salinity maximum is found. Below the salinity maximum, salinity decreased to a depth of about 600-800 m where the salinity minimum is located.

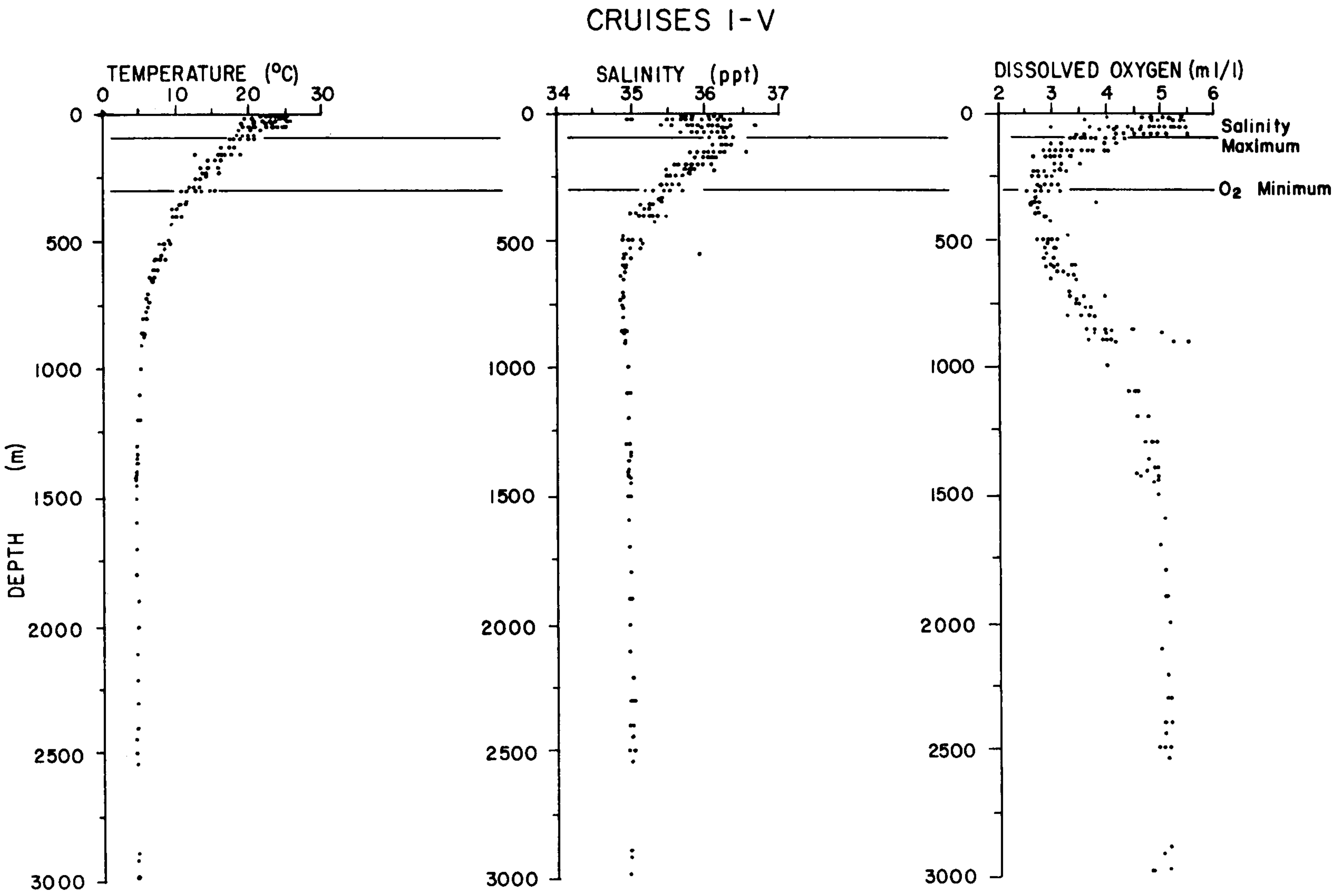

Figure 2-1. Hydrographic profiles of temperature, salinity, and dissolved oxygen, all cruises combined.

Similarly to temperature, salinity varied little over time at similar depths. Along the central transect, salinity showed the following variability among fall 1983, spring 1984, and fall 1984 measurements:

Depth	Extreme	Range
300 m	35.16-35.70 $^{o}/_{oo}$	0.54 $^{o}/_{oo}$
600 m	34.90-34.94	0.04
900 m	34.89-34.95	0.06
1400 m	34.94-34.98	0.04

Depth-specific variations in salinity based on measurements taken in spring 1984 at similar depths from stations in the western, central and eastern Gulf were likewise low. At 275 and 400 m, salinity was slightly higher in the eastern Gulf, with the central Gulf station (C4) having the lowest salinity at these depths (extreme difference of 0.07 ppt). At 775 m and below (1,100-1,400 m) there was a slight but general decrease in salinity from west to east (less than 0.04 ppt difference).

Dissolved Oxygen

Dissolved oxygen (D.O.) concentration (Fig. 2-1) ranged from about 2.5 to 5.5 ml/l (= ~3.6-7.8 mg/l). None of the concentrations found are considered to be limiting to aerobic fauna found in the ocean. Dissolved oxygen concentrations were higher in the surface waters (<50 m) decreasing to the oxygen minimum layer (about 400 m depth). In the eastern Gulf, a secondary oxygen minimum layer at 150 to 300 m is sometimes found (Nowlin and McLellan, 1967). This phenomenon was apparently present during spring 1984 on the eastern transect station E4, where two oxygen minima were observed (one at 174 and one at 400 m).

Below the oxygen minimum, D.O. concentrations increased to a depth of approximately 1,500 m then remained relatively constant (at 5 ml/l) to 2,200 m.

Trans-Gulf dissolved oxygen levels varied less than 0.2 ml/l at a given depth except for measurements made at 1,400 m, but this depth is an area of increasing D.O. levels and small-scale differences in depth of measurement could cause relatively large differences in D.O.

SEDIMENT CHARACTERISTICS

Sediment samples were collected at 45 locations on the continental slope (see Fig. 1-7, Chapter 1). Five of these locations (C1-C5) were sampled during three different cruises and four (E1-E3, E5) were sampled during two different cruises; others were sampled only once. This resulted in a total of 59 collections treated statistically as different samples for most analyses. Each of these 59 samples were replicated, usually six (but sometimes three) times for statistical purposes. Samples were analyzed for several components including grain size, total organic carbon, calcium carbonate, organic matter carbon isotope composition, and various hydrocarbon measures (which will be discussed separately below). A summary of findings is presented below, complete accounts can be found in Gallaway et al. (1988).

Grain Size

Sediment samples were classified into categories using the graphical sediment triangle representing percentages of sand, silt and clay in the sample (Fig. 2-2). The most common sediment type (at over 55% of the locations) was silty-clay, found in all geographic areas. There were small amounts of variation in the ratios of sand:silt:clay within this type, depending on the areas sampled. In the eastern Gulf slope this type had slightly higher percentages of sand than in the western or central areas. Along the central transect, there were slightly higher percentages of silt than clay at the deeper locations (C5 and C12).

Other common sediment types were clay, sandy clay, and sand-silt-clay. Clay was found at nine locations (C1, C6, WC2, WC3, WC4, WC8, WC9, WC10, WC11) in the western and central Gulf, all relatively shallow (<1,226 m). Samples with clay sediments had little variation in the sand-silt-clay proportions. Sandy clay was observed in the western Gulf at Stations W1, W2 and W5, and in the eastern Gulf at Station E5. Sand-silt-clay sediment was found in the eastern Gulf at Stations E1, E1b, E1c, E2d and E4.

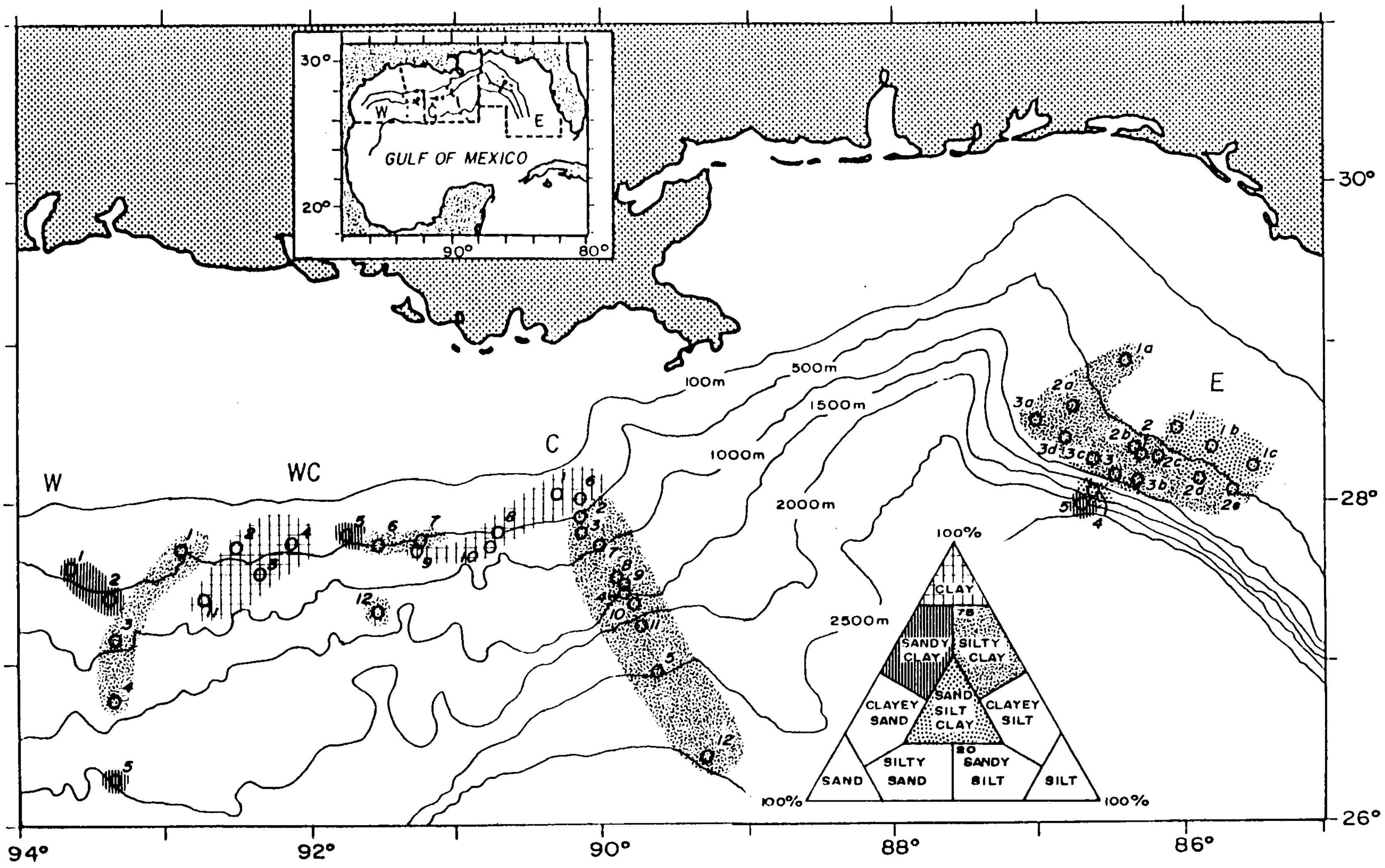

Figure 2-2. Distribution of sediment types on the continental slope as determined from samples at 45 stations (o).

Station WC6 was difficult to characterize because of the variation among the six replicates. Silty clay is probably the best classification based on average values.

Total Organic Carbon

Total organic carbon (TOC) content of sediments varied considerably among stations, with a range of 0.17 to 1.26% by weight. Mean TOC was 0.74% with a standard deviation of 0.21%.

Calcium Carbonate

Percent calcium carbonate in sediment samples varied from 8% to 80%, with a mean of 38.6% and a standard deviation of 19.5%. The lowest value came from samples at approximately 350-m depths in the central region; the highest from between 1,000 and 1,500 m in the eastern region.

Delta ^{13}C

Delta ^{13}C values varied little among samples. The low value of -25.2 and the high value of -17.5 were outliers. Other than these values, there was a general tendency for values to cluster about the mean of -20.9. Standard deviation among samples was 1.19.

SEDIMENT HYDROCARBONS

Sediments on the Gulf of Mexico slope were found to contain a mixture of terrestrial, petrogenic and planktonic sourced hydrocarbons. Alkane distributions are similar at all locations sampled whereas the quantitative importance of the three major inputs varies with location, time of sampling and water depth. However, hydrocarbon concentrations were relatively uniform across the slope given the large geographical area sampled. Extractable organic matter, aliphatic hydrocarbon concentrations and the aliphatic unresolved complex mixture (UCM) range from 4.0 to 94.2, 0.1 to 5.2, and 0.7 to 81.4 ppm dry weight of sediment, respectively (Table 2-1). These concentrations are generally lower than previously

Table 2-1. The ranges and averages for selected hydrocarbon parameters in Gulf of Mexico continental slope sediments (ppm dry weight of sediment).

Cruise	Location (Transect)	Extractable Organic Matter (ppm)	Aliphatic Hydrocarbons (ppm)	Aliphatic Unresolved-Complex-Mixture (ppm)
I (Fall, 1983)	Central	28.4 (13.9 - 61.3)[1]	1.6 (1.3 - 2.0)	23.3 (19.3 - 29.8)
II (Spring/ Summer, 1984)	Central	21.7 (18.0 - 25.2)	1.7 (1.6 - 1.8)	8.9 (6.0 - 14.0)
	Western	26.0 (14.0 - 55.2)	1.1 (0.8 - 1.3)	11.1 (5.2 - 11.4)
	Eastern	8.6 (7.6 - 10.9)	0.7 (0.5 - 1.0)	5.4 (3.2 - 7.3)
III (Fall, 1984)	Central	18.1 (4.0 - 44.4)	1.4 (0.6 - 4.6)	9.7 (4.4 - 17.4)
IV (Spring/ Summer, 1985)	Eastern	7.2 (4.7 - 13.4)	0.2 (0.1 - 0.4)	2.0 (0.7 - 5.0)
V (Spring/ Summer, 1985)	West/Central	30.0 (17.7 - 94.2)	0.9 (0.4 - 5.2)	16.8 (4.2 - 81.4)

[1] Ranges in values.

reported for Gulf of Mexico sediments (Table 2-2). Individual hydrocarbons were present at concentrations ranging from <0.01 to 0.5 ppm. In general, qualitative alkane distributions were similar at all sites sampled. The dominant n-alkane in the 15 to 22 carbon range was variable, whereas the normal alkanes with 23 to 32 carbons were consistently dominated by n-C_{29} or n-C_{31}.

Molecular level and bulk parameters can be used to estimate the relative importance of hydrocarbon sources at a given location. These parameters are based on the premise that hydrocarbon sources have unique fingerprints, i.e., certain recognizable suites of compounds. In nature however, few unique end-members occur. To better understand the dynamics of hydrocarbons in Gulf of Mexico slope sediments several diagnostic parameters were calculated:

Source	Indicator Compound	Abbreviation
Planktonic/Petroleum	n-C_{15}, 17, 19; pristane	PL-1
Petroleum/(Planktonic?)	n-C_{16}, 18, 20; phytane	PE-Lo
Land/(Petroleum)	n-C_{25}, 27, 29, 31	TERR
Petroleum/(Biogenic)	n-C_{24}, 26, 28, 30	PE-Hi
Petroleum/(Biogenic?)/Recycled	Unresolved Complex Mixture	UCM

The assumptions made in evaluating the observed distributions of these parameters are detailed in the Year 3 Annual Report (Gallaway et al., 1988).

These parameters are used to assess the dynamics of hydrocarbons on the slope as a function of water depth, location, and time of sampling. These indicator parameters are also evaluated in terms of other parameters such as the UCM, an indicator of petroleum input; carbon preference index, an indicator of the relative amounts of odd and even normal alkanes; and bulk sediment parameters such as carbon isotopic compositions in order to more fully understand the observed distributions.

Regional Comparisons

Sampling during Cruise II was undertaken to assess the distribution of sediment hydrocarbons on transects from the central, western, and

Table 2-2. Summary of Gulf of Mexico sediment hydrocarbon analyses.

Location	Concentrations in ppm		Predominant Source	Reference
	Total HC	Saturated HC		
Texas/Louisiana - Coastal	20-190		B(P)	Smith, 1952
Texas/Louisiana - Coastal	Low Concentrations[1]		B	Stevens et al., 1956
Gulf of Mexico - Coastal	Biogenic Waxes[2]		B	Bray and Evans, 1961
Florida (Bay) - Sandy Sediments	Ave.=4.4[2]	Ave.=2.0[2]	B	Palacas et al., 1972
- Muddy Sediments	Ave.=86.0[2]	Ave.=30.0[2]	B	
N.E. Coast - Sandy Sediments	0.2-10.0[2] Ave.=6.25	0.1-3.8[2] Ave.=1.4	B(P)	Palacas et al., 1976
STOCS* - Coastal	Very low levels[2]		B(P)	Palacas et al., 1976
STOCS - Coastal (Before, during and after drilling activities)	0.22-5.60[2] Ave.=1.14	(0.1-0.5)[2] Ave.=0.2	B(P)	Parker et al., 1976
Texas/Louisiana - Coastal Banks	0.02-0.80[2]		B	Parker, 1978
MAFLA**- Nearshore Florida (<40 m)	Ave.=1.90[2]	0.29-1.60[2] Ave.=0.86	B	Boehm, 1979
- >40 m Florida	Ave.=1.39[2]	0.29-1.89[2] Ave.=0.83	B(P)	
- Mississippi/Alabama Shelf	Ave.=1.61[2]	0.28-2.89[2] Ave.=1.1	B(P)	
Freeport, Texas - Coastal	0.9-45[2] Ave.=39.7	0.1-2.4[2] Ave.=0.71	B	Slowey, 1980
Texas/Louisiana - Coastal	5.71-87.2[2] Ave.=39.7	3.13-49.5[2] Ave.=21.4	B(P)	Nulton et al., 1981
Texas Shelf	Ave.=1.3[2]		B	Lytle and Lytle, 1979
Florida Coastal (<60 m)	Ave.=3.1[2]		B	Gearing et al., 1976
W of Mississippi R. Coastal (<60 m)	Ave.=11.7[2]		B(P)	Gearing et al., 1976

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[1] Method - gravimetry (expressed as a percentage of the total organic extract recovered from the silica gel).
[2] Method - GC, GC/MS.
* South Texas Outer Continental Shelf
**Mississippi Alabama Florida
B Biogenic.
P Petrogenic.

eastern Gulf of Mexico continental slope. Extractable organic matter (EOM) is a composite of both biologically produced and petroleum related lipid material. In general, EOM was lowest on the eastern transect and nearly equal on the western and central transects, with the exception of Station W1 (Fig. 2-3). The aliphatic UCM, a petroleum indicator, is similar for all three transects though slightly elevated in central transect sediments (see Table 2-1). The elevated EOM at Station W1 corresponded to an increased UCM (i.e., petrogenic component). The UCM, which is used to indicate the presence of petroleum, does not delineate the source of the petroleum, i.e., seepage, the overlying water column or recycled organic matter.

The influence of land-derived material decreased from the central to the western to the eastern transect (Figs. 2-4 and 2-5). Terrestrial hydrocarbon concentrations, as indicated by the Σ n-$C_{25,\ 27,\ 29,\ 31}$ (TERR), were relatively uniform with water depth on the central and western transects, where terrestrial content increased with water depth on the eastern transect. The influence of the land/or river derived material as suggested by the predominance of odd n-alkanes from C_{23} to C_{31}, was readily apparent at all three locations and accounts for a majority of the GC-resolvable alkanes.

Plankton derived hydrocarbons were low compared to the terrigenous and petroleum hydrocarbons and were often difficult to discern at the central and western transects (Figs. 2-4 and 2-5). In general, the planktonic input was higher at the shallower stations of these two transects. The low planktonic hydrocarbon concentrations in the western and central transects may have been due to the high sedimentation rate and/or dilution with terrestrial material. On the eastern transect, the planktonic input was discernible and relatively constant with depth. In general planktonic inputs accounted for less than 10% of the GC resolvable alkanes. Sediment biogenic hydrocarbons on the slope were dominated by the more microbially resistant terrestrial components and the degree of dominance was a function of proximity to the Mississippi River and the topography of the slope.

Petroleum inputs, measured both by alkane parameters and the UCM, were present at all sites (Figs. 2-3, 2-4 and 2-5). In general, however, less petroleum was indicated in the eastern than in the western region,

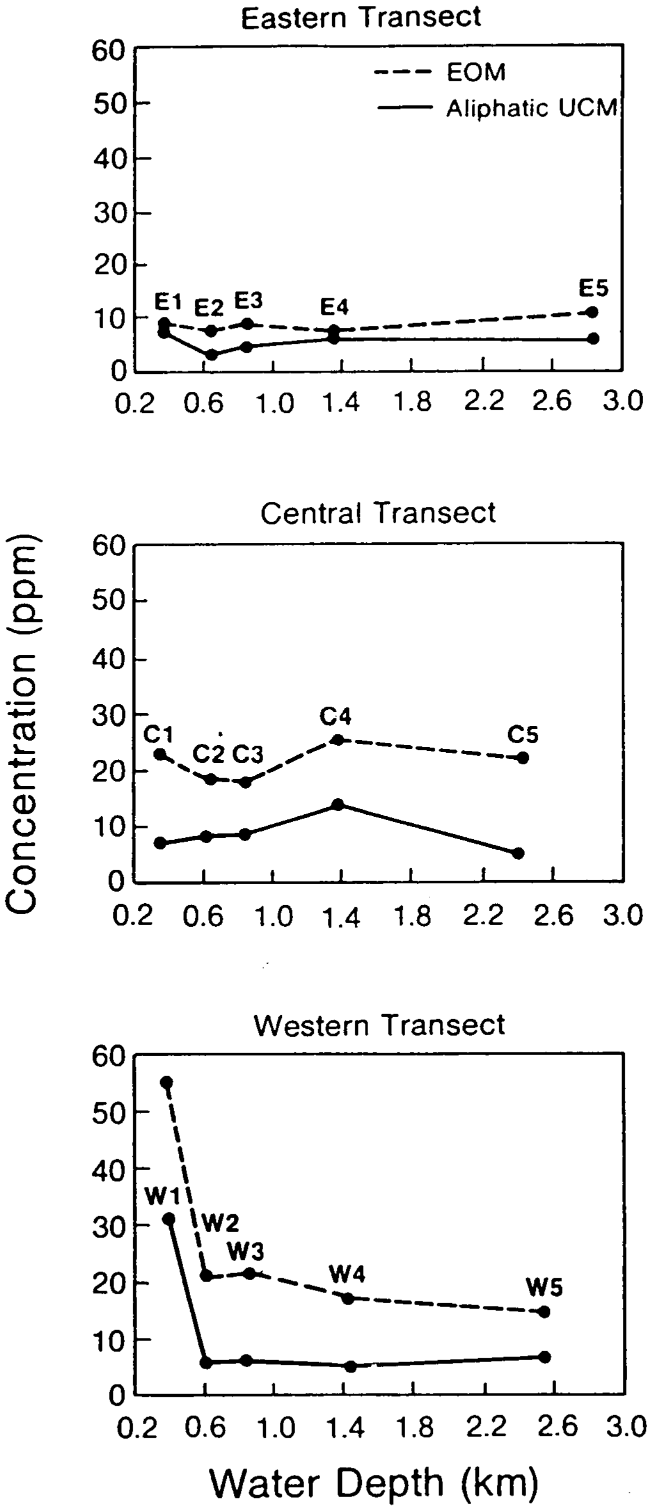


Figure 2-3. Variation in extractable organic matter and the aliphatic unresolved complex mixture along transects in the eastern, central, and western Gulf of Mexico continental slope.

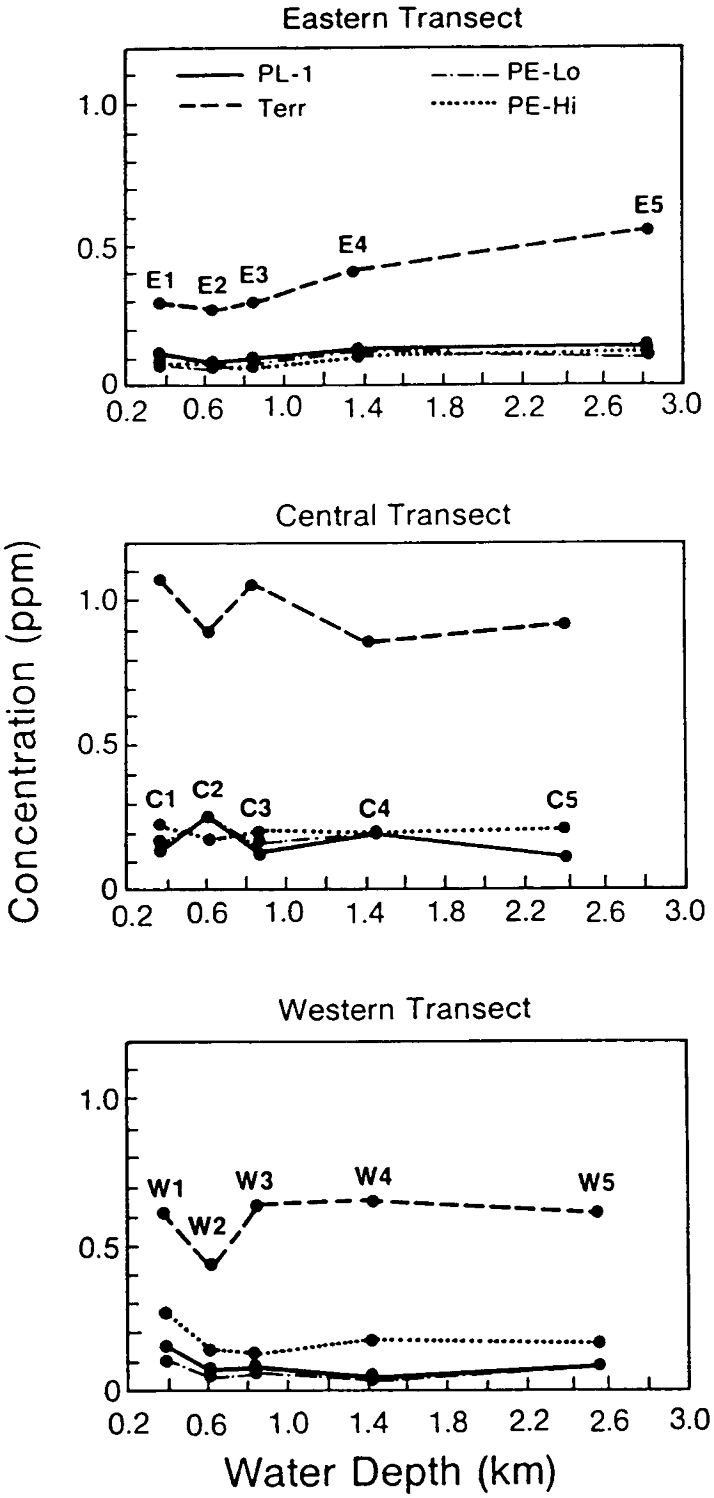


Figure 2-4. Variation in hydrocarbon source parameters along transects in the eastern, central, and western Gulf of Mexico continental slope (for definition of abbreviations see the text).

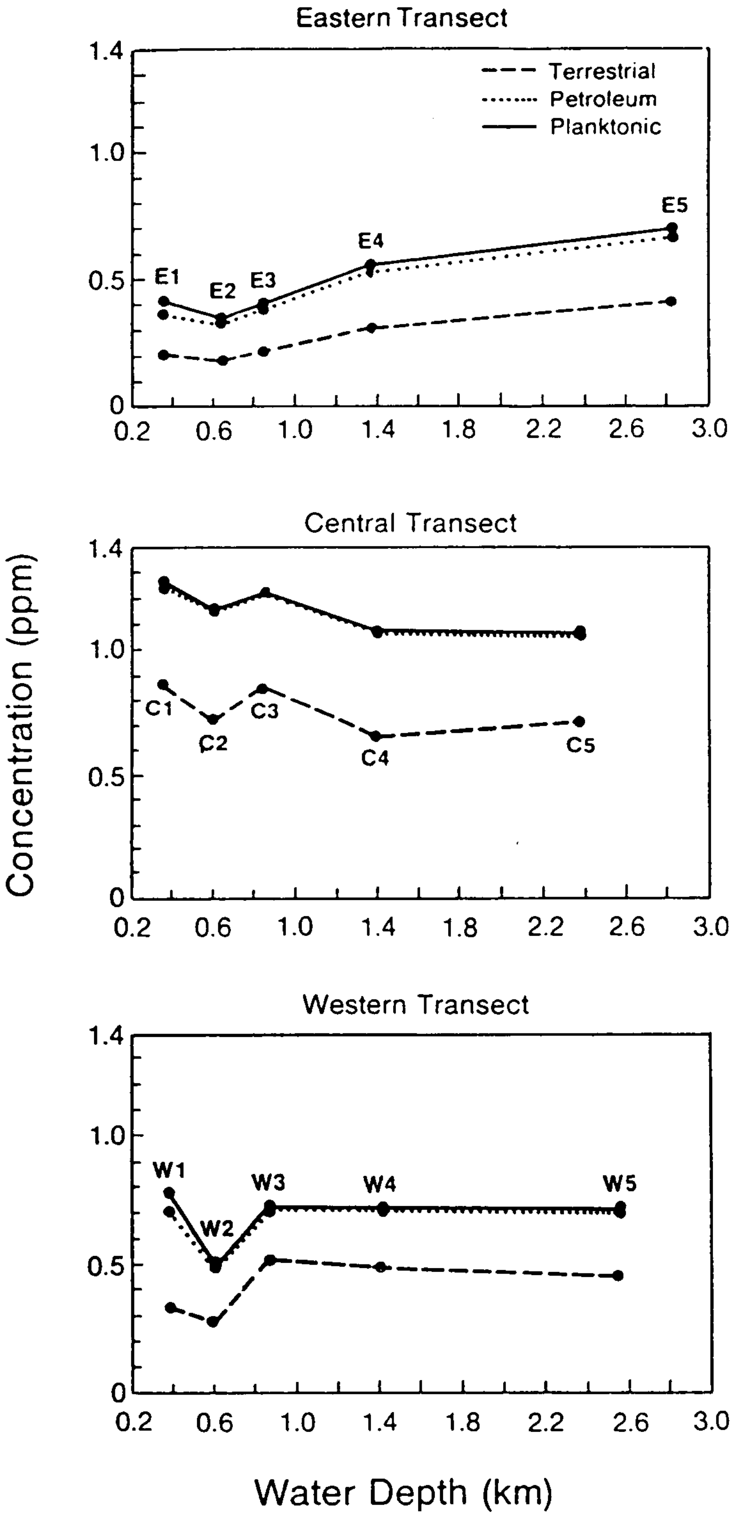


Figure 2-5. Variation in planktonic, terrestrial, and petroleum hydrocarbons along three transects presented as a cumulative concentration.

with highest values at the central transect. Petroleum hydrocarbons (a maximum estimate) were observed at low concentrations at all locations. In an effort to determine if the petroleum hydrocarbons detected were sourced in transported particles or due to upward migration from subsurface reservoirs, the petroleum indicators were compared to terrestrial and planktonic indicator distributions (Fig. 2-6). The general relationships might suggest a dual source for petroleum hydrocarbons. Lower molecular weight hydrocarbons (PE-Lo) tended to increase with an increased terrestrial input on the eastern transect, but this trend was not observed on the central and western transects. The higher molecular weight petroleum indicator (PE-Hi) strongly correlated with the terrestrial indicator (TERR). In this case, this simply reflects the large biogenic contribution to PE-Hi indicator. From this cross-plot, the ratio of the two parameters corresponds to a carbon preference index (CPI) of ~4.3 indicating that a majority of the PE-Hi in these samples is biogenic in origin. Pre-industrial revolution sediments show a similar CPI of 4.9 (Wade and Quinn, 1979).

Compared with Stations W2 to W5, Station W1 contained significantly elevated petroleum hydrocarbon concentrations (Fig. 2-7). The UCM varied independently of the planktonic or terrestrial input (Fig. 2-7). This may suggest an indigenous source such as upward migration from deeper reservoirs. However, any attempt to correlate petroleum and terrestrial inputs assumes that the relative amount of petroleum to terrestrial hydrocarbons transported to the location is constant with time, which may or may not be true. However, extensive natural hydrocarbon seepage documented on the Gulf of Mexico continental slope supports natural seepage as a significant petroleum hydrocarbon input to Gulf of Mexico slope sediments (Anderson et al., 1983; Brooks et al., 1984; 1986). Piston coring on the Gulf slope has shown that petroleum hydrocarbons increase in concentration with depth in areas of known seepage (i.e., separate phase oil droplets in the sediment) and that the bitumens match isotopically and compositionally the deep reservoired fluids (Kennicutt et al., 1987; Lacerda et al., 1987). It is also evident that some fraction of the petroleum hydrocarbons are transported to the slope by river/land derived particles. The UCM can also be due to recycled material and is not distinguishable as a single source.

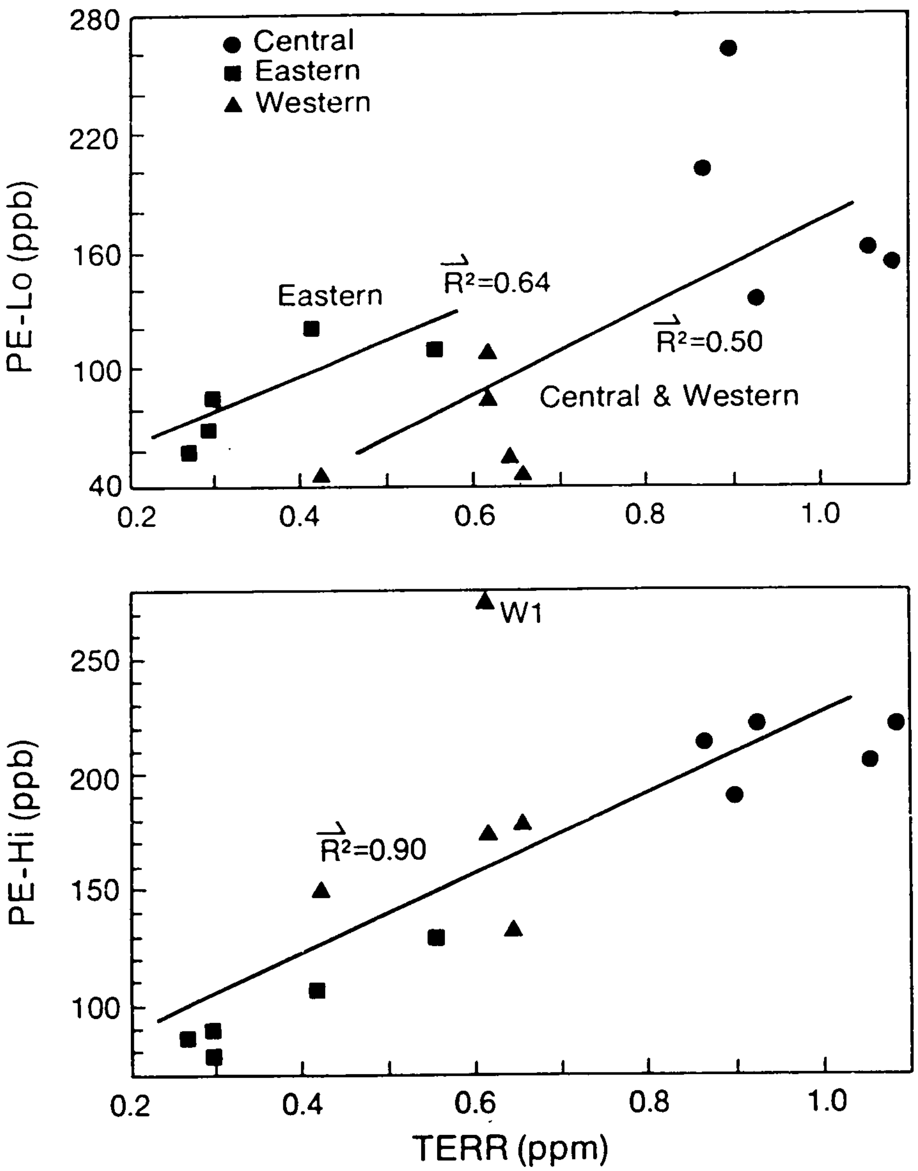


Figure 2-6. The relationship between alkane petroleum indicators and a terrestrial indicator.

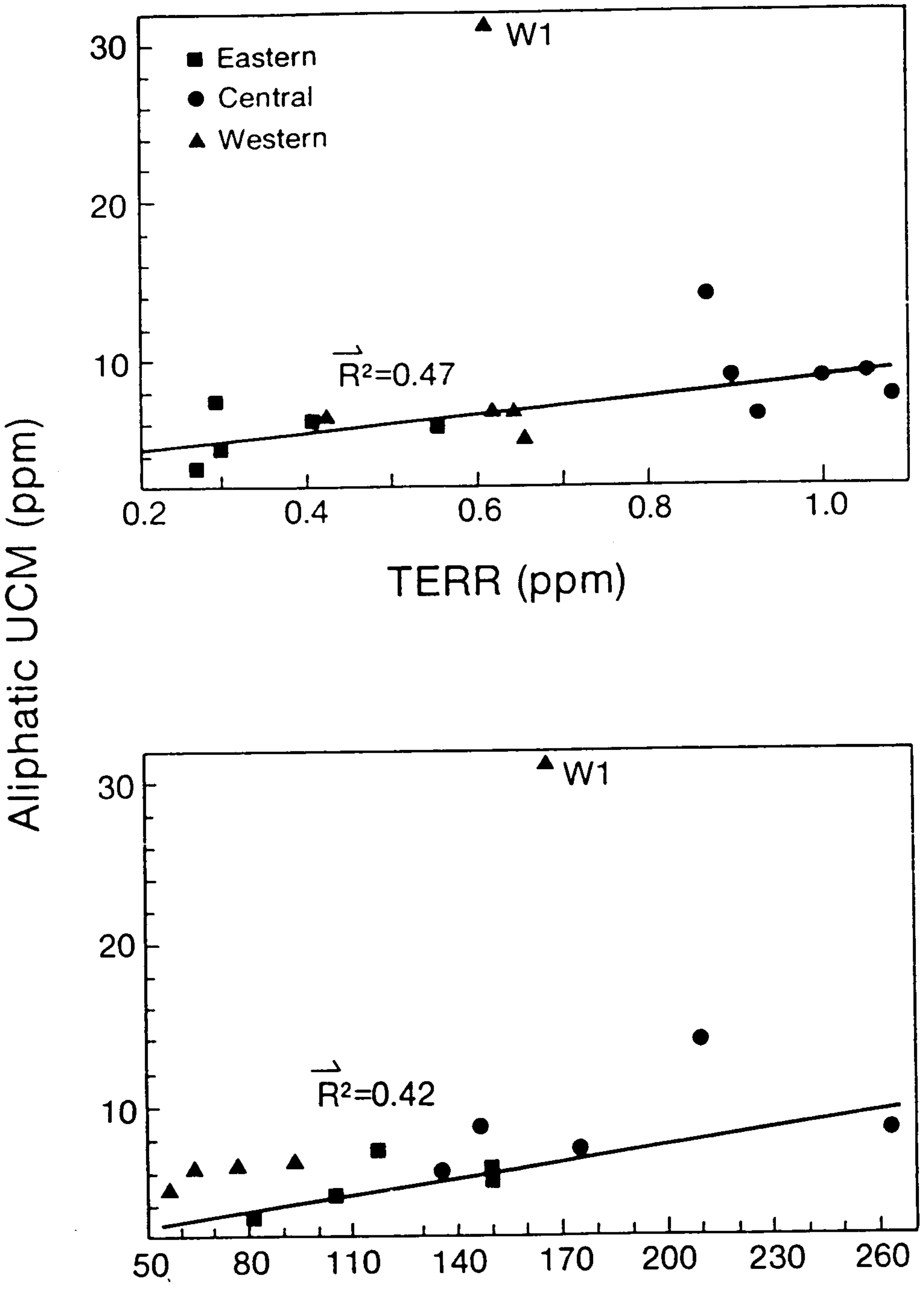


Figure 2-7. The relationship between the aliphatic unresolved complex mixture and the planktonic and terrestrial alkane indicator.

Temporal Variations

The sampling on Cruise I (November 1983), Cruise II (April 1984), and Cruise III, (November 1984) was conducted at the same stations, on the central transect in an attempt to document changes in hydrocarbon distributions over time. The distribution of EOM and aliphatic UCM during three samplings is shown in Figure 2-8. On an average, the aliphatic UCM was highest on Cruise I primarily due to the elevated levels measured at Station C1 (Fig. 2-8). The UCM concentrations during Cruise II and at the shallower stations of Cruise III (<1,500 m) were similar. During Cruise III the UCM was higher than Cruise II by a factor of 1.5 to 2.2 at stations deeper than 1,500 m. Molecular indicators were similar at all depths along the central transect during Cruises I and II (Figs. 2-9 and 2-10), but marked variations in hydrocarbon distributions with depth were observed during Cruise III sampling. Shallower stations had a decreased hydrocarbon content as compared to deeper stations, possibly due to dilution with inorganic material. Terrestrially sourced hydrocarbon concentrations were reduced over the entire Cruise III transect as compared to Cruises I and II, but the deepest stations (>1,500 m) on Cruise III exhibited elevated levels of petroleum hydrocarbons. This is substantiated by the differences in hydrocarbon source parameters previously discussed (Figs. 2-9 and 2-10). Examination of carbon preference index distributions and gas chromatograms suggest the presence of relatively fresh petroleum hydrocarbons, probably from oil seepage, at the deepest stations (Fig. 2-11). Station C7 also has the lowest CPI of this transect, suggesting anomalously high petroleum hydrocarbons. The presence of a high CPI associated with mature petroleum can be explained by the mixing of an oil substantially depleted in $>C_{25}$ alkanes (typical Gulf oil) with a sediment dominated by odd carbon terrestrially derived hydrocarbons $>C_{25}$. Recycled organic matter tends to be significantly reworked by evaporation, dissolution and microbial degradation leading to a depletion in aliphatic hydrocarbon. These differences between samplings most likely represent the patchiness associated with hydrocarbon distributions and do not reflect a temporal change (i.e., flux).

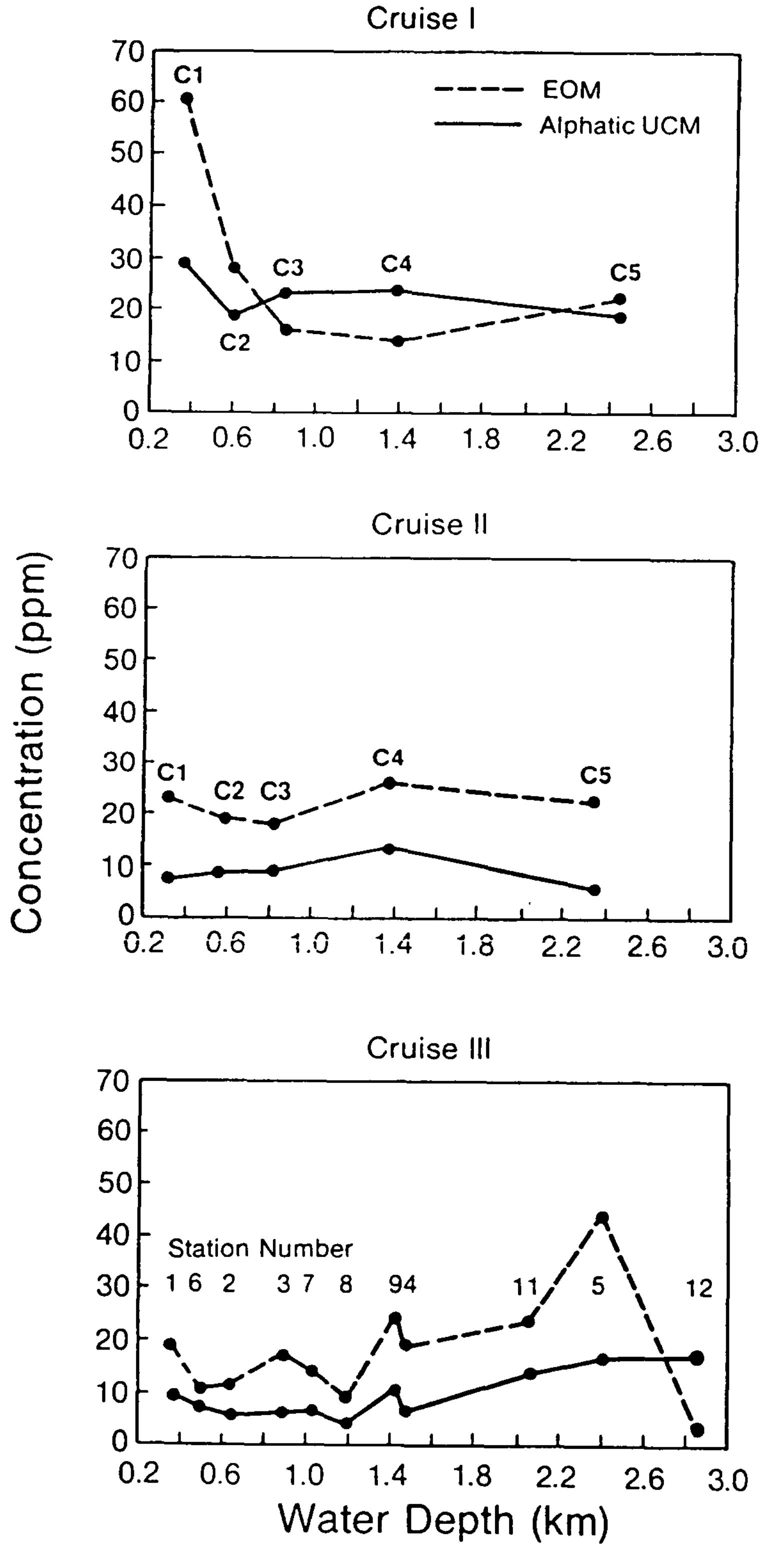


Figure 2-8. Variations in extractable organic matter and the aliphatic unresolved complex mixture during three samplings of the central transect.

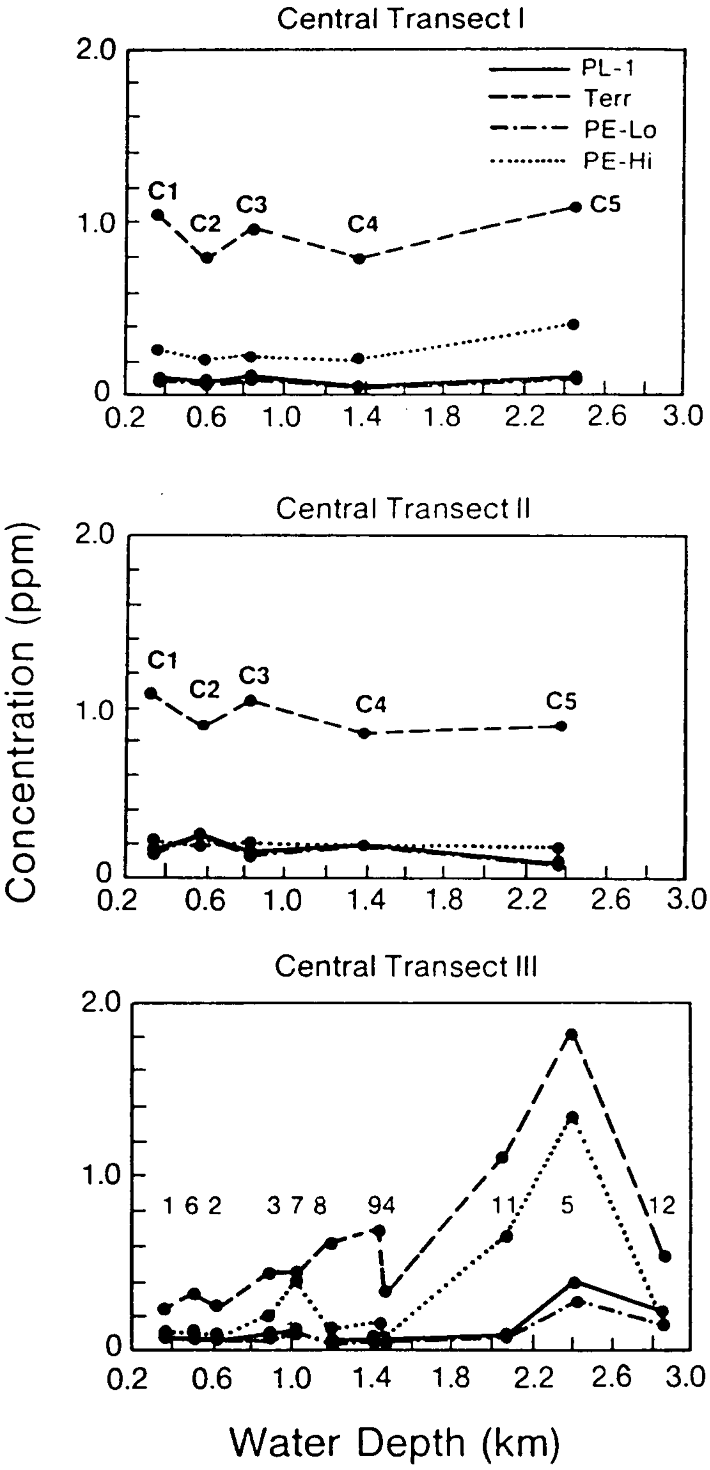


Figure 2-9. Variations in hydrocarbon source parameters during three samplings of the central transect.

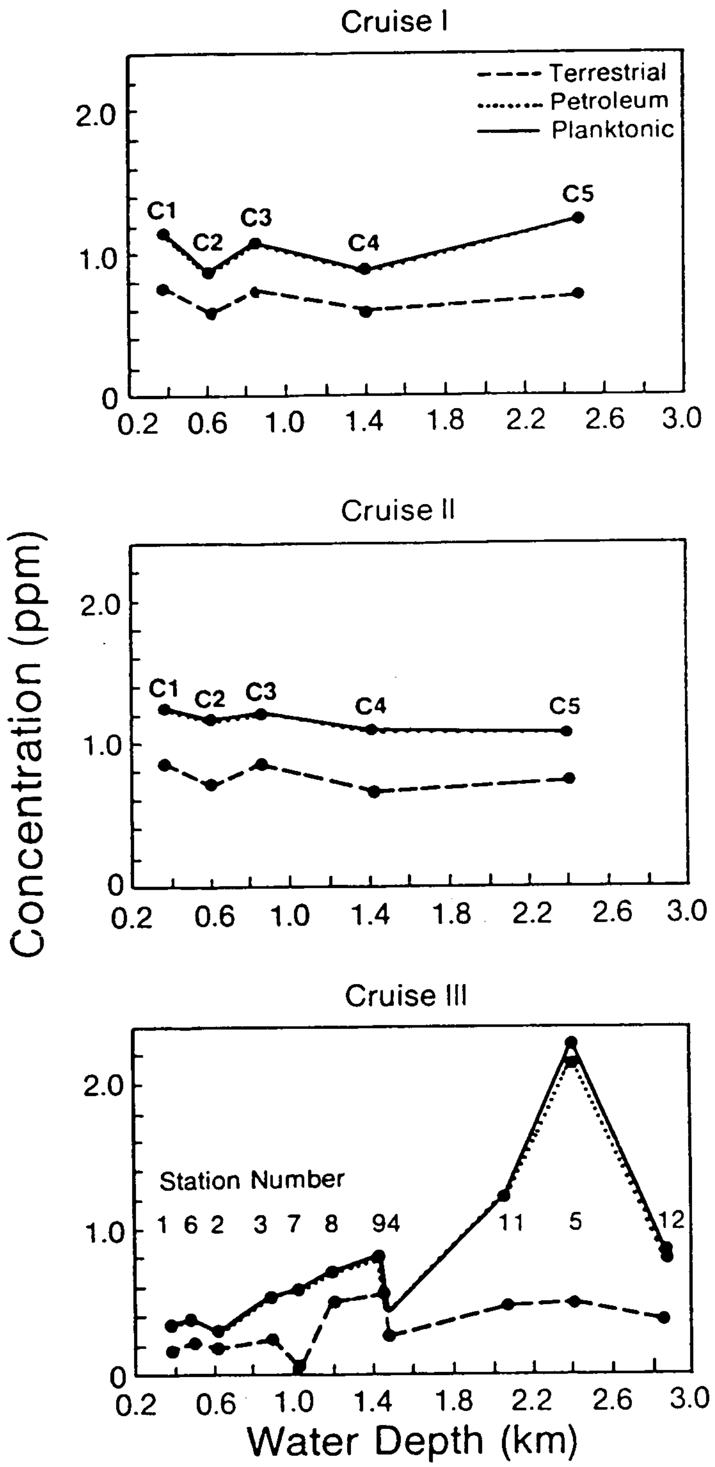
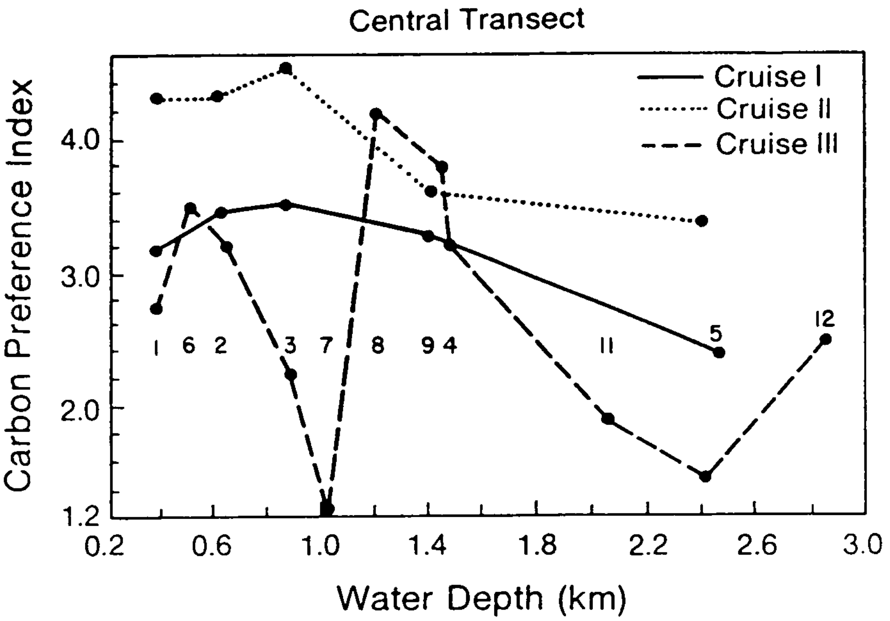


Figure 2-10. Variation in plankton, terrestrial and petroleum hydrocarbons during three samplings of the central transect presented as a cumulative concentration.



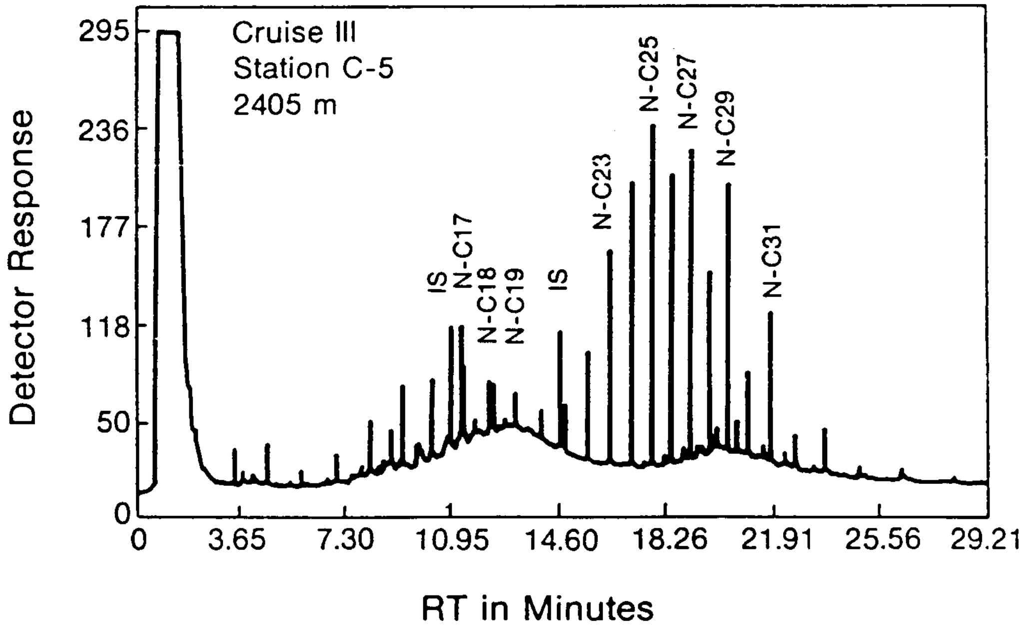


Figure 2-11. Variation in the carbon preference index as a function of depth along the central transect during Cruises I-III (numbers 1-12 represent Cruise III stations) and a representative fused silica gas chromatogram of the aliphatic hydrocarbons from Station C5, Cruise III.

Variability Along Isobaths

Cruise IV in the eastern Gulf of Mexico occupied stations along three isobaths to assess lateral variations in hydrocarbon parameters (Table 2-3). Bulk and molecular parameters were low compared with previous samplings and represent some of the lowest values measured during this study (see Table 2-1); as such the variability (as a percentage) observed along this transect is probably a maximum value. These sampling sites were also chosen to contrast sediment texture which also contributes to the observed variability in hydrocarbon parameters. The aliphatic UCM and total EOM vary by factors of 1.7 to 7.6 at a given depth. Molecular level indicators (i.e., individual component sums) vary by a factor of 2.0 to 7.6 along a given isobath. These data suggest that, at these low concentrations, hydrocarbons are as variable along isobaths in the eastern Gulf as they are with water depth. These data also emphasize the patchy nature of hydrocarbon distributions. Bulk sediment parameters, such as percent sand, varied by as much as a factor of 3 along an isobath, illustrating marked variations in sediment texture as well.

Samples along isobaths in the central and western Gulf were also taken. Data from Stations sampled on Cruises I, II, III and V at ~350 m are compared in Table 2-4. The variability in hydrocarbon parameters reflecting terrestrial input show the greatest variation, as much as 40-fold. The plankton indicators are also highly variable most likely due to dilution with terrestrially sourced material. Bulk parameters such as clay content vary by a factor of 2 and sand content varies from 0.5 to 36.6% at these six locations. These variations again reflect the substantial influence of river/terrestrial derived material. Three samples from Cruise V along the 550 and ~750 m isobath were uniform. The lateral extent covered is relatively small as compared to the 350 m isobath sampling. Bulk sediment parameters were also uniform at these locations.

Seep to Non-seep Comparison

Sediment hydrocarbon levels at stations occupied in known seep areas of the west/central Gulf of Mexico were compared to hydrocarbon levels at

Table 2-3. Variability in hydrocarbon parameters along isobaths - eastern Gulf of Mexico.

	Variable Ranges		
Depth (m):	342-383 m	619-630 m	819-859 m
No. of Stations:	n=4	n=6	n=5
Variable			
Total EOM (ppm)	5.8 - 13.4 (9.7)[1]	4.7 - 9.9 (6.8)	4.9 - 8.2 (5.8)
Aliphatic UCM (ppm)	0.7 - 5.0 (3.0)	0.5 - 3.8 (1.8)	0.7 - 3.1 (1.7)
PL-1[2] (ppb)	11.5 - 94.1 (54.3)	8.1 - 59.1 (29.9)	6.9 - 44.8 (23.4)
TERR[2] (ppb)	36.0 - 74.0 (55.9)	55.9 - 119.8 (78.6)	23.4 - 147.5 (121.6)
PE-Lo[2] (ppb)	13.3 - 100.7 (56.2)	13.5 - 39.8 (21.1)	11.0 - 27.3 (18.8)
PE-Hi[2] (ppb)	14.4 - 30.3 (22.3)	20.4 - 53.1 (33.1)	17.5 - 77.6 (48.6)
Terrigenous[3] (ppb)	21.6 - 49.8 (33.6)	24.0 - 66.7 (45.4)	5.9 - 99.5 (72.8)
Petroleum[3] (ppb)	33.5 - 118.3 (78.5)	34.6 - 67.9 (54.3)	28.5 - 103.5 (67.4)
Planktonic[3] (ppb)	0.0 - 2.8 (0.7)	0.0 - 20.1 (9.5)	0.0 - 17.5 (7.3)

---

[1] Average.

[2] PL-1 = Σn-$C_{15, 17, 19}$ and Pristane; TERR = Σ n-$C_{25, 27, 29, 31}$; PE-Lo = Σ n-$C_{16, 18, 20}$ and Phytane; PE-Hi = Σ n-$C_{24, 26, 28, 30}$.

[3] Terrigenous = (TERR) - (PE-Hi); Petroleum = PE-Lo + PE-Hi); Planktonic = (PL-1) - (PE-Lo).

Table 2-4. Variability in hydrocarbon parameters along isobaths - west/central Gulf of Mexico (for definitions of hydrocarbon parameters see Table 2-3).

	Variable Ranges		
Depth (m):	298-371 m[1]	547-550 m[2]	748-759 m[3]
No. of Stations:	n=6	n=3	n=3
Variable			
Total EOM (ppm)	15.9 - 61.3 (34.5)	17.4 - 23.9 (20.6)	17.0 - 57.9 (30.9)
Aliphatic UCM (ppm)	6.0 - 31.4 (15.6)	6.9 - 7.9 (7.6)	5.6 - 11.9 (8.4)
PL-1 (ppb)	36.3 - 174.9 (121.8)	47.4 - 65.3 (56.4)	50.0 - 68.0 (59.9)
TERR (ppb)	93.4 - 1082.8 (546.7)	109.8 - 273.1 (201.2)	169.7 - 180.5 (176.3)
PE-Lo (ppb)	36.2 - 154.5 (100.3)	39.1 - 52.5 (43.7)	43.4 - 48.9 (45.2)
PE-Hi (ppb)	70.9 - 279.7 (172.2)	80.6 -121.9 (99.4)	48.0 - 96.6 (64.8)
Terrigenous (ppb)	22.5 - 860.6 (374.5)	29.2 - 252.2 (101.7)	83.9 - 130.8 (111.5)
Petroleum (ppb)	123.3 - 388.0 (127.4)	119.7 - 161.5 (143.2)	91.4 - 140.0 (110.1)
Planktonic 9ppb)	0.1 - 57.7 (21.5)	4.0 - 26.2 (12.7)	6.6 - 19.1 (14.7)

---

[1] Cruises I, II and III, Stations E1 and W1; Cruise IV, Stations WC1 and WC2.

[2] Stations WC2, WC4, WC8.

[3] Stations WC3, WC9, WC10.

nearby stations. In general the petroleum indicators were elevated by a factor of two to three at the seep versus the non-seep sites (Table 2-5). This suggests that the petroleum was substantially biodegraded. Variability in hydrocarbon concentrations at the seep/non-seep areas was of the same order of magnitude as along isobaths with varying sediment type. However, previous samplings at seep locations have retrieved sediments with total EOM as high as 150,000 ppm as contrasted to the average of 60.3 ppm for the two "seep" sites sampled in this study. This again emphasizes the patchy nature of hydrocarbon distributions and in particular the non-uniform distribution of petroleum seepage in any given area. The potential extremes of petroleum hydrocarbon input to slope sediments are not represented in this sample set, though previous work documented that these samples were taken in an area of active, natural, oil seepage.

Topographic Features

One set of paired stations (WC11 and WC12) were taken to compare bottom topography effects. The sediment sample at a topographic (WC1) high was elevated in petroleum hydrocarbons (Table 2-6). This difference cannot be ascribed simply to topographic differences and more likely suggests that an additional input of hydrocarbons has occurred at Station WC11. More detailed studies would need to be performed to understand the relationship between hydrocarbons and topographic expressions.

Relationship to Bulk Parameters

In general, the highest aliphatic hydrocarbon concentrations were associated with the more clayey/organic carbon-rich sediments. To more fully understand the sedimentological relationships, the three primary hydrocarbon sources were considered individually since their distribution is controlled by different factors. The data must also be considered in the context of the sampling design, i.e., areal, temporal and water depth dependencies. Overall, however, the terrigenous or land-derived hydrocarbon component tends to increase with clay content within a given sampling period (Fig. 2-12), but when the data are considered as a

Table 2-5. Comparison of sediment hydrocarbon parameters at seep and non-seep locations on the western/central Gulf of Mexico continental slope (for definitions of hydrocarbon parameters see Table 2-3).

Station Type: No. of Stations: Variable	Variable Ranges Seep[1] n=2	Variable Ranges Non-Seep[2] n=3	Ratio[3]
Total EOM (ppm)	26.3 - 94.2 (60.3)	17.4 - 23.9 (20.6)	2.9
Aliphatic UCM (ppm)	6.8 - 46.2 (26.5)	6.9 - 7.9 (7.6)	3.5
PL-1 (ppb)	153 - 272 (212)	47.4 - 65.3 (56.4)	3.8
TERR (ppb)	147 - 237 (192)	110 - 273 (201)	0.95
Petro-Lo (ppb)	92.7 - 219 (156)	39.1 - 52.5 (43.7)	3.6
Petro-Hi (ppb)	99.9 - 119 (110)	80.6 - 122 (99.4)	1.1
Terrigenous (ppb)	46.8 - 117 (82.1)	29.2 - 151 (102)	0.8
Petroleum (ppb)	193 - 457 (266)	120 - 174 (144)	1.9
Planktonic (ppb)	52.1 - 60.0 (56.1)	4.0 - 26.2 (12.7)	4.4

[1] Stations WC6, WC7

[2] Stations WC2, WC4, WC8

[3] Ratio of seep parameter/non-seep parameter

Table 2-6. Comparison of sediment hydrocarbon parameters at two different topographic settings (for definitions of hydrocarbon parameters see Table 2-3).

Station: Station Type: Depth (m): Variable	WC-11 Topo-Hi (1226 m)	WC-12 Topo-Low (1236 m)
Total EOM (ppm)	18.9	17.1
Aliphatic UCM (ppm)	81.4	4.2
PL-1 (ppb)	266.6	67.5
TERR (ppb)	3068.3	182.6
Petro-Lo (ppb)	248.2	45.7
Petro-Hi (ppb)	852.7	44.9
Terrestrial (ppb)	2233.7	137.7
Planktonic (ppb)	18.4	21.8
Petroleum (ppb)	1100.9	90.6

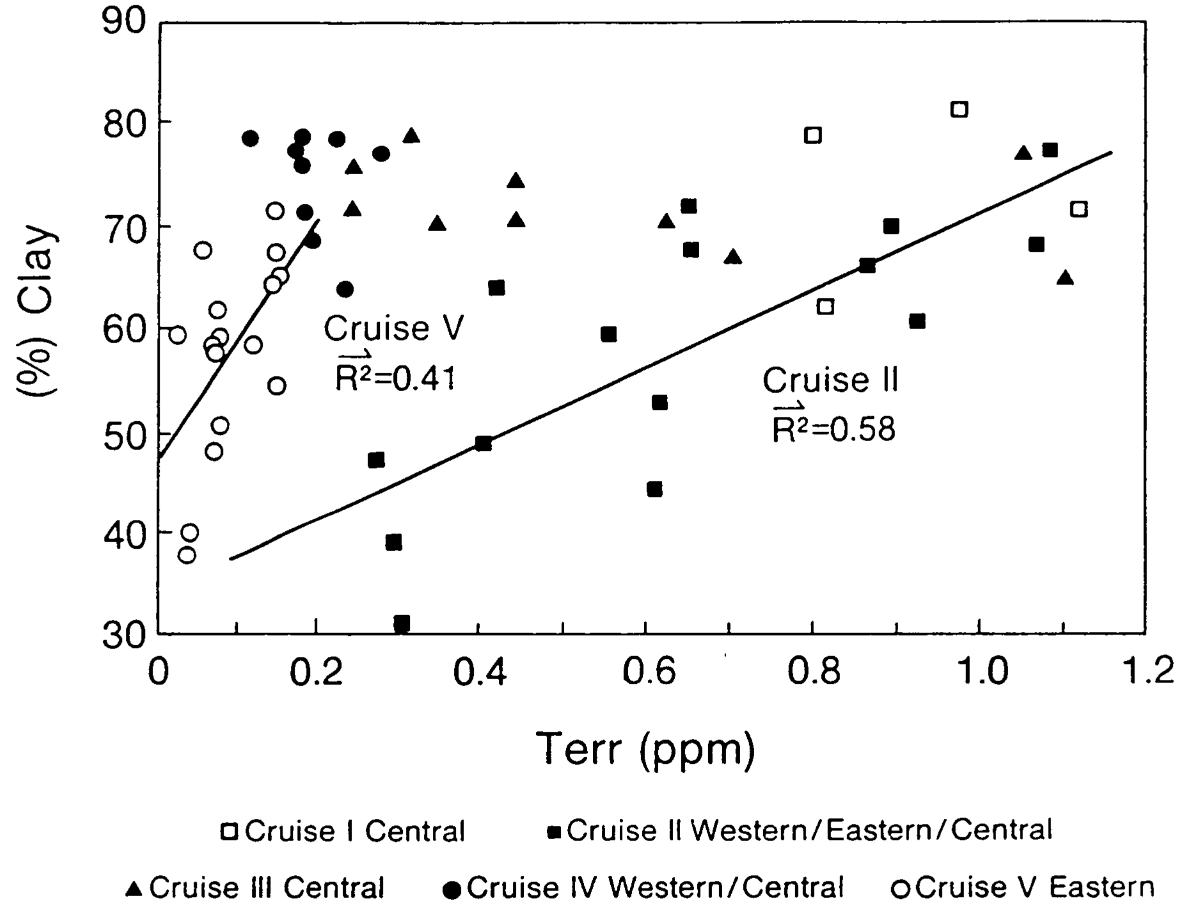


Figure 2-12. The relationship between a terrestrial hydrocarbon indicator and sediment clay content.

complete set, no trend is apparent. This may be due to changing clay to terrigenous organic matter ratios with time and location. Among the samples, the Cruise III central transect and the west/central samplings correlated least with grain size. This may have been due, in part, to a substantial petroleum input to the TERR indicator that is independent of the Mississippi River or a variable terrestrial input. It is also probable that the distance the material is transported and the composition of the transported material varies with time. The largest range in clay content was observed during Cruise II when the western, central and eastern transects were also sampled (Fig. 2-13). In this case, TERR generally increases with clay content and decreases with sand content. Within a given transect no correlation was evident. In general, the relative importance of riverine material between geographical areas can be estimated, though variability within a given area (i.e., along a transect) can be substantial. Petroleum indicators were generally independent of grain size, though as previously mentioned some component of the petroleum was apparently related to river associated particles (Fig. 2-14). Phytoplankton derived hydrocarbons did not correlate with grain size.

Aromatic Hydrocarbons

Sediment aromatic hydrocarbons were below the GC/FID detection limit (~5 ppb) at all locations sampled. This low level of individual aromatic compounds is consistent with the low level of aliphatic hydrocarbons. The aromatics, though a significant fraction of the total weight of a petroleum, are generally measured on an individual compound basis, an order of magnitude less concentrated than the n-alkanes. The presence of aromatic hydrocarbons at low concentrations was inferred from total scanning fluorescence analyses supporting the conclusion that a low level chronic petroleum input is present at all locations sampled. This petroleum input could be due to sedimentation from the overlying water column, transport of recycled organic matter from shallow water sediments (i.e., turbidity flows), or petroleum seepage.

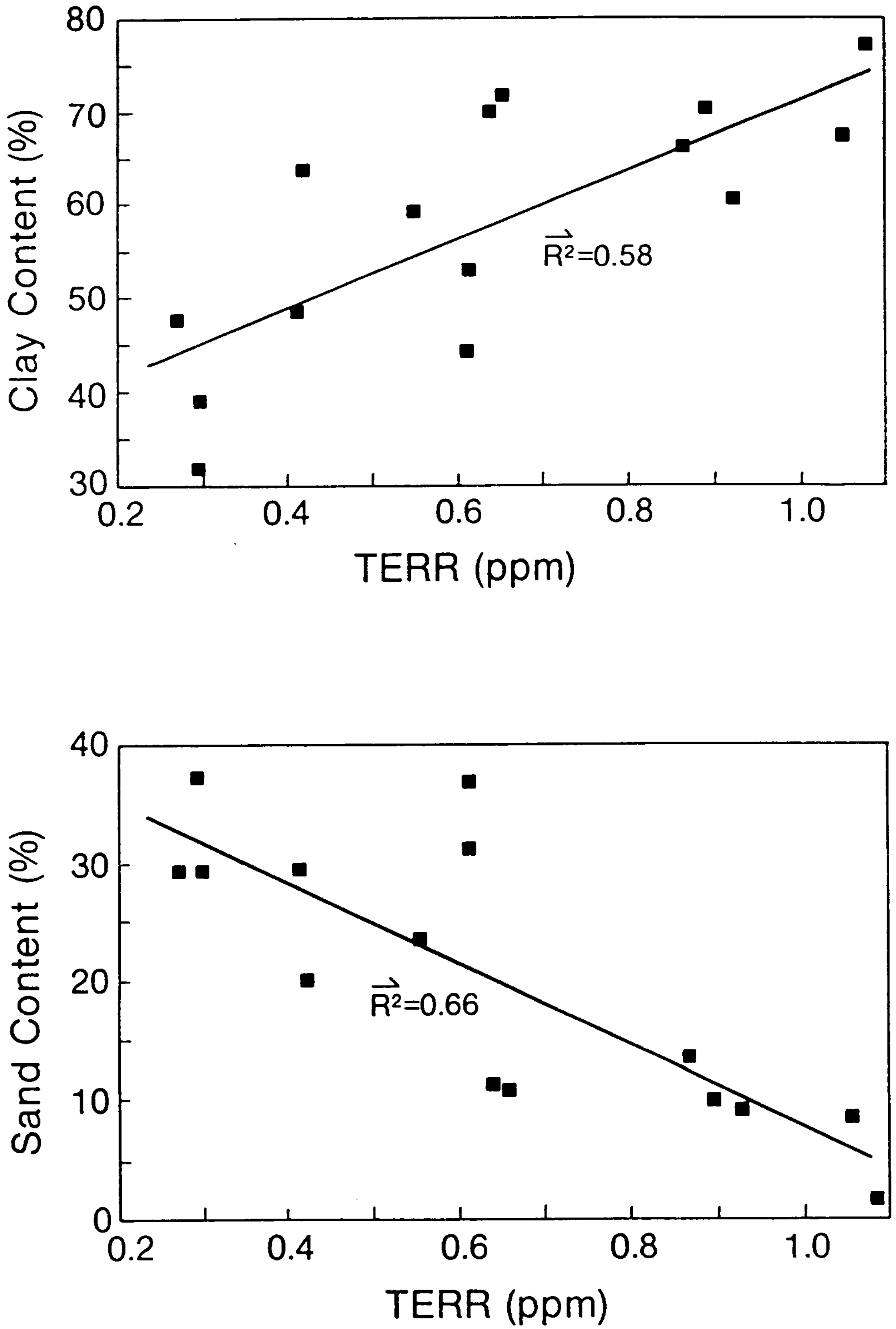


Figure 2-13. The relationship between a terrestrial hydrocarbon indicator and the clay and sand content of sediments from Cruise II.

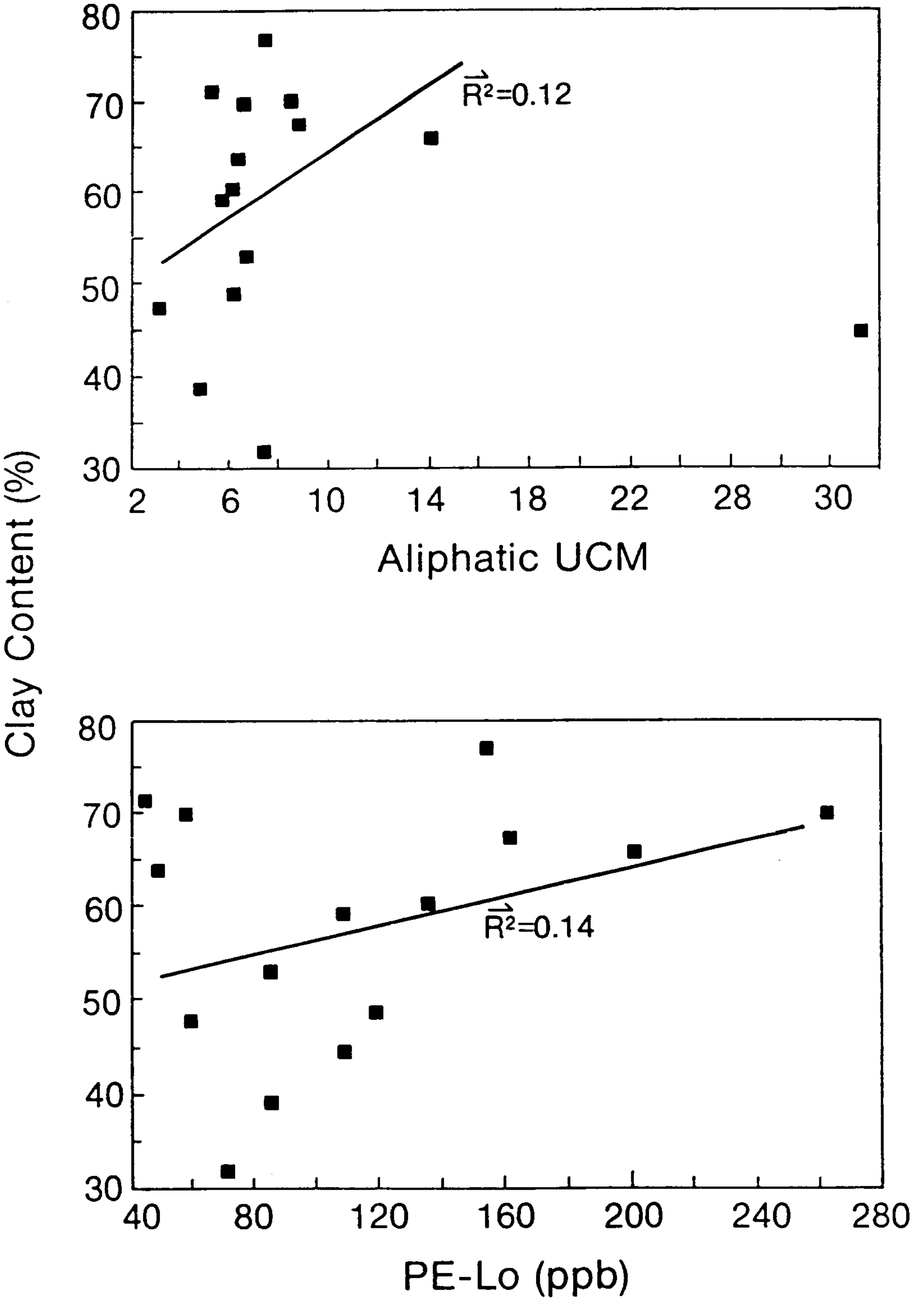


Figure 2-14. The relationship between two petroleum hydrocarbon indicators and the clay content of sediments from Cruise II.

HYDROCARBONS IN ORGANISMS

Hydrocarbon analyses in organisms were primarily restricted to megafauna taken by trawling, namely fish and decapod crustaceans. Due to the wide range in sampling depths no single species was available to provide definitive comparison of trophic levels or variations in concentrations with water depth. A broad survey of many species from throughout the trawl catches was provided (see Gallaway et al., 1988). In general organism tissue hydrocarbon concentrations were low level, and devoid of any obvious petroleum-related inputs. The dominant alkanes were pristane, n-C_{17}, n-C_{15} and n-C_{19}. These hydrocarbons have a presumed planktonic origin. The total extractable organic matter (EOM) was predominantly biogenic lipid material and the concentrations varied widely. The gas chromatograms of the lipid material revealed the presence of the hydrocarbons mentioned above, as well as a second group of compounds tentatively identified as endogenous C_{28} to C_{30} steroidal compounds.

Hydrocarbon levels in Gulf of Mexico slope organisms were highly variable. Total resolved alkanes in tissues varied from <50 ppb to >8,000 ppb. No trends in hydrocarbon distributions were evident as a function of organism type. Of the organisms analyzed, decapod crustaceans had the lowest incidence of hydrocarbon occurrence in muscle tissues with 58 to 63% being hydrocarbon free (Gallaway et al., 1988). In contrast, more than ~75% of fish muscle tissues analyzed contained detectable hydrocarbons. It should be noted, however, that the samples for a given species were often limited to a single individual.

As previously stated, tissue hydrocarbons, when present, were generally dominated by pristane, n-C_{17}, n-C_{15}, and n-C_{19}, all having a planktonic origin. However, n-C_{16}, n-C_{18} and phytane were also present. These compounds are components of petroleum, but due to the low concentrations observed their source is unclear. A few organisms also contained measurable amounts of higher molecular weight petroleum and plant biowax hydrocarbons. All of these organisms were collected at the Central Transect except for one shrimp taken at Station E3 during Cruise II that contained primarily petroleum hydrocarbons. The presence of the plant biowaxes suggests that these organisms have assimilated hydrocarbons from the sediments that they live in. These hydrocarbons presumably reside in the sediments and not in the water column at these water depths. In two organisms, the plant biowaxes were detected in the liver and/or gonads as well as the muscle tissue. The presence of the sediment hydrocarbons in tissues suggest that these organisms either ingested sediments and/or other organisms that had previously ingested sediments. On average the highest alkane concentrations were detected in liver and gonad tissues, though there are high hydrocarbon levels present in some muscle tissues as well.

RESULTS OF PRINCIPAL COMPONENT ANALYSES

Although some 40 physical/chemical habitat variables were measured, some of these were considered unlikely as potential factors directly affecting benthic biota of the continental slope (e.g., inorganic nutrients in bottom waters measured to identify water masses). Ultimately the PCA was run using 22 bottom sediment and water column variables:

Bottom Sediments	Water Column
Percent Sand	Surface Transmissivity
Percent Silt	Bottom Transmissivity
Percent Clay	Surface Particulate Organic Carbon
Total Organic Carbon	Bottom Particulate Organic Carbon
Calcium Carbonate	Surface Dissolved Organic Carbon
Delta ^{13}C	Bottom Dissolved Organic Carbon
Carbon Preference Index	Bottom Temperature
Hydrocarbon Indices	Bottom Salinity
Unresolved Complex Mixture (UCM)	Bottom Dissolved Oxygen
Total Extractable Organic Material (TOTEOM)	
n-$C_{15,17,19}$ and Pristane (PL-1)	
n-$C_{16,18,20}$ and Phytane (PE-LO)	
n-$C_{25,27,29,31}$ (TERR)	
n-$C_{24,26,28,30}$ (PE-Hi)	

In each of the four PCA analyses, corresponding to the four experiments, principal components 1 and 2 accounted for 45 to 63% of the total sample variance:

PCA 1: Region/Season/Year Comparison - 45%
PCA 2: Depth Comparison - 63%
PCA 3: Latitude by Depth Comparison - 59%
PCA 4: Longitude by Depth Comparison - 61%

In PCA 1, stations from each region generally clustered together and separated on the x-axis by levels of organic carbon and hydrocarbons versus percent sand and bottom water transparency, and on the y-axis by plankton and high molecular weight hydrocarbons versus bottom temperature and surface water dissolved organic carbon (Fig. 2-15). Station C5 on Cruise III was the most disparate of all the stations due mainly to relatively high organic carbon and hydrocarbon concentrations. Related depth data suggest that the location of this station on this cruise was at a marked change in declivity where organic matter might be expected to accumulate. In general, organic carbon and hydrocarbon levels were highest in the central region and lowest in the eastern region.

The results of PCA 2, an analysis of variation among 11 central transect stations by depth, yielded three general groupings on the x-axis separated mainly by hydrocarbon levels (Fig. 2-16). One group included two stations shallower than 500 m, and another group included the three stations greater than 2,000 m in depth. Stations between these depth ranges clustered together with regard to placement on the x-axis (Principal Component 1) but were divided into two groups along the y-axis (Principal Component 2). On the latter axis the separation was mainly attributable to sand content and bottom dissolved organic carbon levels.

The results of PCA 3, conducted on eastern transect stations sampled on Cruise IV, yielded six station groupings separated on the x-axis mainly by clay content and on the y-axis by sand content and bottom water levels of dissolved organic carbon (Fig. 2-17). In general, the groupings reflected four depth related environments: one represented by stations shallower than 500 m; one by stations about 650 m in depth; one by

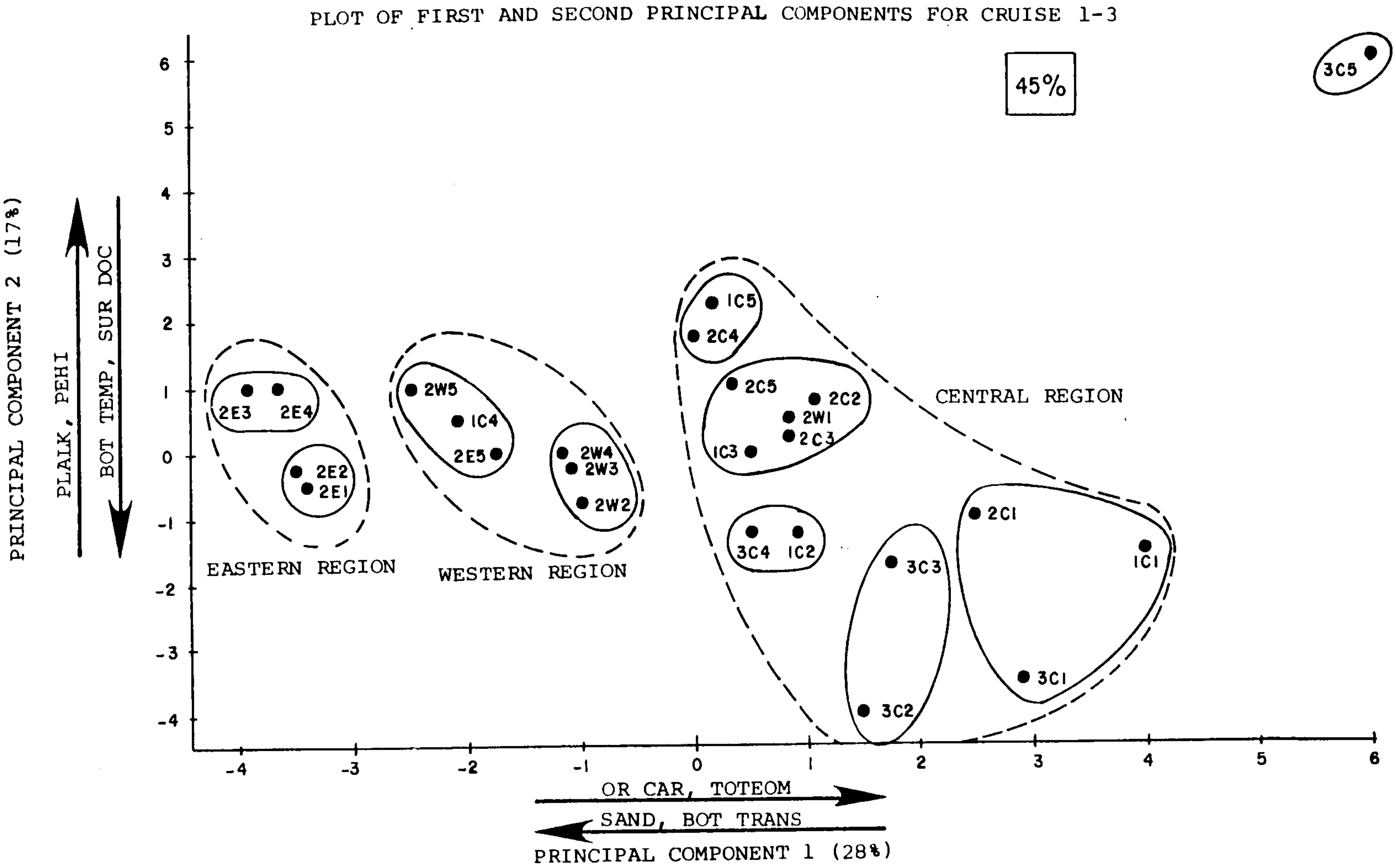


Figure 2-15. Results of Principal Component Analysis of physical/chemical variables showing similarities of Stations C1-C5, E1-E5, and W1-W5 sampled during Cruises I (fall 1983), II (spring 1984) and III (fall 1984).

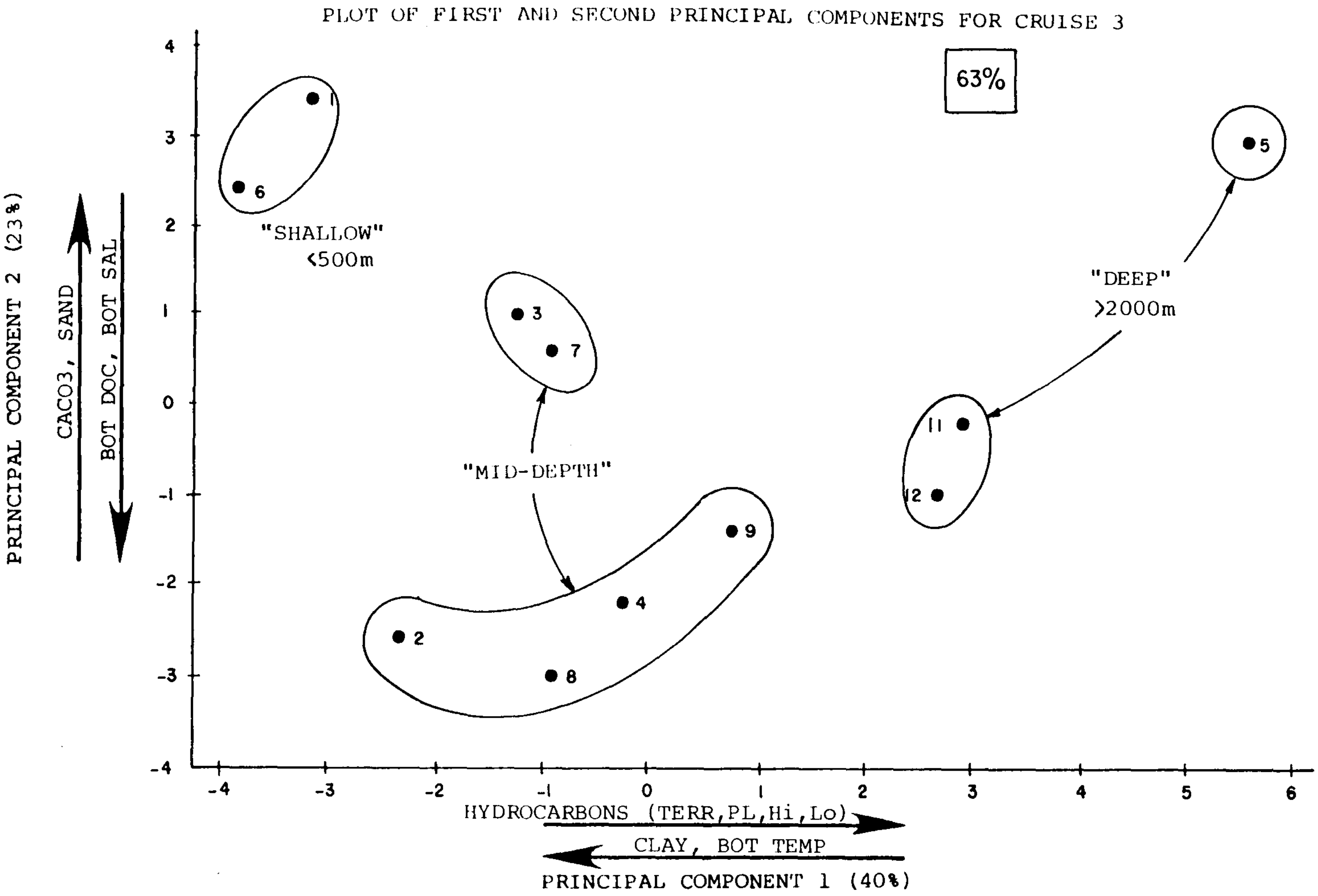


Figure 2-16. Results of Principal Component Analysis of physical/chemical variables showing similarities of Stations C2-C12 sampled during Cruise III (fall 1984).

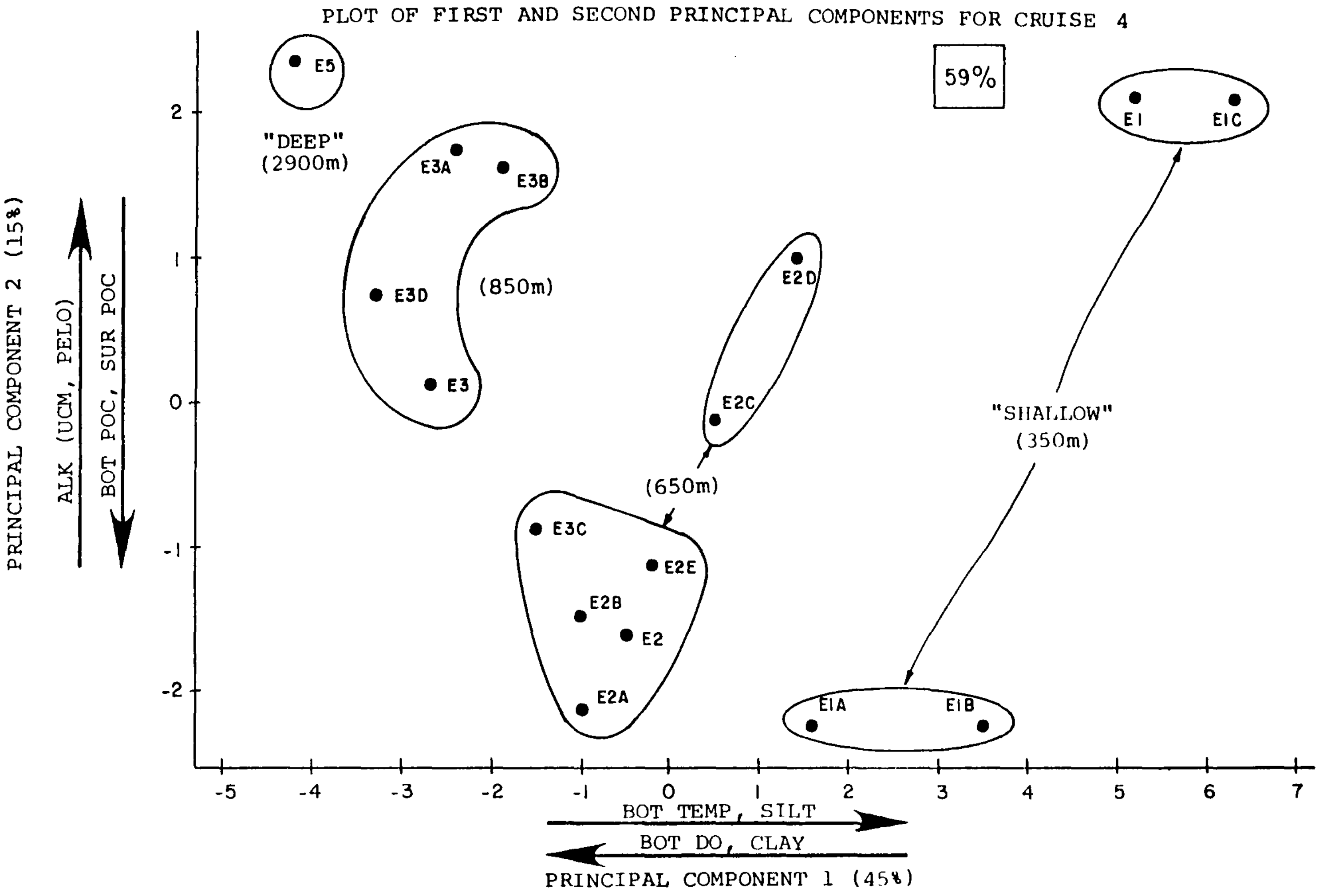


Figure 2-17. Results of Principal Component Analysis of physical/chemical variables showing similarities of 16 eastern Gulf of Mexico stations sampled on Cruise IV during Spring 1985.

stations about 850 m in depth; and the last by a single station located in 2,900 m of water.

PCA 4 included stations sampled in the west-central Gulf on Cruise V. Analysis yielded three station groupings that reflected station depth even though depth was not an input variable (Fig. 2-18). The depth groups were generally stations in the 300-, 500- and 750-, and 1,200-m depth ranges. Of interest here is that two 500-m deep stations clustered with the 300-m deep stations, mainly due to hydrocarbon content. These two stations were located near areas of petroleum seeps.

GENERAL DISCUSSION AND SUMMARY

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

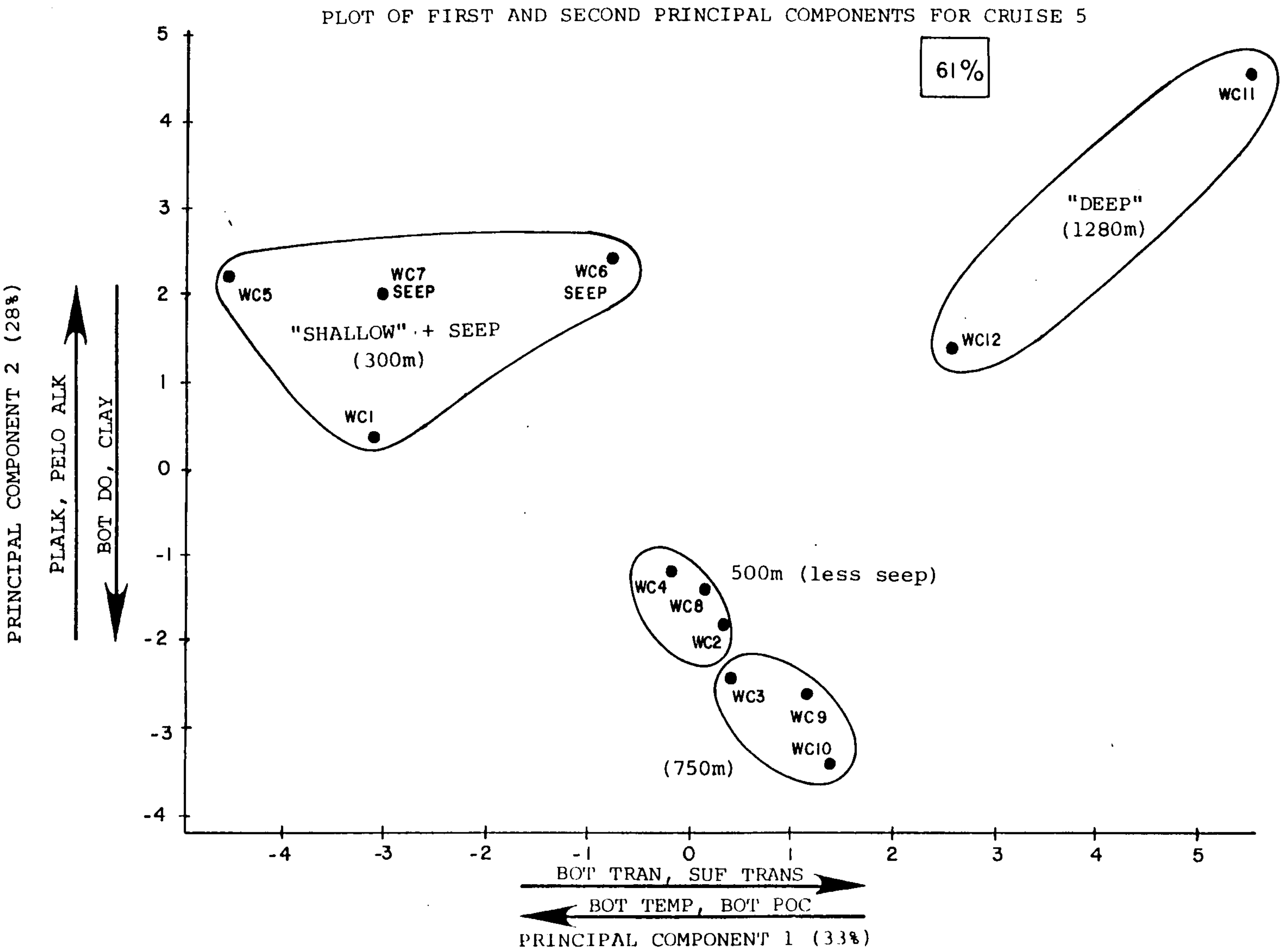


Figure 2-18. Results of Principal Component Analysis of physical/chemical variables showing similarities of 12 stations sampled in the west-central (WC) Gulf of Mexico during Summer 1985.

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 (see Chapters 6 and 7), was lower than previous reports for shelf and coastal sediments but no regular 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 clayish, 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. Terrigeneous hydrocarbons were common but the majority of the hydrocarbons appeared of plankton origin.

Results of the PCA analyses 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 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.

CONCLUSIONS

Based upon the results of this study, we conclude that:

(1) Water masses over the Gulf of Mexico continental slope have been adequately described and differ little either temporally or spatially.

(2) Benthic habitats of the slope differ significantly by region, with the eastern Gulf habitats being most different from those of the similar central and western Gulf. The effects of the Mississippi River discharge and petroleum seeps likely account for most of the observed differences (petroleum seep communities are described below in Chapters 6 and 7).

(3) Slope environments differ significantly by depth. Shallow and deep habitats are connected by a broad transitional zone. Subtle hydrocarbon differences account for most of the variation.

(4) Hydrocarbon levels are greater in the central and western Gulf than in the eastern Gulf.

In subsequent sections, comparisons of environmental to faunal differences are presented and discussed.

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CHAPTER 3. OBSERVATIONS ON THE DISTRIBUTION AND ABUNDANCE OF THE MEIOFAUNA OF THE CONTINENTAL SLOPE OF THE NORTHERN GULF OF MEXICO

B.J. Gallaway, R.L. Howard, and G.F. Hubbard

INTRODUCTION

Energy or food availability is generally considered the major factor controlling distributional patterns in the deep sea. Both within and between localities (and on a wide scale), it has been generally apparent that food availability is one of the prime factors explaining the differences in faunal densities in the deep sea. Observations of decreases in standing stocks with increasing depth and/or distance from the continents have been made by many deep sea researchers (e.g., Sanders and Hessler, 1969; Rowe, 1971; Rowe, 1983; and Thiel, 1983). The exceptions, such as the highly productive chemosynthetic communities in the northern Gulf of Mexico (see Chapter 6 of this report), particularly "prove the rule."

Thiel (1975) hypothesized that, for the deep-sea benthos, small organisms gained importance in total community metabolism as depth increases and food decreases. He defined the deep sea as a "small organism habitat", speaking in the broad sense at the community level. (It should be noted, as Thiel [1983] subsequently made clear, that the hypothesis did not say that all the species in the deep sea are smaller, size decrease must occur in all taxa and gigantism does not occur.) Independently of Thiel, Rowe and Menzel (1971) in a discussion of the depauparate nature of benthic samples from the deep Gulf of Mexico, concluded that where the fauna is sparse, the biomass must be parcelled into small packages of equivalent size. Schoener (1969) also provides evidence that food limitation would favor small size.

Studies of the meiofauna were included in this study to better understand benthic community structure and function on the continental slope of the northern Gulf of Mexico. Of particular interest was the comparative rates of decrease in meiofaunal and macrofaunal standing stocks with depth. The specific objectives were to:

(1) Describe, over time and space, the composition, distribution and abundance of the meiofauna of the continental slope of the northern Gulf of Mexico;

(2) Relate observed trends to environmental features and the macrofauna, comparing results to other deep-sea regions; and

(3) Identify any unusual or important meiofaunal resources.

For the purposes of this report, the meiofauna were defined as those metazoan organisms retained on a 0.063 mm sieve after the sample had been rinsed through a 0.300 mm sieve to remove larger macrofaunal organisms.

STUDY AREA AND METHODS

Samples were collected as described in Chapter 1 of this report using a box core. Two replicates were taken from each of the 324 grabs taken at 59 stations. Twelve replicates were obtained for each station, except those sampled on the eastern and western transects on Cruise II when only six replicates were obtained (by design).

Individuals were identified to major group and enumerated. Biomass was estimated based upon published literature values for the size ranges of organisms in the samples (Fauble, 1982; Rowe et al., 1974). Results are presented as densities per 10 cm^2 following Thiel (1983).

RESULTS

The meiofaunal collections contained in excess of 230,000 individuals representing 43 major groups of animals (see Gallaway et al., 1988 for a complete listing of the data). 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 (Table 3-1). 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).

Table 3-1. Overall abundance and estimated biomass of the meiofaunal collection.

Taxa	Overall Abundance	Mean Density per 10 sq. cm	Standard Error	Wet Weight Multiplier	Approximate Wet Weight µg
Nematoda	135,167	414.62	10.25	0.85	114,892
Harpactacoida	41,826	128.3	3.11	2.8	117,113
Nauplii	30,119	92.39	2.75	2.15	64,756
Polychaeta	9,648	29.6	1.56	55.25	533,052
Ostracoda	6,118	18.77	0.58	39.15	239,520
Kinorhynch	2,222	6.82	0.41	2.8	6,222
All other taxa	5,648	0.91	0.13	NA	75,730
Total	230,748	707.82	16.2		1,151,283

Abundance Patterns

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 (Fig. 3-1). Also, there was an overall trend of decrease in abundance with depth, but this was not always the case (e.g., abundance on the eastern Gulf transect in spring 1984, Fig. 3-1).

A more detailed examination of depth distribution was enabled from the fall 1984 sampling on the central transect (Fig. 3-2). 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 (Figs. 3-3 and 3-4). The samples reflected remarkable constancy.

Mean density of meiofauna across all stations in this study was 700 organisms/10 cm^2, with individual station values ranging from about 200 to 1,100 organisms/10 cm^2. 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 cm^2. 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.

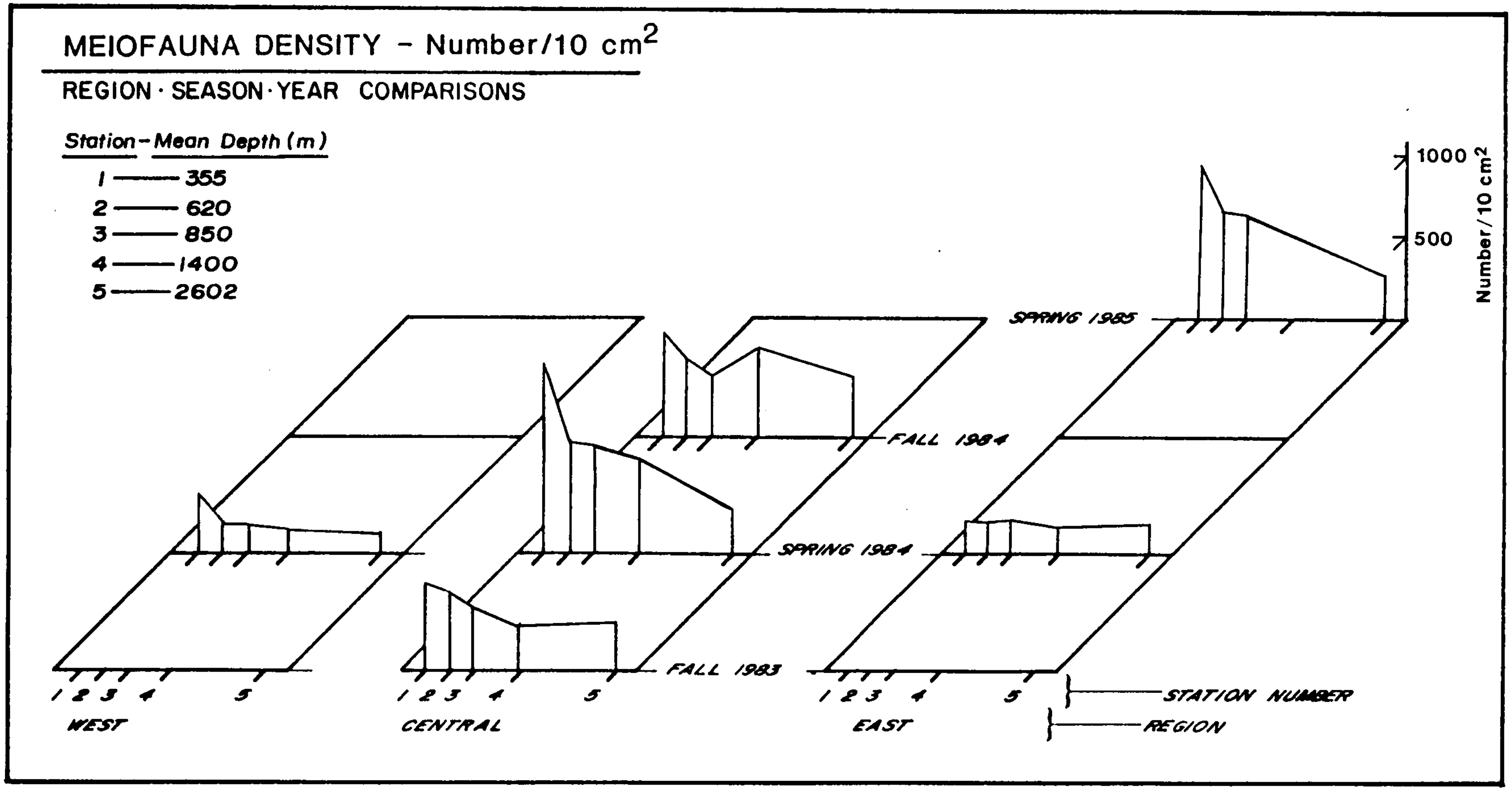

Figure 3-1. Comparative levels of meiofaunal densities by region, season, year, and selected depth interval.

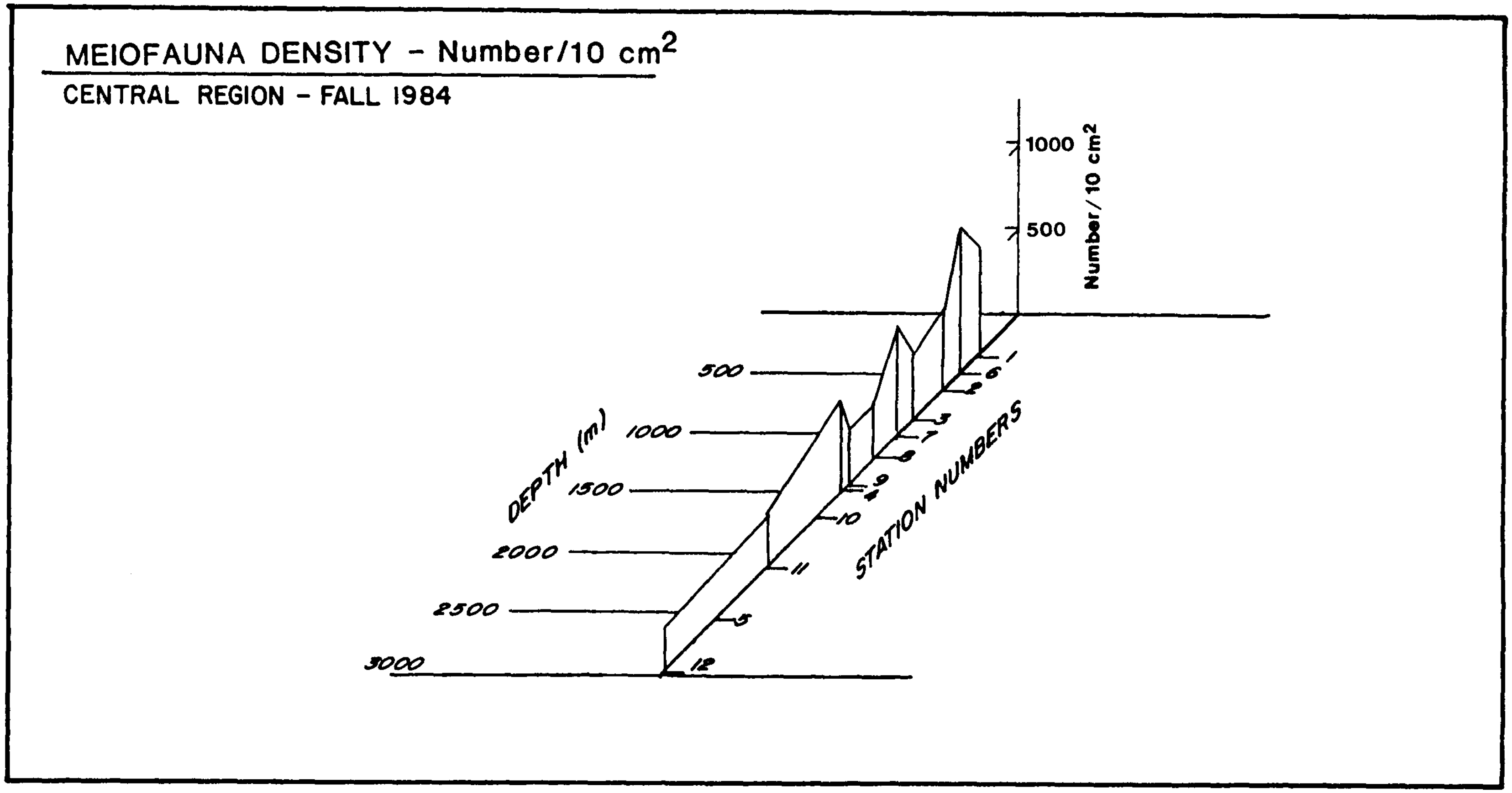

Figure 3-2. Comparative levels of meiofaunal densities by depth on the central transect, fall 1984.

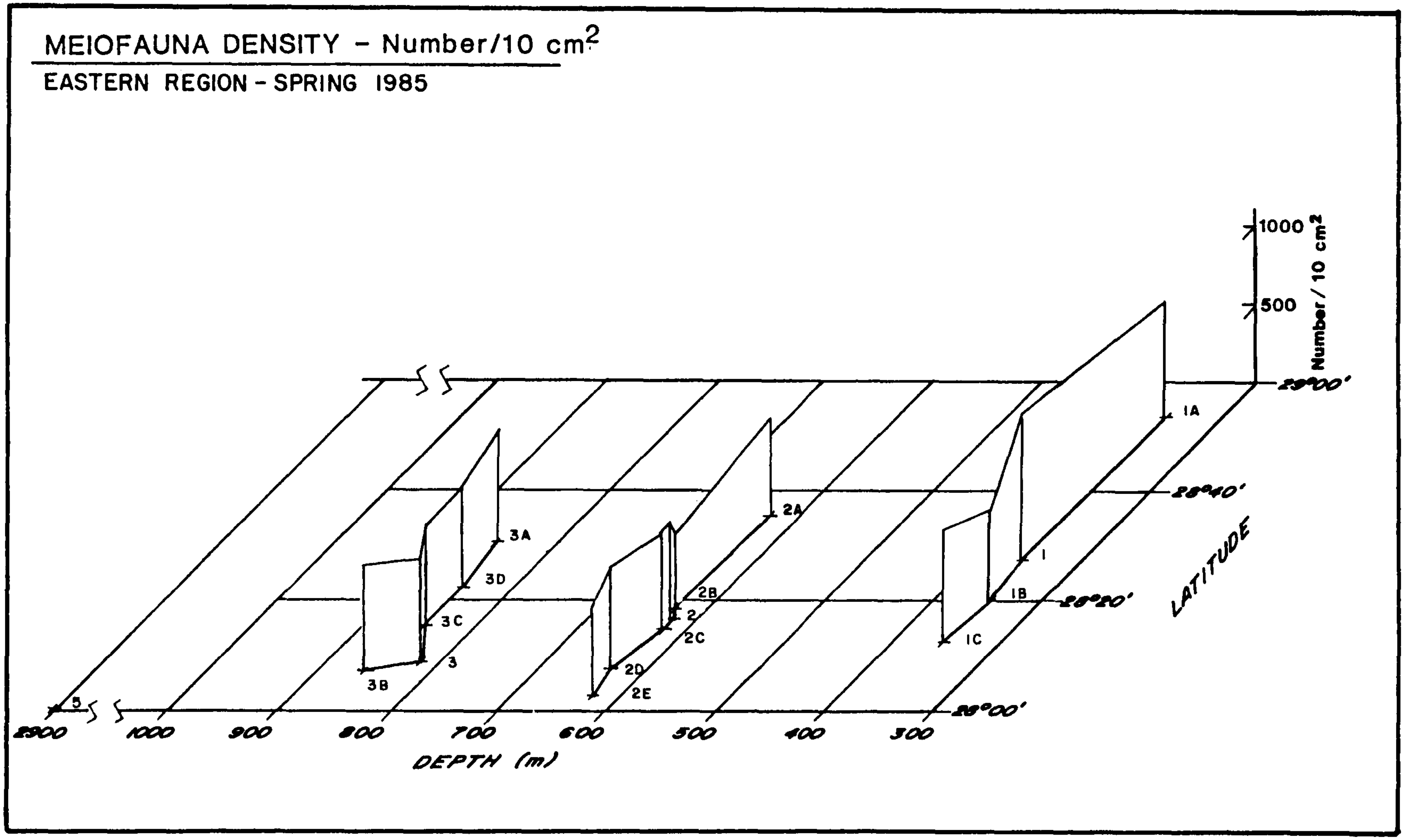

Figure 3-3. Comparative levels of meiofaunal densities along selected isobaths in the eastern Gulf of Mexico, spring 1985.

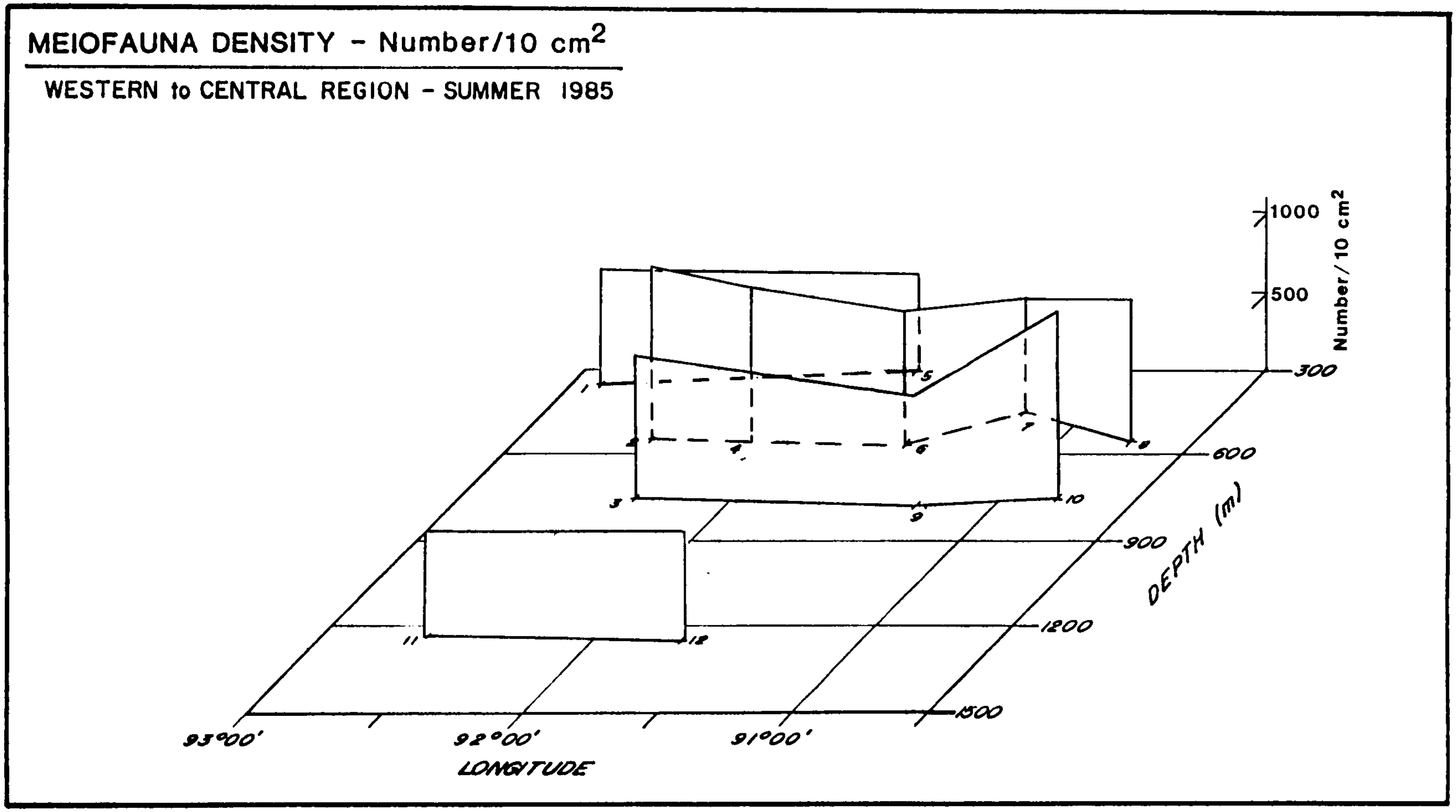

Figure 3-4. Comparative levels of meiofaunal densities along isobaths between the central and western Gulf of Mexico sampling transects, summer 1985.

Relation to Macrofauna

Both macrofauna and meiofauna numbers and biomass deceased overall with depth (Fig. 3-5). 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.

Relation to Environment

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.

Studies in coastal habitats have indicated that sediment grain size influences the relative abundance of nematodes and harpacticoids (Tietjen, 1969; Coull, 1970). Because these were the most abundant groups found in the present collections, changes in their relative density would influence the overall meiofaunal density. Figure 3-6 shows a comparison of the abundance of nematodes and harpacticoids plotted against percent sand and percent clay. Linear regression of these points shows that the abundance

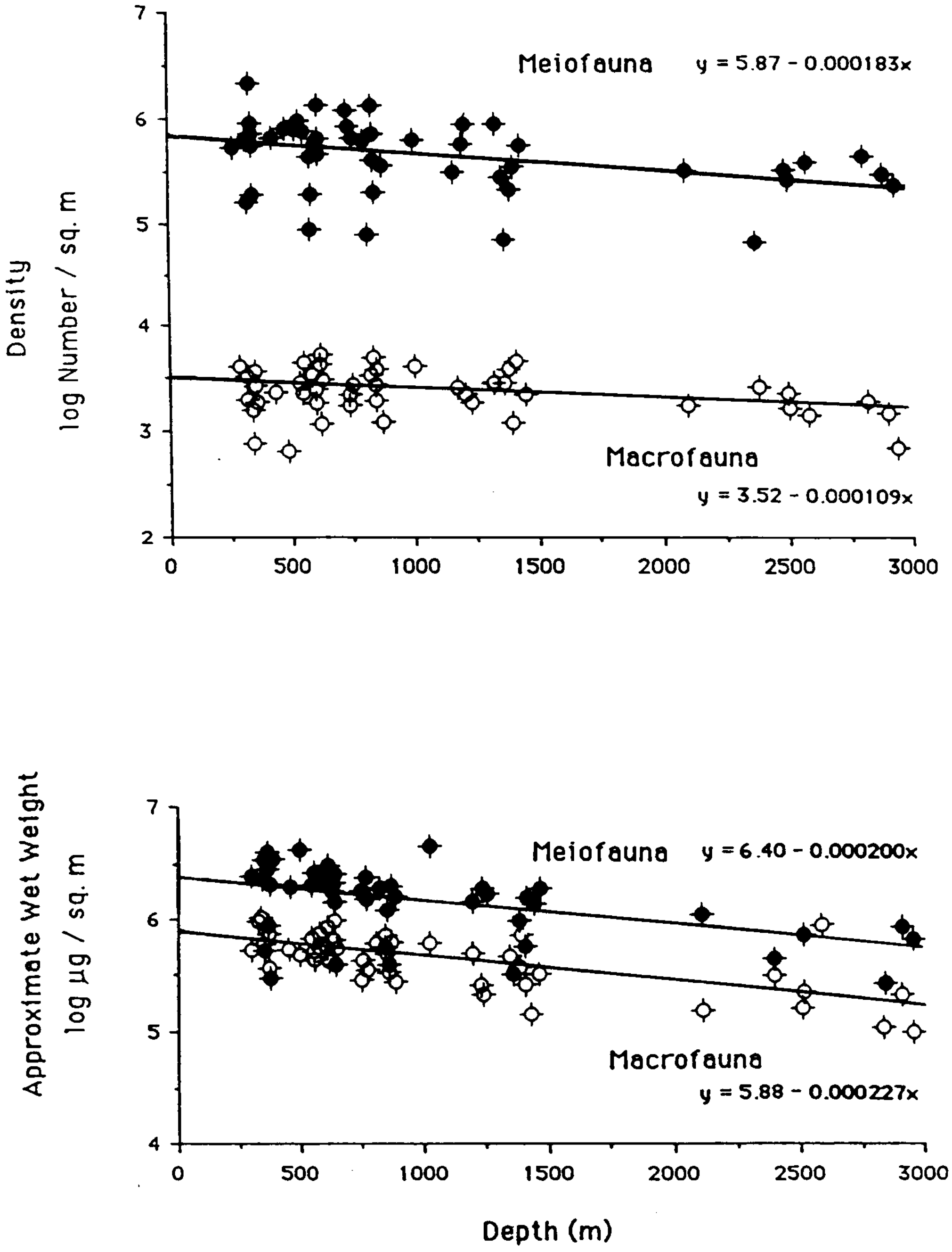

Figure 3-5. Relative occurrence of meiofauna and macrofauna with depth at all sampling stations. Upper plot shows log of density per square meter. Lower plot shows log of approximate biomass per square meter.

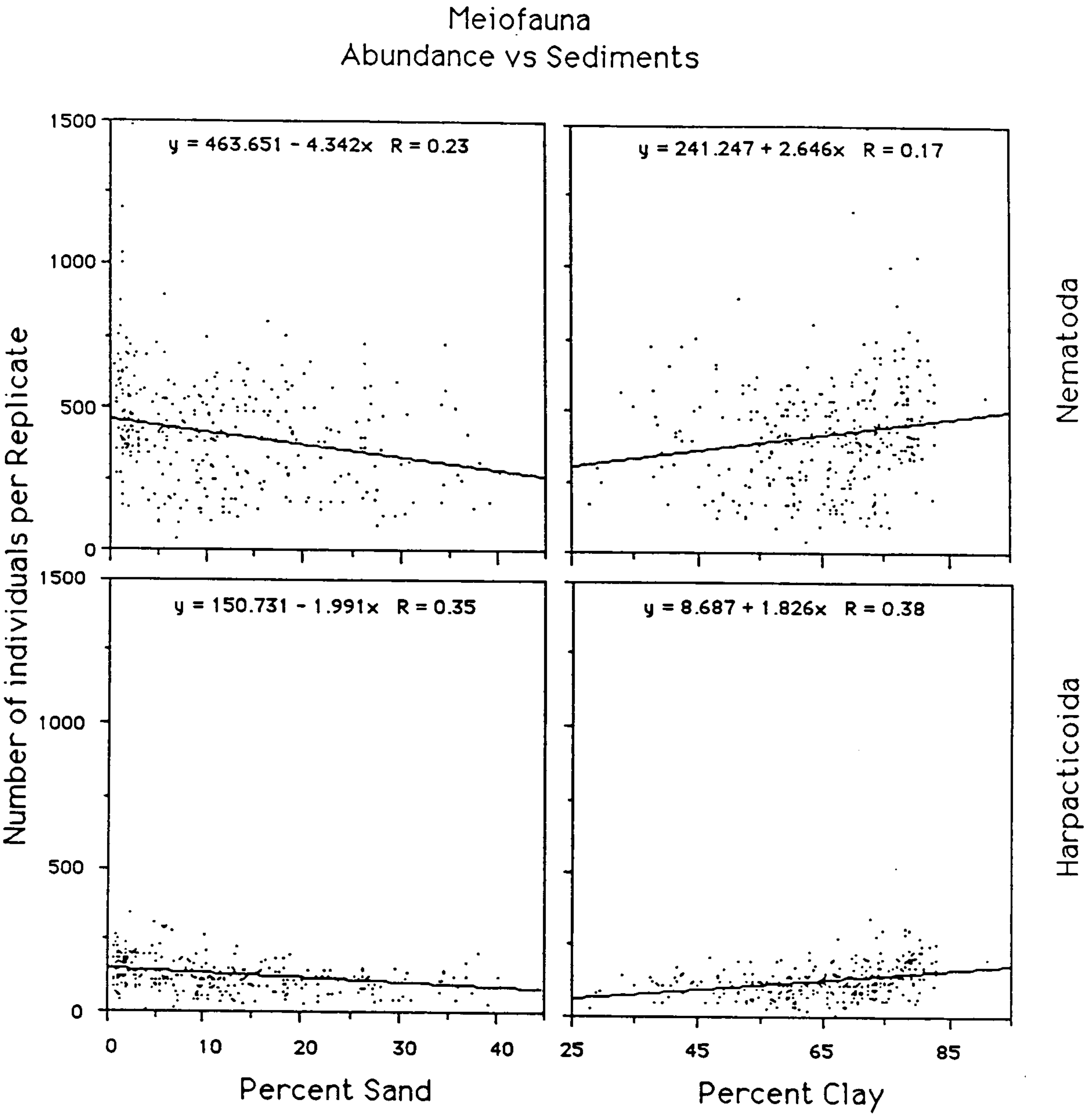

Figure 3-6. Abundance of Nematoda and Harpacticoida plotted against percent sand and clay.

of both groups decreased as the sediments became coarser, and increased as they became finer. The rate of change was more acute for the nematodes than for the harpacticoids, particularly in the case of increasingly sandy sediments. The fit of these regressions are poor, however, which suggests that other factors also influenced the composition of the meiofauna.

Unusual Findings

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 (Fig. 3-7). 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.

CONCLUSIONS

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.

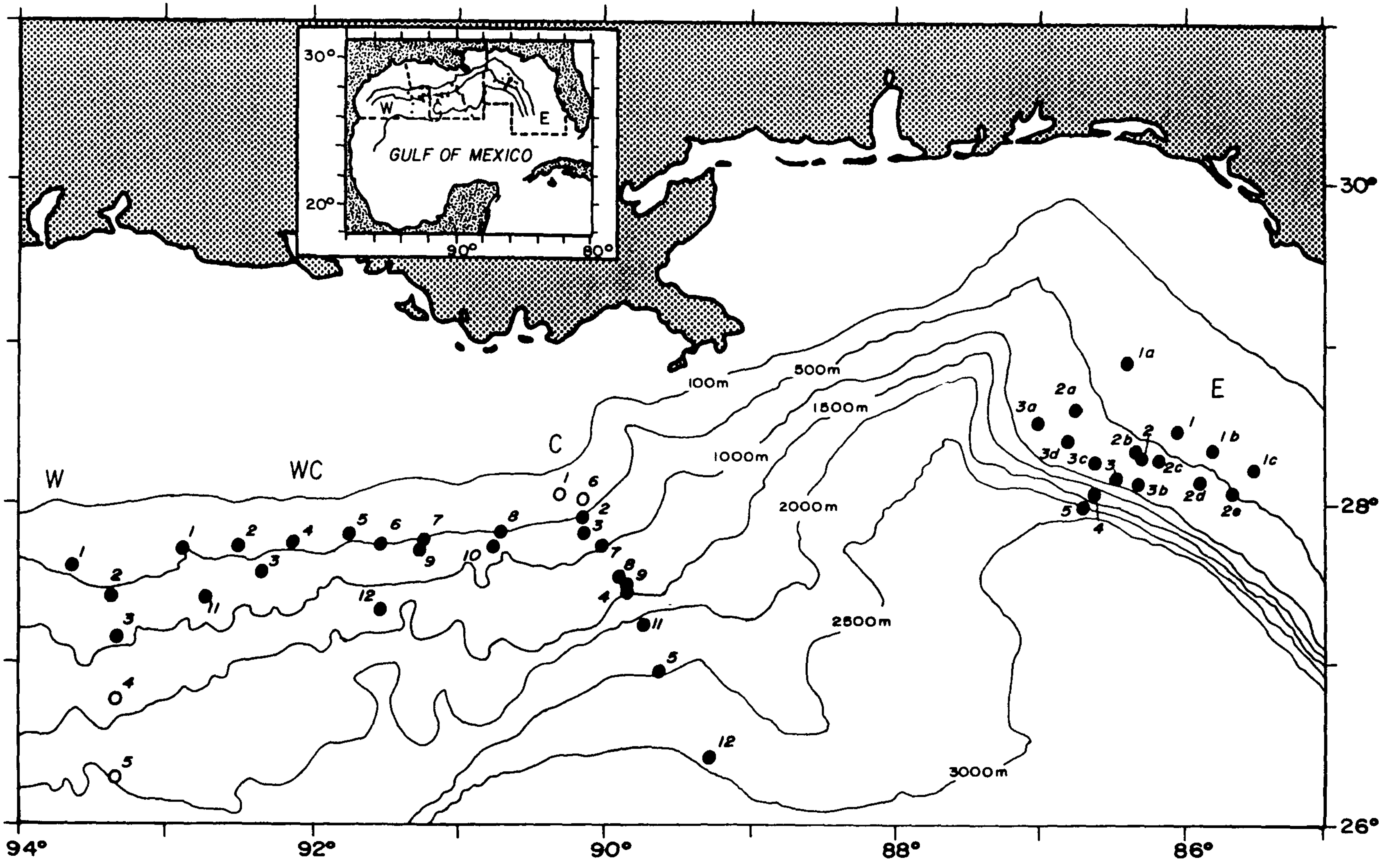

Figure 3-7. Distribution of the phylum Loricifera among continental slope sampling stations, 1983-1985. Open dots indicate no specimens were collected, closed dots indicate Loricifera was present.

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CHAPTER 4. THE MACROFAUNA OF THE CONTINENTAL SLOPE OF THE NORTHERN GULF OF MEXICO--COMMUNITY STRUCTURE, DIVERSITY AND ABUNDANCE AS COMPARED TO ENVIRONMENTAL FEATURES

B.J. Gallaway, R.L. Howard, and G.F. Hubbard

INTRODUCTION

As part of an overall objective to develop a regional data base for the continental slope of the northwestern Gulf of Mexico prior to oil and gas development, continental slope macrofauna were studied. Immediately prior to this study, a review of the literature (Pequegnat, 1983) had shown that very little information was available describing the macrofauna characteristic of the slope in this region. Therefore, macrofauna studies received high priority due to their known importance in other ecosystems. The primary objectives of the macrofauna investigations were to:

(1) Describe, over time and space, the composition and abundance of slope macrofauna;
(2) Relate any observed trends to environmental features;
(3) Compare results to other deep sea regions; and
(4) Identify any unusual or important macrofaunal resources.

In this study, macrofauna were defined as those organisms collected with box corers and retained on a 0.300 mm sieve; the group thus included much smaller individuals than one typically finds in other macrofauna samplings in the deep Gulf which have used 0.500 mm or 0.42 mm sieves. However, the findings are directly comparable to the Minerals Management Service's studies of the U.S. Atlantic continental slope.

Specimens were routinely identified to the lowest possible taxon, except for those belonging to four major groups in which severe taxonomic difficulties were encountered: Nematoda, Copepoda (primarily harpacticoid copepods), Aplacophora, and Scyphozoa. For the remaining groups, approximately 89% of the individuals were identified either to genus or to species; 71% of the taxa were identified to species. Specimens that could not be identified to species were usually either a) juveniles that had not yet developed the requisite taxonomic characteristics, or b) specimens that no longer possessed intact the morphological structures necessary for positive identification.

STUDY AREA AND METHODS

A description of the study area sampled and the methods used in sample collection and analyses is provided in Chapter 1. The conceptual study design included 60 stations (see Fig. 1-7), of which 59 were actually sampled. Samples were replicated (usually six but there were only three for eastern and western transect stations during Cruise II) and 324 of the planned 330 samples were obtained.

Statistical treatment of the data included numerical classification (cluster analysis), calculation of diversity indices, and analysis of variance (ANOVA) on density values for 61 of the most abundant individual species using a square root transformation. Also, correlation analyses (Pearsons Product Moment) were conducted, relating the density of the 61 most abundant species to the 22 water and sediment quality data variables (Table 4-1) upon which the PCA analyses were based as described in Chapter 2.

The cluster analyses were based upon presence/absence information for species represented by ten or more individuals using the Dice index of similarity. While many ecologists have disdained the use of binary data in interactions where quantitative data are available, others have noted that if there are many zeros in the data matrix (as was the case here), use of binary rather than quantitative data involves the loss of relatively little information (Boesch, 1977). An agglomerative cluster technique was used, based upon the group average method to define intergroup resemblance. According to Boesch (1977), group average agglomeration clustering is now the most widely used method in ecology.

Benthic community parameters, including Shannon-Weiner (H') diversity and its associated evenness (E) and richness values were calculated for each station. The H" index was calculated:

$$H''(s) = - \Sigma pj \log_e p_j$$

in which (s) is the total number of species and p_j the observed proportion of individuals belonging to the jth species (j = 1,2,....s).

Table 4-1. Environmental variables measured in sediment and water on the northern Gulf of Mexico continental slope.

Variable	Abbreviation	Unit of Measure	Where Measured
HYDROCARBONS			
Planktonic-derived alkanes	PL1ALK	ppb	Sediments
Low-molecular-weight alkanes	PELOALK	"	"
Petroleum-derived alkanes	PLHIALK	"	"
Terrigenous primary productivity	TERRI	"	"
Total extractable organic matter	TOTEOM	ppm	"
Aliphatic unresolved complex mixture	ALUCM	"	"
Carbon preference index	CPI	ratio	"
SEDIMENT GRAIN SIZE			
Sand	SAND	% by wt.	"
Silt	SILT	"	"
Clay	CLAY	"	"
OTHER CARBON MEASURES			
Organic carbon	ORCAR	"	"
Calcium carbonate	CACO3	"	"
Delta carbon-13	DELC13	ppt	"
WATER QUALITY			
Bottom water temperature	BOTTEM	°C	Water
Bottom water salinity	BOTSAL	ppt	"
Bottom water dissolved oxygen	BOTDO	ml/l	"
Bottom water transmissivity	BOTTRAN	percent	"
Bottom water particulate organic carbon	BOTPOC	μgC/l	"
Bottom water dissolved organic carbon	BOTDOC	μgC/l	"
Surface water transmissivity	SURTRAN	percent	"
Surface water particulate organic carbon	SURPOC	μgC/l	"
Surface water dissolved organic carbon	SURDOC	μgC/l	"

Hurlbert's modification (1971) of the rarefaction method (Sanders, 1968) was used to predict the number of species in a random sample without replacement, given a population N:

$$E\left[S_m \middle| N\right] = \sum_{i=1}^{k} 1 - \frac{(N_m - N_i)}{\binom{N}{m}}$$

in which N_i is the finite population of species i; N is $(N_1, N_2, \ldots, N_k)$, a vector representing the entire finite population; and S_m is the random variable denoting the number of species in a sample of size m (Smith and Grassle, 1977). N is the total number of individuals in the finite population:

$$\sum_{i=1}^{k} N_i$$

For the species diversity results, we used m=50 or the number of species per 50 individuals, m=100 or the number of species per 100 individuals, m=500, m=1,000, and m=5,000.

The ANOVAs and correlation analyses were accomplished using SAS statistical packages and the Texas A&M University Amdahl computer. Four ANOVAs were conducted--the first for comparing regional, seasonal and annual differences (by depth); the second to examine variation across isobaths in the central Gulf; the third to examine variation along different isobaths in the eastern Gulf; and the fourth to examine variation along isobaths in the region between our central and western Gulf transects (see Fig. 1-7).

Orthogonal contrasts (Li, 1964) were used to evaluate various a-priori distributional hypotheses. Given 25 stations in ANOVA 1, 24 contrasts were allowed. Stated as hypotheses these were:

(1) There were no significant differences in macrofaunal abundance between the eastern Gulf and the central and western Gulf.

Within the eastern Gulf transect:

(2) Abundance at the shelf-slope transition station (E1, 355 m) was not significantly different than abundance at deeper stations (E2-E5, 620-2,600 m);

(3) Abundance at stations deeper than 500 m but shallower than 1,000 m (Archibenthal Zone, E1, E2) was not significantly different from abundance at stations deeper than 1,000 m (E4, E5);

(4) Abundance at Station E2 (~620 m) in the Archibenthal Horizon A zone of Pequegnat (1983) was not significantly different from abundance at Station E3 (~850 m) in the Archibenthal Horizon B zone of Pequegnat (1983); and

(5) Abundance at Station E4 (1,400 m) in the Upper Abyssal Zone of Pequegnat (1983) was not significantly different from abundance at Station E5 (2,600 m) in the Mesoabyssal Horizon C zone of Pequegnat (1983).

Contrast number six was the second regional hypothesis test:

(6) There were no significant differences in macrofaunal abundance between the central and western Gulf transects.

Contrasts 7-10 were the same as 2-5 listed above except for the western Gulf stations, W1-W5. The balance of the contrasts for ANOVA 1 all involved the central transect. Contrast 11 addressed seasonal differences:

(11) Abundance on the central transect during spring 1984 (Cruise II) was not significantly different from abundance observed there during the fall seasons of 1983 and 1984.

Contrasts 12-15 were the same as listed under 2-5 above except for Cruise II stations, C1-C5.

Contrast 16 was the comparison of annual abundance patterns:

(16) Abundance on the central transect during fall 1983 was not significantly different from abundance observed during fall 1984.

Contrasts 17-20 and 21-24 were the same as listed under 2-5 above except for Stations C1-C5 for fall 1983 and fall 1984, respectively.

ANOVA 2 incorporated data from the 11 stations sampled on the central transect during fall 1984. Before describing these contrasts, a review of the stations by depth as they compare to fine-scale (e.g., Pequegnat, 1983) versus coarse-scale (e.g., Carney et al., 1983) views of faunal zonation patterns on the slope is presented below.

Station	Depth (m)	Fine-Scale Zone	Coarse-Scale Zone
C1	357	Shelf/Slope Transition	Distinct Shelf
C6	492	Shelf/Slope Transition	"
C2	633	Archibenthal, Horizon A	"
C3	881	Archibenthal, Horizon B	"
C7	1021	Upper Abyssal	Transition
C8	1192	Upper Abyssal	"
C9	1430	Upper Abyssal	"
C4	1465	Upper Abyssal	"
C11	2101	Upper Abyssal	"
C5	2518	Mesoabyssal, Horizon C	Distinct Slope
C12	2945	Mesoabyssal, Horizon D	"

Overall the views are the same, except for the question of whether fine-scale faunal differences occur at depths shallower than 1,000 m and deeper than 2,000 m.

The specific contrasts for this ANOVA were:

(1) Macrofaunal abundance at stations between 350 and 1,000 m in depth (shallow) was not significantly different from abundance at stations deeper than 1,000 m.

And within the shallow group of stations:

(2) Abundance at stations in the Shelf/Slope Transition Zone (C1, C6) was not significantly different from abundance at stations in the Archibenthal Zone (C2, C3);

(3) Abundance at C1 was not significantly different from abundance at C6; and

(4) Abundance at C2 was not significantly different from abundance at C3.

The next contrast (5) dealt with stations deeper than 1,000 m:

(5) Abundance at stations in the Upper Abyssal Zone (C7, C8, C9, C4, C11) was not significantly different from abundance at stations in the Mseoabyssal Zone (C5, C12).

Within the Mesoabyssal Zone, contrast 6 was used to evaluate differences between the proposed Horizons C and D.

(6) Abundance at C5 was not significantly different from abundance at C12.

The remainder of the contrasts for ANOVA 2 dealt with comparisons of abundance within the Upper Abyssal Zone:

(7) Abundance at C11, at the approximate boundary between the Abyssal and Mesoabyssal Zones (~2,000 m), was not significantly different from the shallower stations sampled in the Upper Abyssal Zone (C7, C8, C9, C4);

(8) Abundance at Stations C7 and C8 (about 1,000- and 1,200-m deep, respectively) was not significantly different from abundance at Stations C9 and C4, both about 1,450 m deep;

(9) Abundance at C7 was not significantly different from abundance at C8; and

(10) Abundance at C9 was not significantly different from abundance at C4.

These contrasts provide a direct examination of macrofaunal abundance patterns within variously defined faunal zones.

ANOVA 3 was based upon data collected in the eastern Gulf of Mexico on Cruise IV during spring 1985. The primary objective of this cruise was to obtain data enabling an evaluation of whether variation along isobaths was as great as variation observed downslope across isobaths. Given the orientation of peninsular Florida, the along-isobath sampling also provided some measure of latitudinal variation, although the latitudes encompassed were not extensive (see Fig. 1-7 in Chapter 1).

In review, 16 stations were sampled, four (E1, E1A, E1B E1C) along the 350-m depth contour (Shelf/Slope Transition Zone), six (E2, E2A, E2B, E2C, E2D, E2E) along the 620-630-m depth contour (Archibenthal Horizon A), five (E3, E3A, E3B, E3C, E3D) along the 850-m depth contour (Archibenthal Horizon B) and one station at 2,900 m (E5).

This design enabled 15 contrasts as will be described below. The first contrast was:

(1) Macrofaunal abundance at stations in the Shelf/Slope Transition Zone was not significantly different from abundance in the Archibenthal and Abyssal Zones.

Within the Shelf/Slope Transition Zone, one station (E1A) was located in silty-clay sediments whereas the others had sand-silt-clay, enabling the hypothesis that:

(2) Abundance of macrofauna in silty-clay sediments (E1A) was not significantly different from abundance in sand-silt-clay sediments (E1, EB, EC).

With this source of possible variation removed, the remaining contrasts for this group were:

(3) Abundance at the northeastern-most of the stations (E1) was not significantly different from the abundance at stations more northwest (E1B, E1C); and

(4) Abundance at Station E1B was not significantly different from abundance at Station E1C.

Contrast (5) tested for abundance differences between the deepest station (E5, Mesoabyssal Horizon C Zone) and the two sets of stations in the Archibenthal Zone. Within the Archibenthal Zone, the first hypothesis tested was:

(6) Abundance in Horizon A (E2, E2A, E2B, E2C, E2D, and E2E) was not significantly different from abundance in Horizon B (E3, E3A, E3B, E3C, E3D).

Within Horizon A, the following hypotheses were tested:

(7) Abundance at the closely grouped "core" stations (E2, E2B and E2C) was not significantly different from abundance at more distant stations in either direction (E2A, E2D, E2E);

(8) Abundance at Station E2C was not significantly different from abundance at closely-spaced Stations E2 and E2B;

(9) Abundance at Station E2 was not significantly different from abundance at Station E2B;

(10) Abundance at distal Station E2A was not significantly different from abundance at Stations E2D and E2E, located some 55 nautical miles (nmi) to the southeast; and

(11) Abundance at Station E2D (sand-silt-clay sediments) was not significantly different from abundance at Station E2E (silty clay sediments).

Similarly, the hypotheses tested within the Horizon B stations were tests of abundance between the two southeasternmost stations versus stations further removed to the northwest, namely:

(12) E3B and E3 versus E3A, E3C, E3D;

(13) E3B versus E3;

(14) E3A versus E3C and E3D; and

(15) E3C versus E3D

The distance between stations and station groups can be seen in Figure 1-7 of Chapter 1.

ANOVA 4 was based upon data collected from stations arranged along selected isobaths on the slope in the west-central (WC) Gulf of Mexico. Twelve stations were sampled during a summer 1985 cruise. In review, two stations (WC1, WC5) were in the Shelf/Slope Transition Zone; five (WC2, WC4, WC6, WC7, WC8) were in Horizon A and three (WC3, WC9, WC10) in Horizon B of the Archibenthal Zone; and, lastly , two (WC11, WC12) were in the Upper Abyssal Zone. The first two hypotheses tested using the orthogonal contrast approach were:

(1) Macrofaunal abundance in the Shelf/Slope Transition Zone was not significantly different from abundance in deeper zones; and

(2) Within the Shelf/Slope Transition Zone, abundance at Station WC1 (silty-clay) was not significantly different from abundance at WC5 (sandy clay).

Next, a test was run to evaluate abundance in the Archibenthal Zone as compared to abundance in the Abyssal Zone:

(3) Macrofaunal abundance in the Archibenthal Zone was not significantly different from abundance in the Abyssal Zone; and within the Abyssal Zone; and

(4) Abundance at Station WC11 (a topographic high feature 1,226-m deep) was not significantly different from abundance at WC12 (a topographic depression 1,236-m deep).

Within the Archibenthal Zone, the first hypothesis was to evaluate abundance differences between the two horizons:

(5) Abundance within Horizon A was not significantly different from abundance in Horizon B.

For the three stations within Horizon B, the following contrasts were seen:

(6) Abundance at Station WC3 was not significantly different from abundance at WC9 and WC10, located about 60 nautical miles to the east of WC3 but at the same depth and over the same sediment type; and

(7) Abundance at WC9 was not significantly different from abundance at WC10. These stations were about 30 nautical miles apart.

Within Horizon A, the initial comparison was to determine whether differences could be discerned between samples taken in the known vicinity of natural hydrocarbon seepage on the seabed versus samples taken at non-seep areas at the same approximate depths and having the same sediment types:

(8) Abundance at petroleum seep sites (WC6, WC7) was not significantly different from control sites (WC2, WC4, WC8); and

(9) Abundance at seep Station WC6 was not significantly different from abundance at seep Station WC7.

Stations WC2, WC4 and WC8 were all located on clay sediments and were all about 500-m deep. Stations WC2 and WC4 were separated by about 15 nautical miles with WC8 lying some 75 nautical miles due east (See Fig. 1-7, Chapter 1). The resulting contrasts were:

(10) Abundance at WC8 was not significantly different from abundance at Stations WC2 and WC4; and

(11) Abundance at WC2 was not significantly different from abundance at WC4.

Collectively, the sampling and analysis design enabled evaluation of abundance variation across and along depth contours as well as in relation to special features.

RESULTS

The macrofauna collections contained nearly 50,000 organisms representing 1,569 distinct taxa (Gallaway et al., 1988). Within these groups, 1,121 species were identified with a high proportion being new to science. For example, we were unable to assign existing names to 36 of the 61 most abundant macrofauna species represented in the collections (more than 90 individuals collected). The collections taken on this program have been viewed as highly important, taxonomically speaking, and several of the collections are being accessed from the Smithsonian Institute by taxonomic experts as the basis for group revisions and for dissertation research projects (e.g., the polychaete collection will be used as the basis for a Ph.D. dissertation by one of the program participants, G. Fain Hubbard).

In the following results sections we first describe the overall taxonomy, abundance and diversity patterns reflected by the macrofauna, including results of cluster analyses designed to delineate regional, annual, seasonal and depth differences in macrofaunal assemblages. We next describe the patterns of abundance exhibited by individual species, highlighting significant differences observed among regions, years, seasons, depths and key environmental features (see Study Area and Methods above).

The observed biological differences are related to corresponding environmental features by (1) comparing the results of the Principal Component Analyses (PCA) based upon environmental variables to the results of the biologically-based cluster analyses and (2) by directly correlating the abundance of the 61 "dominant" species to 22 environmental variables believed to be of potential importance to the biota based upon PCA analyses.

A discussion of the results follows. In that section we compare our significant findings to previous work in the Gulf of Mexico and to similar studies being conducted on the U.S. Atlantic continental slope.

Taxonomy and Abundance

The 60 most common species (plus Vesicomya sp. which was included because the specimens potentially represent chemosynthetic forms) represented eight major groups, of which the polychaetes were both most abundant and diverse (Table 4-2). At the species level most macrofauna were represented by very few individuals. For example, only 110 of the 1,121 identified species of the macrofauna were represented by ten or more individuals (Gallaway et al., 1988). It can be seen from the rarefaction curves developed for each station/cruise combination, that the number of species expected at the various sample sizes obtained at each station

Table 4-2. Abundance of the 60 most common macrofauna (and Vesicomya sp.) collected on the continental slope of the northern Gulf of Mexico, 1983-1985.

	Total Count
Polychaeta (32)	
Litocorsa antennata	1209
Aurospio dibranchiata	1190
Tachytrypane sp. A	571
Spiophanes berkeleyorum	505
Exogone sp. A	467
Aricidea suecica	421
Pholoe "sp. C"	417
Maldane "sp. A"	402
Prionospio ehlersi	380
Levinsenia gracilis	371
Fauveliopsis sp. B	283
Sarsonuphis hartmanae	276
Prionospio cirrifera	272
Tharyx marioni	231
Lumbrinerides dayi	229
Ceratocephale oculata	220
Paralacydonia paradoxa	211
Leitoscoloplos sp. A	196
Tharyx annulosus?	191
Paramphinome jeffreysii	188
Terebellides stroemi	173
Diplocirrus capensis	168
Pionosyllis "sp. H"	161
Terebellides atlantis	153
Paramphinome sp. A	130
Spiophanes bombyx	118
Diplocirrus "sp. A"	116
Cirrophorus lyra	116
Lumbrineris verrilli	113
Exogone sp. B	104
Euchone incolor	101
Levinsenia uncinata	91
	9774
Bivalvia (7)	
Eulamellibranchia sp. F	319
?Vesicomya sp.	262
Malletia sp. B	239
Crenella sp. A	225
Nucula sp. A	208
Eulamellibranchia sp. B	105
Yoldiella sp. A	105
	1463
Myodocopan Ostracods (5)	
Euphilomedes sp. A	332
Angulorostrum sp. A	279
Philomedes sp. A	203
Pseudophilomedes sp. A	127
Harbansus sp. A	98
	1039
Tanaidacea (5)	
Pseudotanais sp. 1	299
Mesotanais sp. 1	181
Leptognathia sp. 15	173
Apseudidae sp. A	154
Tanaella sp. 1	119
	926
Isopoda (5)	
Ischnomesus sp. 208	231
Gnathia sp. 201	240
Prochelator sp. 202	118
Prochelator sp. 408	97
Macrostylus sp. 256	94
	780
Bryozoa (3)	
?Nolella monniotae	1772
Euginoma cavillieri	289
Setosellina elegantula	109
	2170
Amphipoda (2)	
Pardisynopia sp. 1	145
Phoxocephalidae sp. 1	143
	288
Nemertea (2)	
Nemertea sp. CL4	130
Nemertea sp. D	193
	323
	16,763

(three to six replicates) never approached an asymptotic value (Fig. 4-1). However, a deflection in the curves was usually evident at sample sizes of about 500 specimens. Results of previous power analyses suggested that on the order of 12 to 24 replicates of 0.05 m^2 sample size would be necessary for truely quantitative work on Gulf of Mexico slope macrofauna.

The overall region, season, and year by depth patterns of overall macrofaunal abundance are shown by Figure 4-2. From inspection, abundance appears somewhat higher on the central transect ($x=3,156/m^2$) than on either the eastern ($x=2,695/m^2$) or western transects ($x=2,100/m^2$). Based upon the data from the central transect, spring abundance levels ($3,156/m^2$) appeared higher than fall abundance levels (x ranged from 1,657 to $1,987/m^2$). The annual differences between the fall collections of 1983 and 1984 on the central transect and the spring collections of 1984 and 1985 on the eastern transect were 330 and 169 organisms/m^2, respectively. This compares to regional differences ranging between 461 and 1,056 organisms/m^2, and seasonal differences ranging from 1,169 to 1,499 organisms/m^2. Annual differences appear to be less than regional and seasonal variation in abundance.

On both the eastern and western transects, an overall decline of macrofaunal density with depth is clearly indicated, even though there are some exceptions at the shallower of the sampled depths. On the central transect, the observed trend of abundance decrease with depth was interrupted by an apparent abundance peak at the 1,400-m deep station (Fig. 4-2). This trend for a mid-depth abundance peak was also reflected by the samples taken at finer intervals across isobaths of the central transect during Cruise III (Fig. 4-3).

Results of sampling along isobaths in both the eastern (Fig. 4-4) and western (Fig. 4-5) transects showed overall density to have been relatively uniform along isobaths.

Species Diversity

The diversity evaluations made in this report are based upon comparisons of the H" and E(S) indices applied to data for species only. From inspection of the H" data and supporting indices (evenness and richness, Table 4-3), it is apparent that most of the differences in the

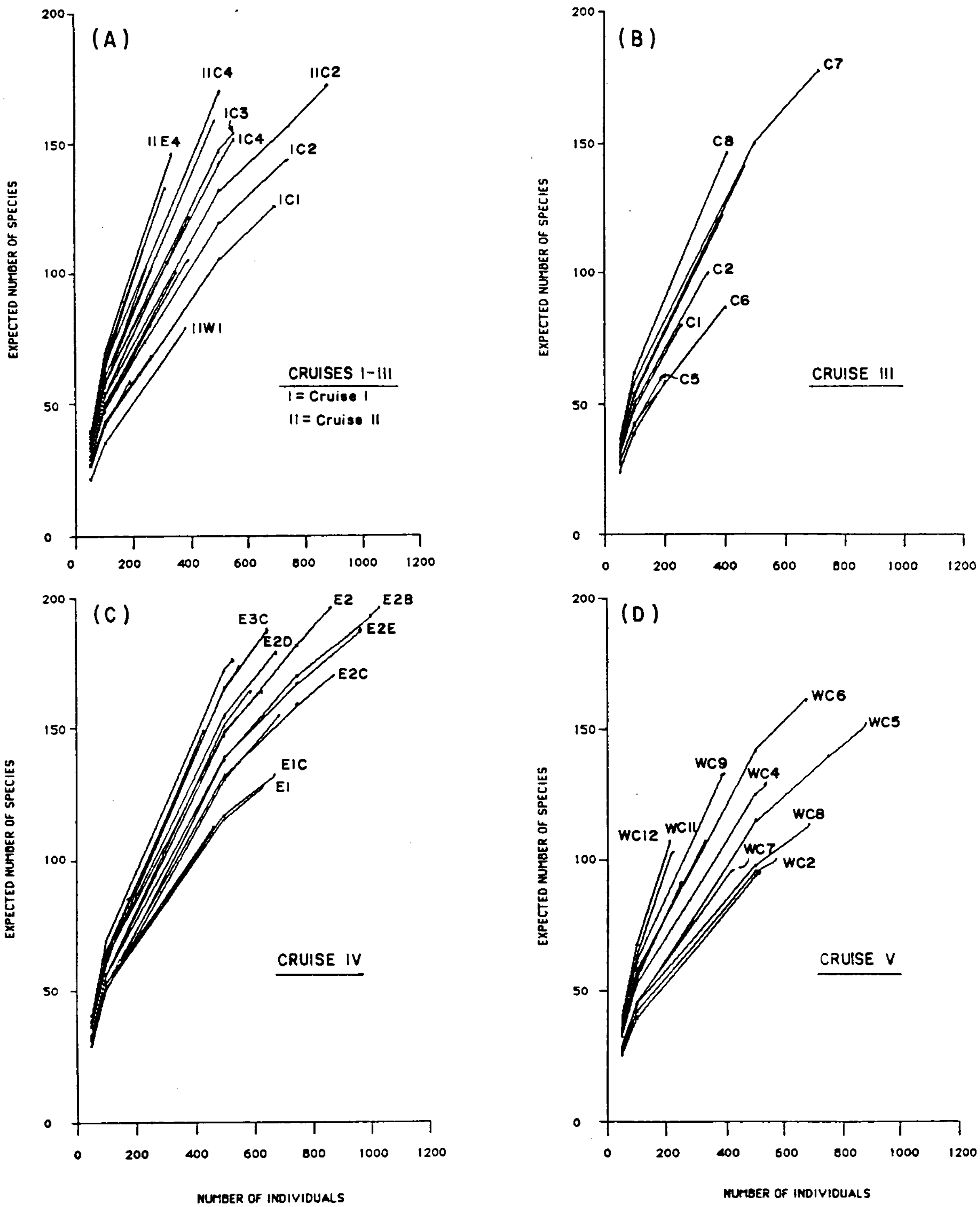

Figure 4-1. Results of rarefaction analyses for samples taken at each station during Cruises I-V. Not all stations are labeled. "C" denotes central transect, "E" denotes eastern transect, and "W" denotes western transect.

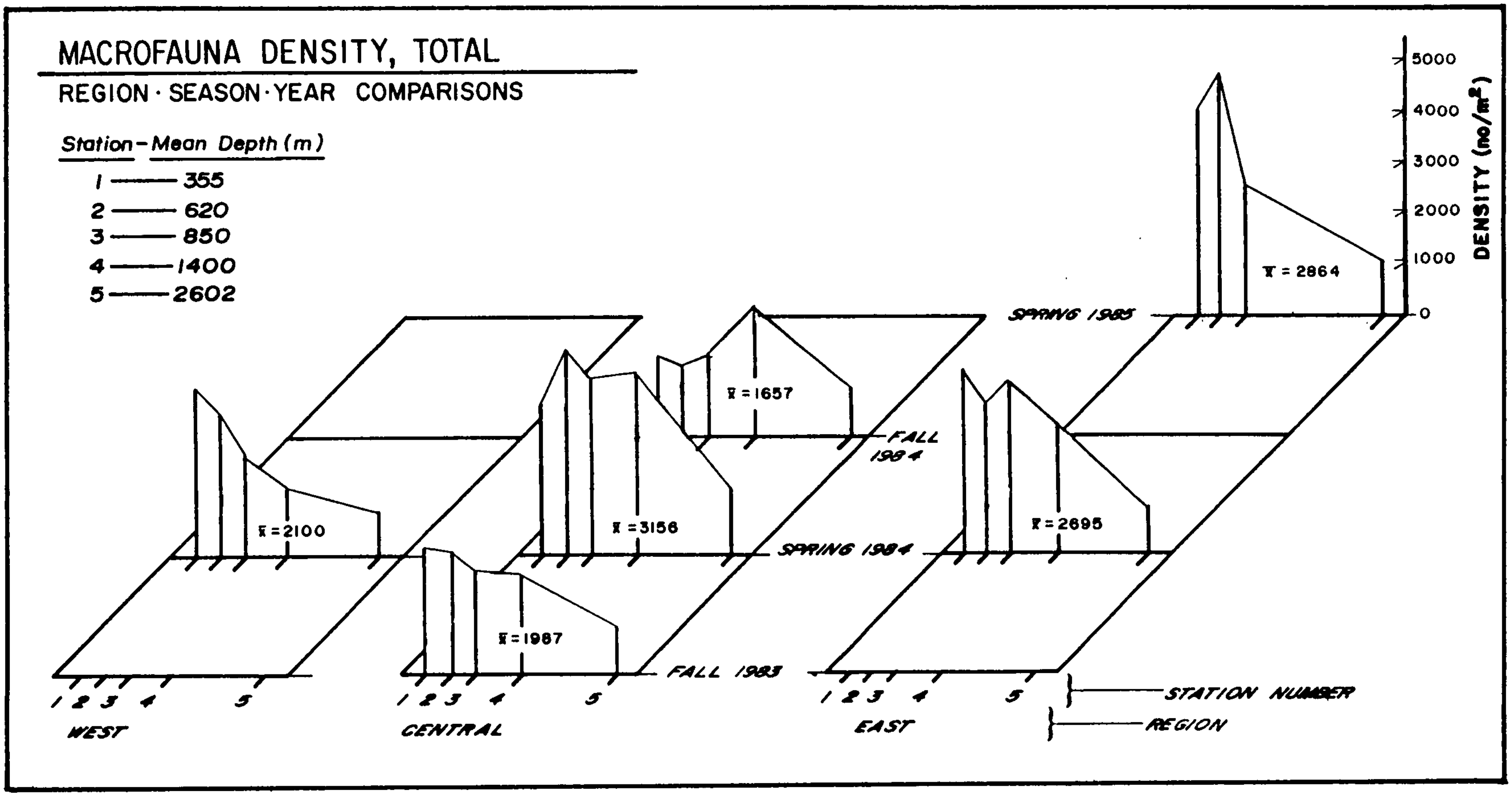

Figure 4-2. Comparative levels of macrofaunal densities by region, season, year and selected depth interval.

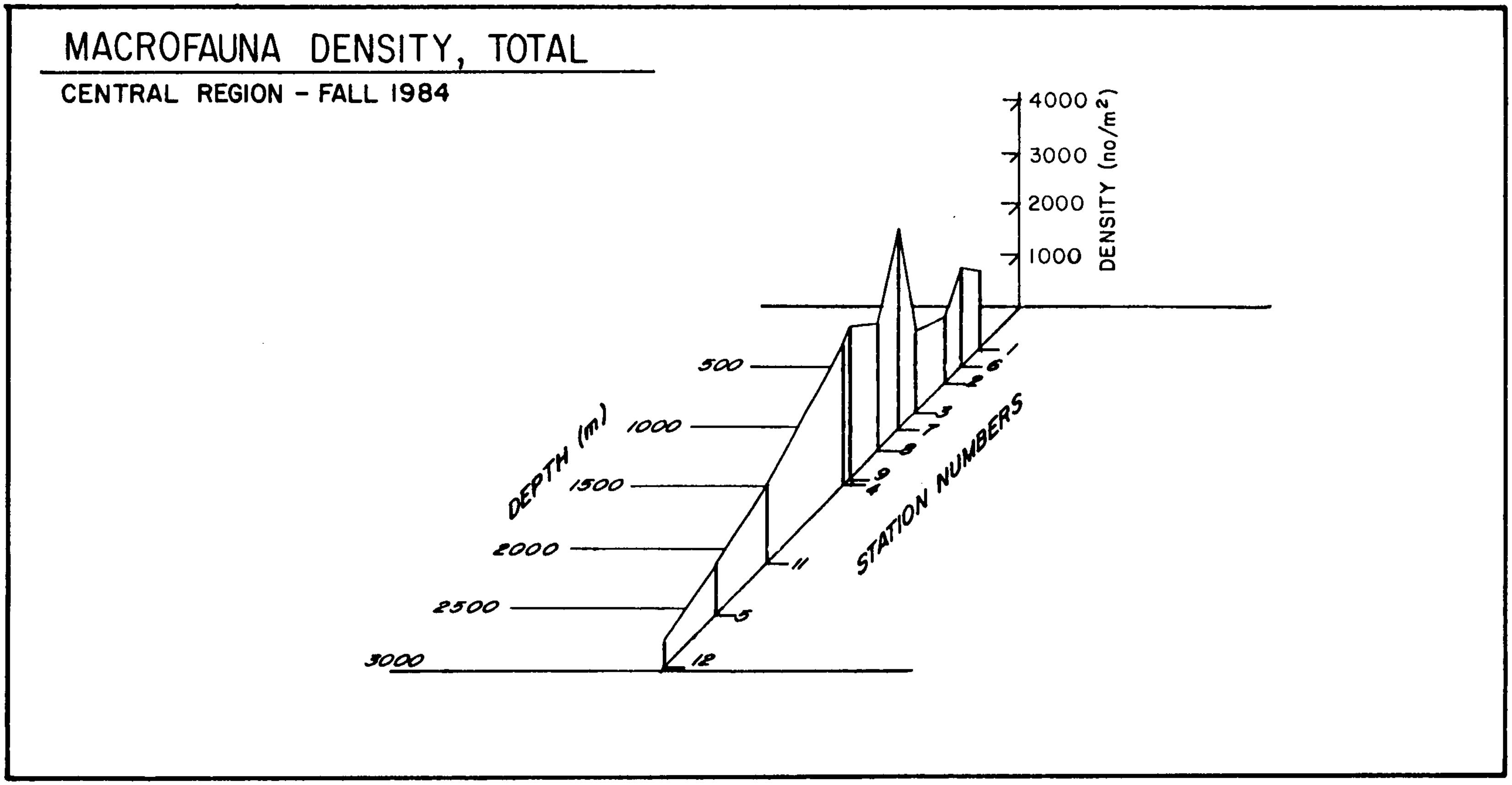

Figure 4-3. Comparative levels of macrofaunal density by depth on the central transect, fall 1984.

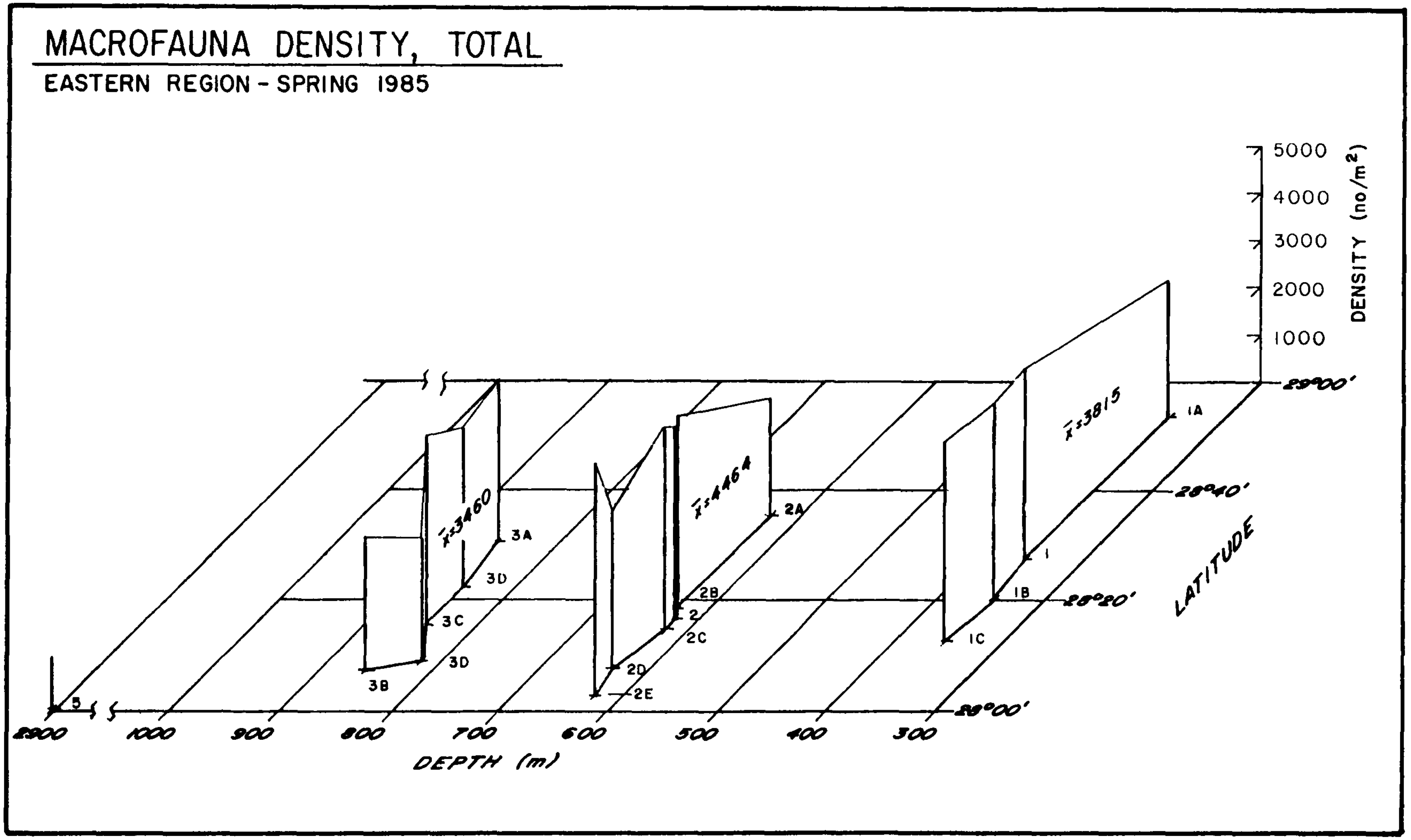

Figure 4-4. Comparative levels of macrofaunal density along selected isobaths in the eastern Gulf of Mexico during spring 1985.

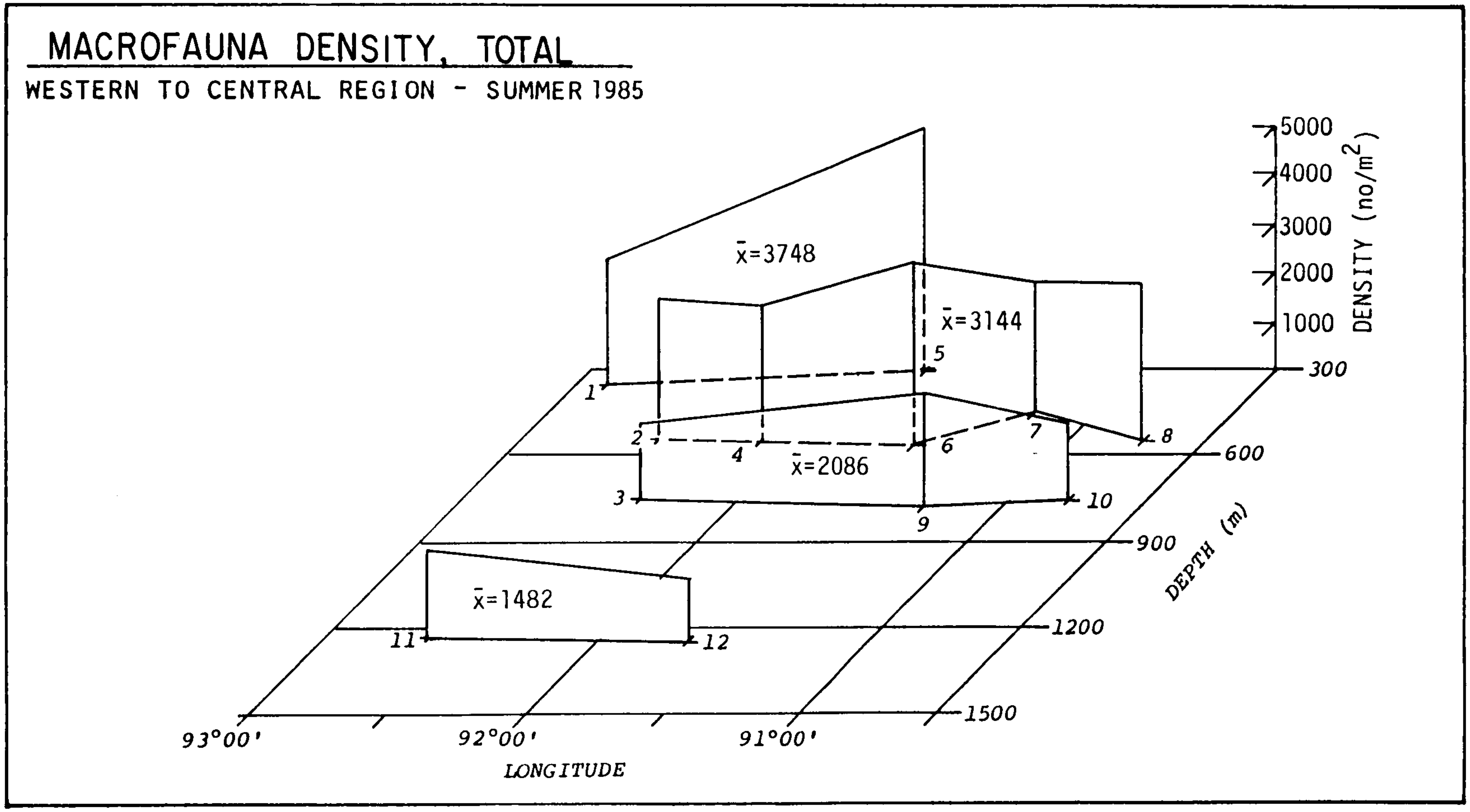

Figure 4-5. Comparative levels of macrofaunal density along isobaths between the central and western Gulf of Mexico sampling transects, summer 1985.

Table 4-3. Species diversity (H") and associated indices for Gulf of Mexico continental slope sampling stations, 1983-1985.

CRUISE I

STATION:	C1	C2	C3	C4	C5
Diversity	3.73	3.85	3.64	3.66	3.27
Evenness	0.77	0.79	0.72	0.73	0.78
Richness	18.77	19.68	23.31	22.35	11.02
Number of Species	124	131	154	149	65
Number of Genera	29	23	32	30	12
Total Taxa	190	188	220	212	93
Total Number	702	740	708	751	333

CRUISE II

STATION:	W1	W2	W3	W4	W5	C1	C2	C3	C4	C5	E1	E2	E3	E4	E5
Diversity	3.13	3.87	3.64	3.75	2.80	3.70	4.04	3.93	3.89	3.43	4.04	4.22	4.26	4.21	3.25
Evenness	0.71	0.82	0.80	0.86	0.70	0.77	0.77	0.77	0.75	0.76	0.85	0.89	0.85	0.82	0.78
Richness	13.64	18.76	15.98	14.69	10.30	18.28	26.10	23.58	26.03	14.36	19.13	20.16	24.40	26.50	11.70
Number of Species	83	110	92	78	54	119	184	162	178	89	118	117	152	170	65
Number of Genera	11	16	25	18	10	21	32	32	37	16	25	17	25	29	17
Total Taxa	109	151	138	112	74	161	251	229	248	124	168	162	198	224	92
Total Number	408	334	297	189	172	637	1110	922	898	458	453	315	487	588	237

CRUISE III

STATION:	C1	C2	C3	C4	C5	C6	C7	C8	C9	C11	C12
Diversity	3.69	3.87	3.90	3.67	3.20	3.68	3.73	3.77	3.47	3.47	3.28
Evenness	0.83	0.82	0.82	0.75	0.77	0.82	0.72	0.75	0.71	0.83	0.84
Richness	14.74	18.21	18.54	20.70	11.12	14.43	25.34	22.21	19.78	11.88	9.83
Number of Species	86	110	113	136	65	90	181	148	134	66	50
Number of Genera	16	20	19	26	17	14	35	41	35	15	13
Total Taxa	119	154	154	183	92	121	249	212	196	91	72
Total Number	319	398	420	679	316	478	1217	750	831	238	146

Table 4-3 (cont'd).

CRUISE IV

STATION:	E1	E1A	E1B)	E1C	E2	E2A	E2B	E2C	E2D	E2E	E3	E3A	E3B	E3C	E3D	E5
Diversity	4.07	4.02	4.24	4.23	4.49	4.01	4.42	4.45	4.53	4.39	4.36	4.33	4.47	4.40	4.48	3.85
Evenness	0.82	0.84	0.83	0.84	0.85	0.77	0.83	0.96	0.86	0.83	0.86	0.82	0.85	0.83	0.85	0.83
Richness	20.63	17.98	25.25	22.57	29.63	26.26	29.10	26.02	28.20	28.83	25.05	29.11	27.95	29.71	29.45	17.66
Number of Species	142	119	171	157	204	182	202	177	191	203	162	198	186	204	200	103
Number of Genera	40	25	37	35	35	35	42	40	41	43	36	36	36	52	36	20
Total Taxa	202	166	235	216	281	243	279	249	266	279	226	263	248	291	271	140
Total Number	931	708	840	1003	945	984	999	866	843	1104	618	869	750	928	860	322

CRUISE V

STATION	WC1	WC2	WC3	WC4	WC5	WC6	WC7	WC8	WC9	WCA	WCB	WCC
Diversity	3.78	3.67	3.82	3.89	4.01	4.25	3.75	3.79	3.90	3.76	3.89	3.96
Evenness	0.80	0.77	0.79	0.78	0.79	0.81	0.78	0.77	0.77	0.78	0.80	0.82
Richness	17.12	17.91	19.89	21.71	23.26	26.62	18.60	19.95	23.16	19.58	20.46	20.07
Number of Species	111	120	127	145	162	185	121	138	154	121	126	122
Number of Genera	25	24	22	28	44	35	22	27	33	20	24	26
Total Taxa	156	164	174	203	235	250	162	189	213	157	171	168
Total Number	618	769	564	760	1014	1004	633	959	739	459	450	415

overall index are attributable to the richness aspect, which is greatly influenced by sample size or abundance.

Regional, seasonal and yearly patterns of macrofaunal diversity by depth were not pronounced, but diversity appeared to decrease from east to west and to have been somewhat higher in fall than in spring on the central transect (Table 4-3). Differences in fall diversity levels between years on the central transect were negligible, but spring 1985 diversity levels on the eastern transect were marginally higher than spring 1984 levels.

The most consistent depth trend in H" was a marked decrease in diversity between the 1,400-m deep and 2,600-m deep stations on each transect (Table 4-3). There also appears a tendency for a slight diversity increase between the shallowest station (~350 m) and some of the sequentially deeper stations, yielding somewhat skewed, dome-shaped diversity curves over the depth range sampled.

The data obtained from sampling a higher density of stations on the central transect in fall 1984 enabled a more detailed examination of macrofauna diversity levels over depth intervals (Table 4-3). Diversity appeared to increase slightly from Station 1 (H"=3.69, 355 m deep) to Station 3 (H"=3.90, 850 m deep), and from there decreased with depth down to Station 9 (H"=3.47, 1,428 m deep). A slight peak (H"=3.67) was observed at Station 4 (1,465 m deep), after which the diversity level once more declined gradually over the depth interval between 1,465 m and 2,945 m (Table 4-3). The observed differences, however, were all marginal, the total range of values being from 3.20 to 3.90 (Table 4-3).

As shown by Table 4-3, macrofauna H" diversity levels were rather constant along the sampled isobaths in both the eastern and western regions where these studies were conducted. Additionally, there appeared very little variation by depth, at least within the intervals sampled.

Diversity indices such as H" often suffer the criticism that they can be biased by sample size. Rarefaction is an approach towards eliminating this bias. In the approach, the sample data are used to estimate the expected number of species represented by a given sample size. Trends in expected number of species, E(S) for a sample of 50 individuals mirrored the findings obtained from use of the H" diversity index (compare Figs. 4-6 through 4-9 to data in Table 4-3). Diversity levels at the shallowed

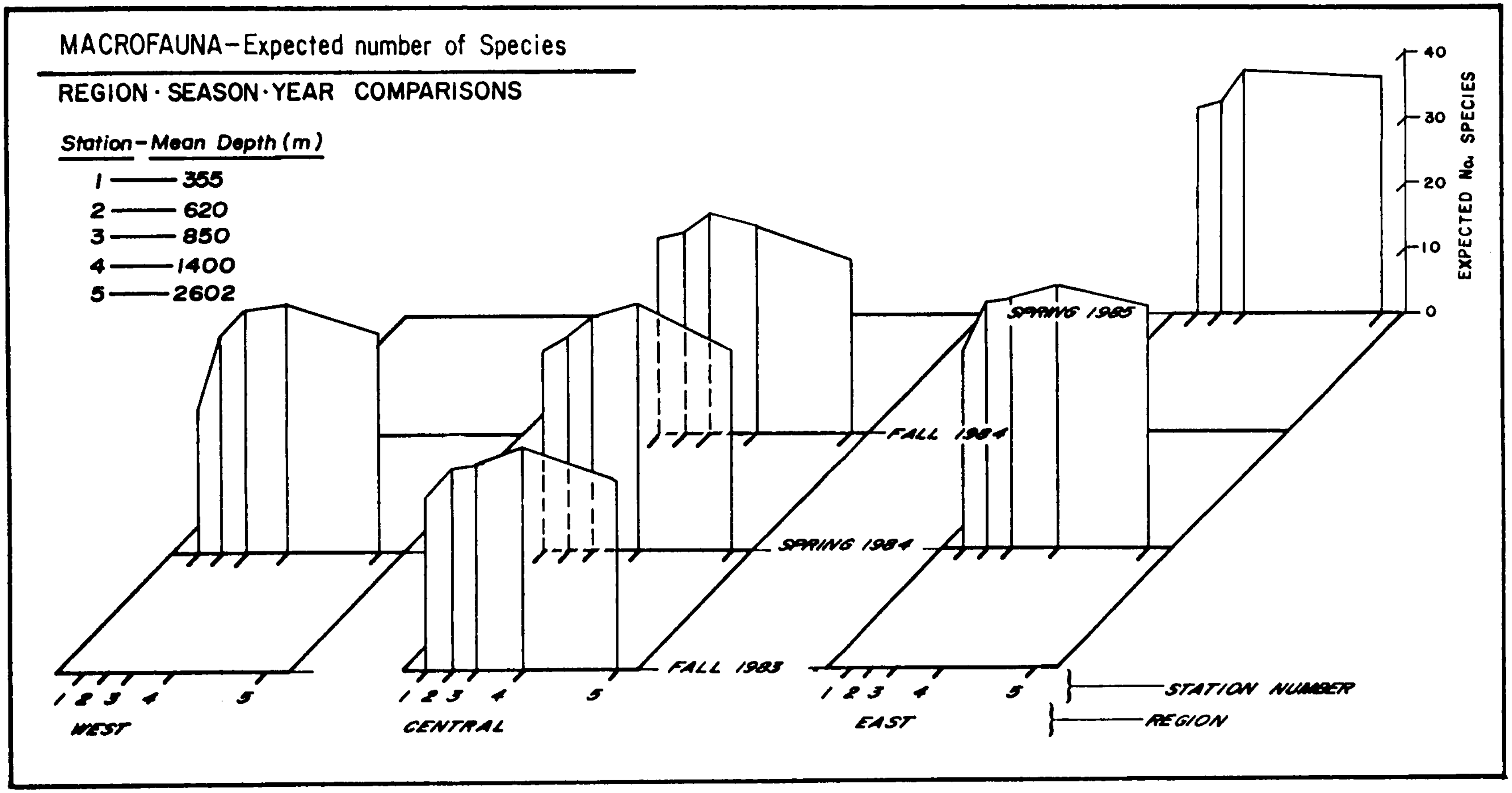

Figure 4-6. Comparative levels of macrofauna expected number of species in a sample size of 50 individuals by region, season, year and selected depth interval.

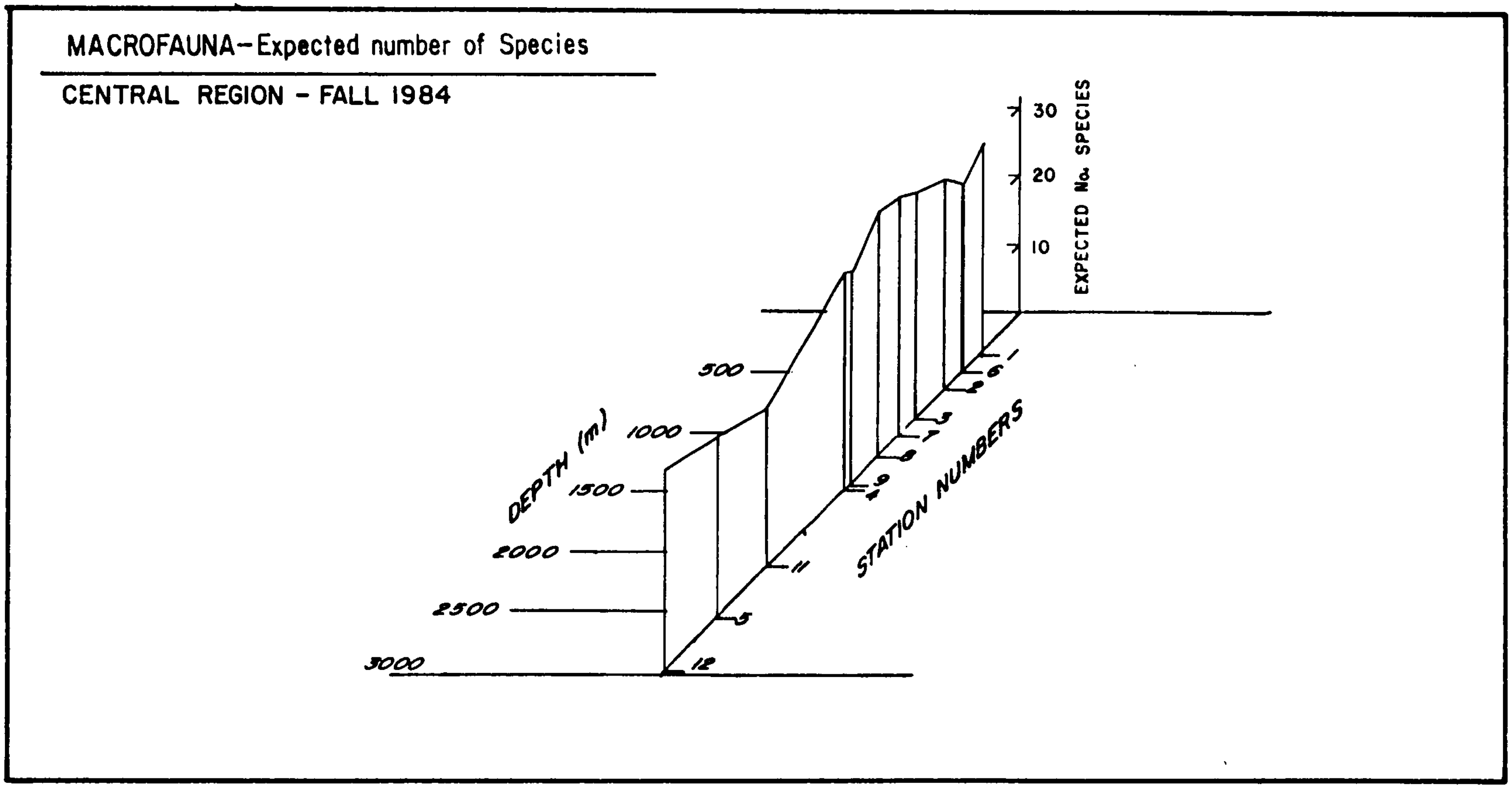

Figure 4-7. Comparative levels of macrofauna expected number of species in a sample size of 50 individuals by depth on the central transect, fall 1984.

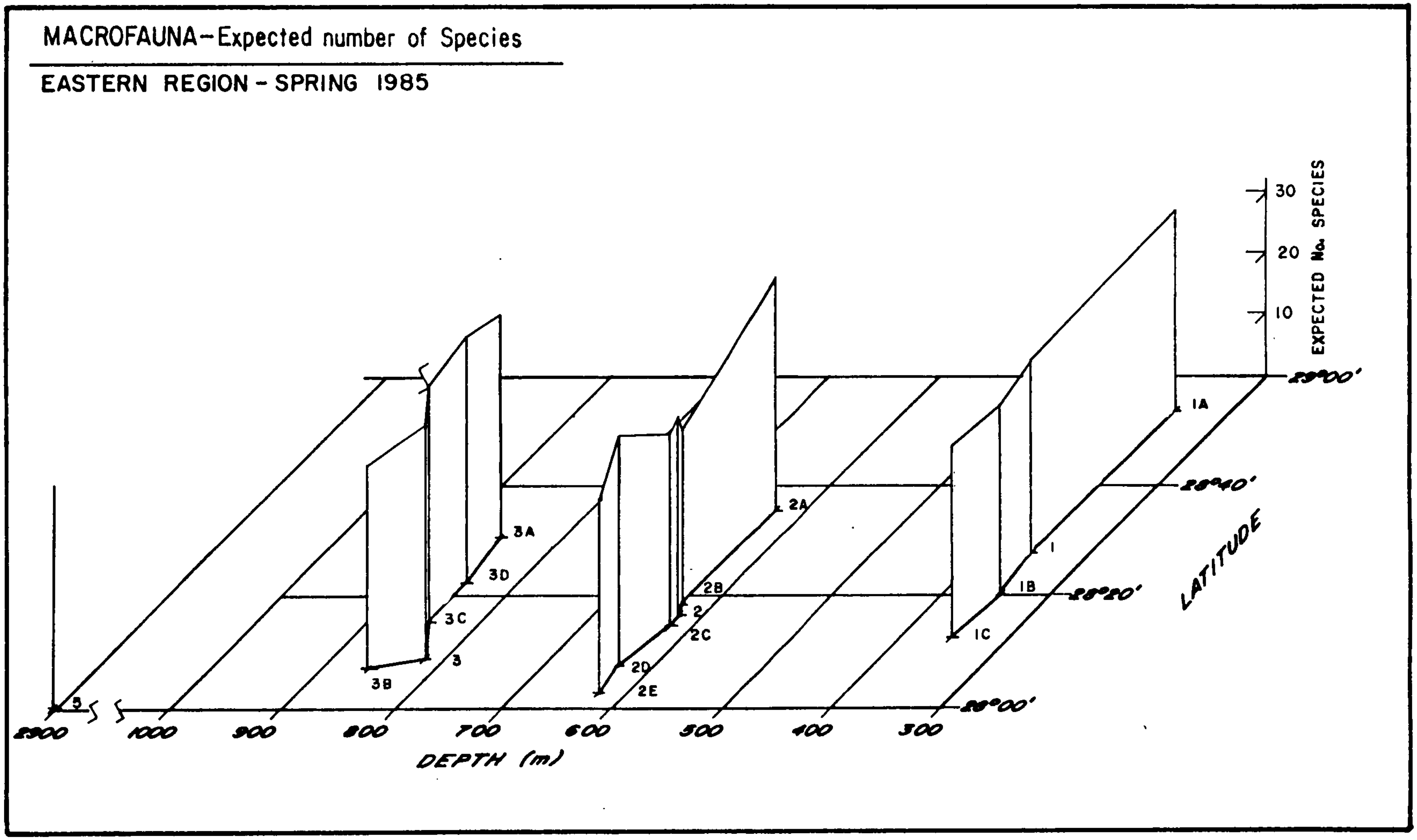

Figure 4-8. Expected number of macrofauna species in a sample size of 50 individuals along selected isobaths in the eastern Gulf of Mexico during spring 1985.

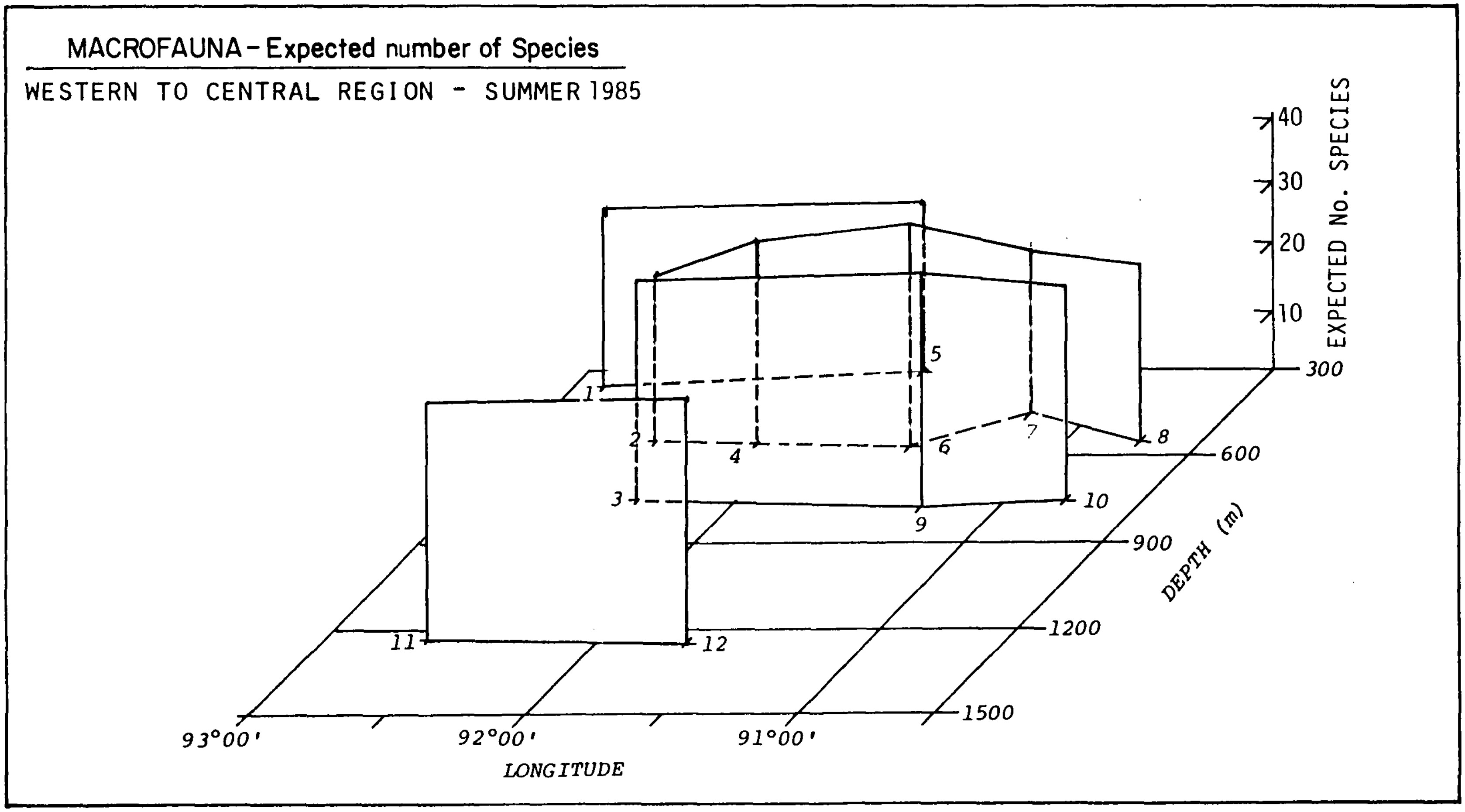

Figure 4-9. Expected number of macrofauna species in a sample size of 50 individuals along isobaths between the central and western Gulf of Mexico sampling transects, summer 1985.

and deepest stations were usually lower than levels observed at the mid-depth ranges; regional, seasonal and annual differences were slight and variation along isobaths appeared less than variation across isobaths.

Cluster Analyses and Relation to Principal Component Analyses

Macrofauna data from Stations E1-E5, C1-C5 and W1-W5 were subjected to cluster analysis in an attempt to discern any species assemblage differences by region, season, year and depth (Fig. 4-10). The results can be interpreted to suggest three major station groups--a distinct deep (>2,000 m) assemblage (Group 3), a distinct shallow (<400 m) assemblage on the central transect (Group 1) and a large intermediate depth group (Group 2) generally ordered by depth but also reflecting regional and seasonal subgroupings.

Within Group 1, similarity at Station C1 was higher for spring and fall 1984 collections than between these two seasonal collections and the fall 1983 collection. The three collections made at C5 also clustered together (in Group 3), but here, the fall 1983 and spring 1984 collections were more similar than these two collections were to the fall 1984 collection. These data may be suggestive that the seasonal and annual differences that occur at different depths on the slope result from different kinds of driving forces. At the deepest stations (Group 3), regional differences were distinctive with the central Gulf area being most dissimilar as compared to the eastern and western Gulf regions (Fig. 4-10).

At least five subgroups can be discerned among the Group 2 stations, generally ordered by depth as noted above. Within this group, the western region stations were the most dissimilar within each subgroup in which they occurred (Fig. 4-10). Three of these stations, in fact, formed two of the separate subgroups, namely 2a (W1, W4) and 2b (W3). These subgroups also accounted for most of the exceptions to the general depth-ordered pattern of clustering.

Groups 2c, 2d and 2e (Fig. 4-10) represented combinations of Shelf/Slope Transition-Archibenthal Horizon A; Archibenthal Horizon A-Archibenthal Horizon B; and Archibenthal Horizon B-Upper Abyssal Zone, respectively. This suggests that Pequegnat's (1983) zonation scheme

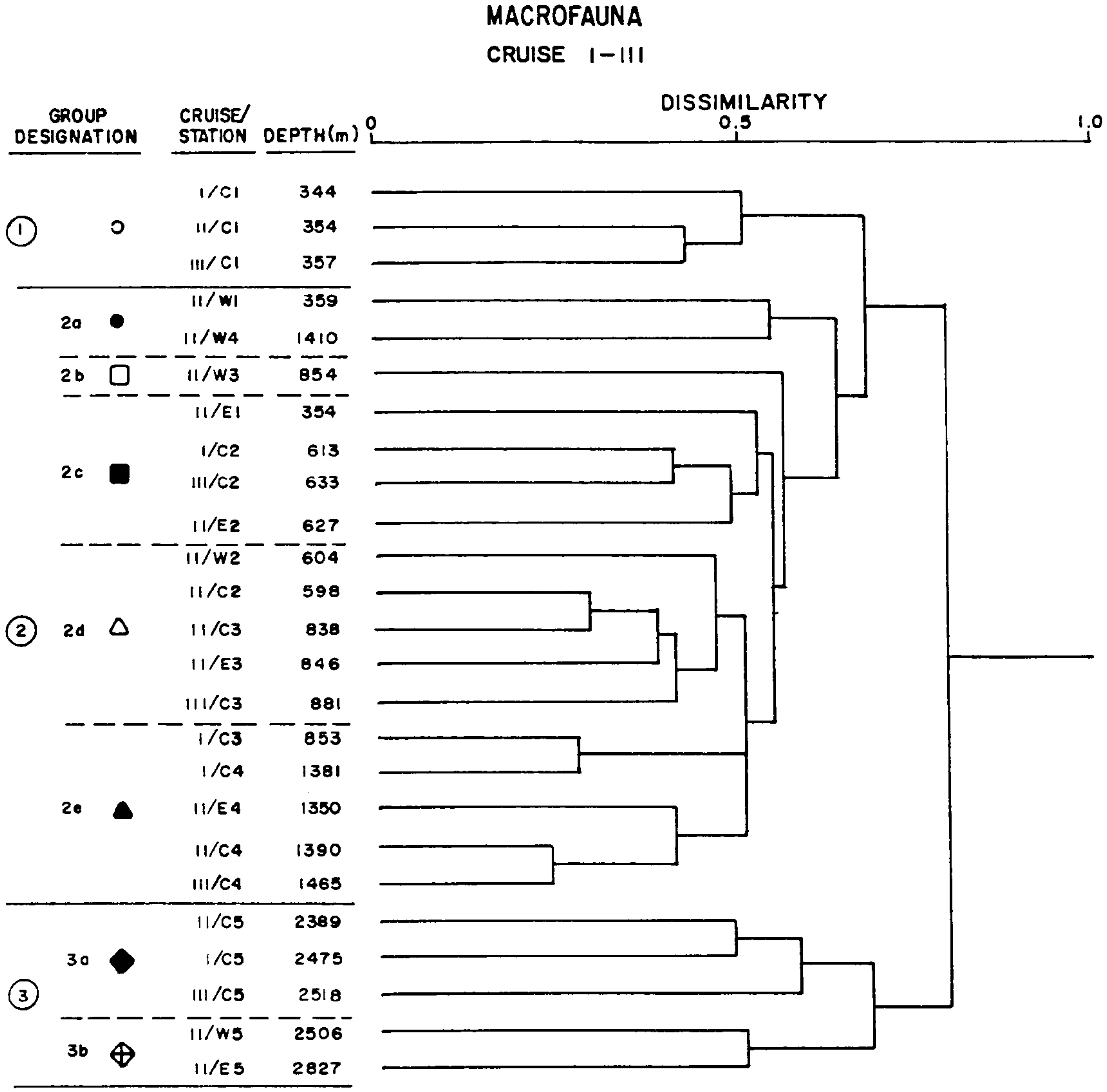

Figure 4-10. Results of cluster analysis for Stations 1-5 sampled on the eastern, western and central transects, Cruises I-V. Roman numerals I-III represent cruises; "E" denotes eastern transect, "C" denotes central transect and "W" denotes western transect.

(developed largely from megafaunal observations) may hold generally true for the macrofauna. This is explored in more detail below based upon the Cruise III data.

Results of station classification for the same set of stations using PCA analysis applied to physical/chemical variables suggested a general grouping of stations by region within which a number of subgroups could be delineated. The results of the biological classification of stations is compared to the corresponding PCA classification by superimposing the symbols for each biological subgroup from Figure 4-10 on the PCA results presented in Chapter 2 (Fig. 4-11). While marked agreement is not suggested, some similarities are evident. These include the distinct groupings of the three seasonal collections taken at Station C1 in both analyses and the regional separation of the deepest stations in both analyses, with Cruise III C5 (fall 1984) data being quite different from environmental and biological data taken there during fall 1983 (Cruise I) and spring 1984 (Cruise II).

The Cruise III sampling design included twelve stations (only eleven were successfully sampled for macrofauna) and examined variation across isobaths on the central transect. The results of the biological cluster analysis showed four groups which exhibited a high degree of depth order (Fig. 4-12). Stations deeper than 2,000 m formed the most dissimilar group and, within this group, Station C5 (2,518 m) which constituted Group 3 was somewhat different from stations C11 (2100 m) and C12 (2,945 m) which constituted Group 4.

Group 1 was a shallow group consisting of stations C1 (Shelf/Slope Transition Zone), C2 (Archibenthal Horizon A) and C6, a station placed at the boundary between these two postulated zones which corresponds to the approximate location of the oxygen minimum layer. Collections from stations C1 and C2 were virtually identical and somewhat dissimilar from C6. These data could be interpreted to suggest that the Shelf/Slope Transition Zone for macrofauna extends to a depth of on the order of at least 650 m.

Group 2 stations all exhibited a relatively high degree of similarity but two subgroups appeared possible (Fig. 4-12). One of these consisted of stations between about 880 and 1,200 m in depth (stations C3, C7, C8), whereas the other consisted of stations on the order of 1,450 m deep (C9,

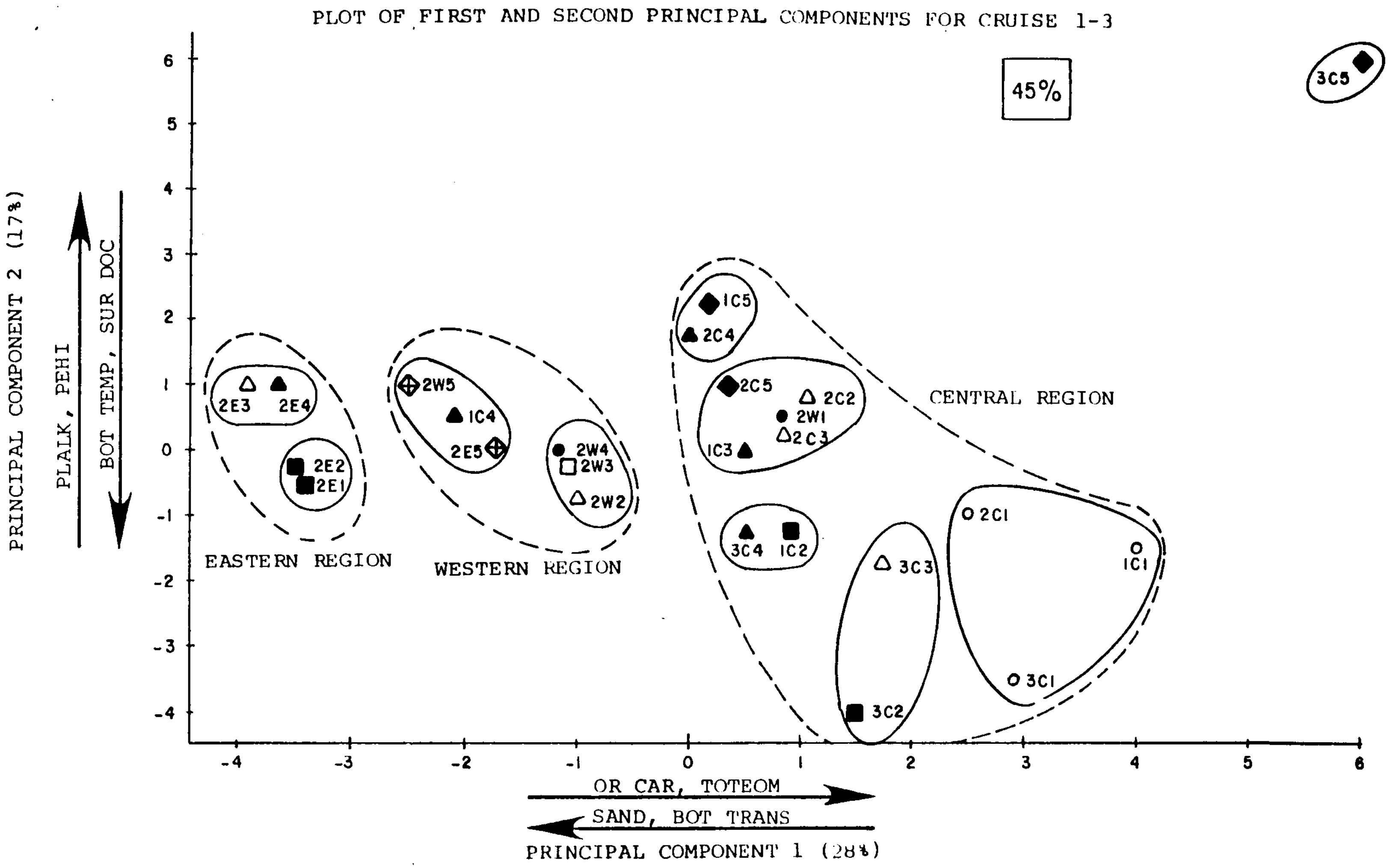

Figure 4-11. Results of biological cluster analysis for Stations 1-5 sampled on Cruises I-III superimposed by overlaying group designation symbol (see Fig. 4-10) on the results of the corresponding PCA analysis (see Fig. 2-15 in Chapter 2).

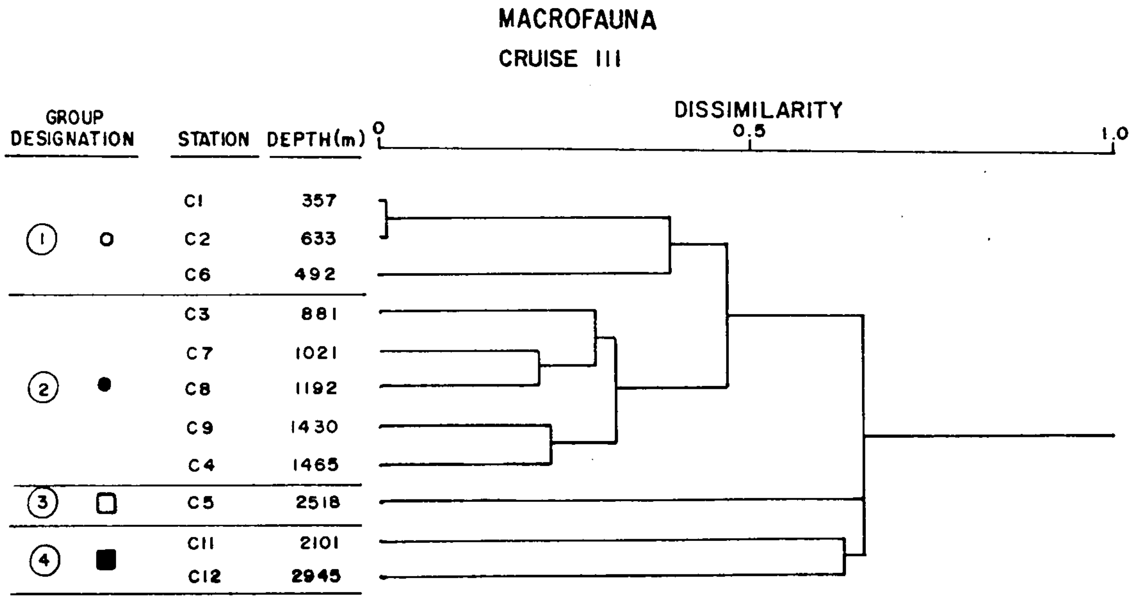

Figure 4-12. Results of cluster analysis for central transect stations sampled on Cruise III, fall 1984.

C4). This apparent break in biological similarity (somewhere between 1,200 and 1,400 m) corresponds to the point where bottom water temperature drops from about 4.5 to 5°C to a uniform 4.2°C.

From these results, one might hypothesize that, for macrofauna, four faunal zones might be represented on the Gulf of Mexico continental slope, at least in the central Gulf. These are (1) a Shelf or Slope Transition Zone, generally extending between 300 to 750 m; (2) the Upper Archibenthal Zone between 750 and 1,200 m; (3) the Lower Archibenthal Zone between 1,200 and 1,650 m; and the Abyssal Zone greater than 2,000 m.

Comparison of the PCA and biological cluster analyses for Cruise III show good agreement, even to the subbroup levels for the most part (Fig. 4-13). The only notable exception is that Station C2 grouped with mid-depth stations in the PCA analyses and with the "shallow" group of stations in the biological analysis. (While we characterize the station classifications by depth group for discussion purposes, neither depth nor hydrostatic pressure were used directly in the analyses.) Environmental variables that were indicated to be of importance in the classification included bottom temperature and salinity, hydrocarbon levels and sediment characteristics.

The cluster analyses for stations sampled on Cruise IV were designed to evaluate whether variation in community similarity along isobaths was as great as variation across isobaths. From Figure 4-14, can be seen that community similarity along isobaths was remarkably similar with the clusters ordered almost entirely by depth. Some five groups were formed, the most dissimilar being the one deep station (E5) and the four stations (E1, E1A, E1B, E1C) located along the 350-m depth contour. Likewise all of the ~600-m deep stations clustered together, with Station E2D being most dissimilar within this group. This station was over sand-silt-clay sediments whereas all the rest were over silty clay sediments (See Fig. 2-2 in Chapter 2).

Stations along the "800"-m deep (819-860 m) contour exhibited more dissimilarity within an isobath than the stations along the 300- and 600-m deep contours. The southeasternmost stations (E3, E3B) actually formed a distinct group (Group 4) being less similar to the other 800-m deep stations than to the ~600-m deep stations. Nevertheless, the overall degree of dissimilarity observed among stations for Cruise IV was markedly

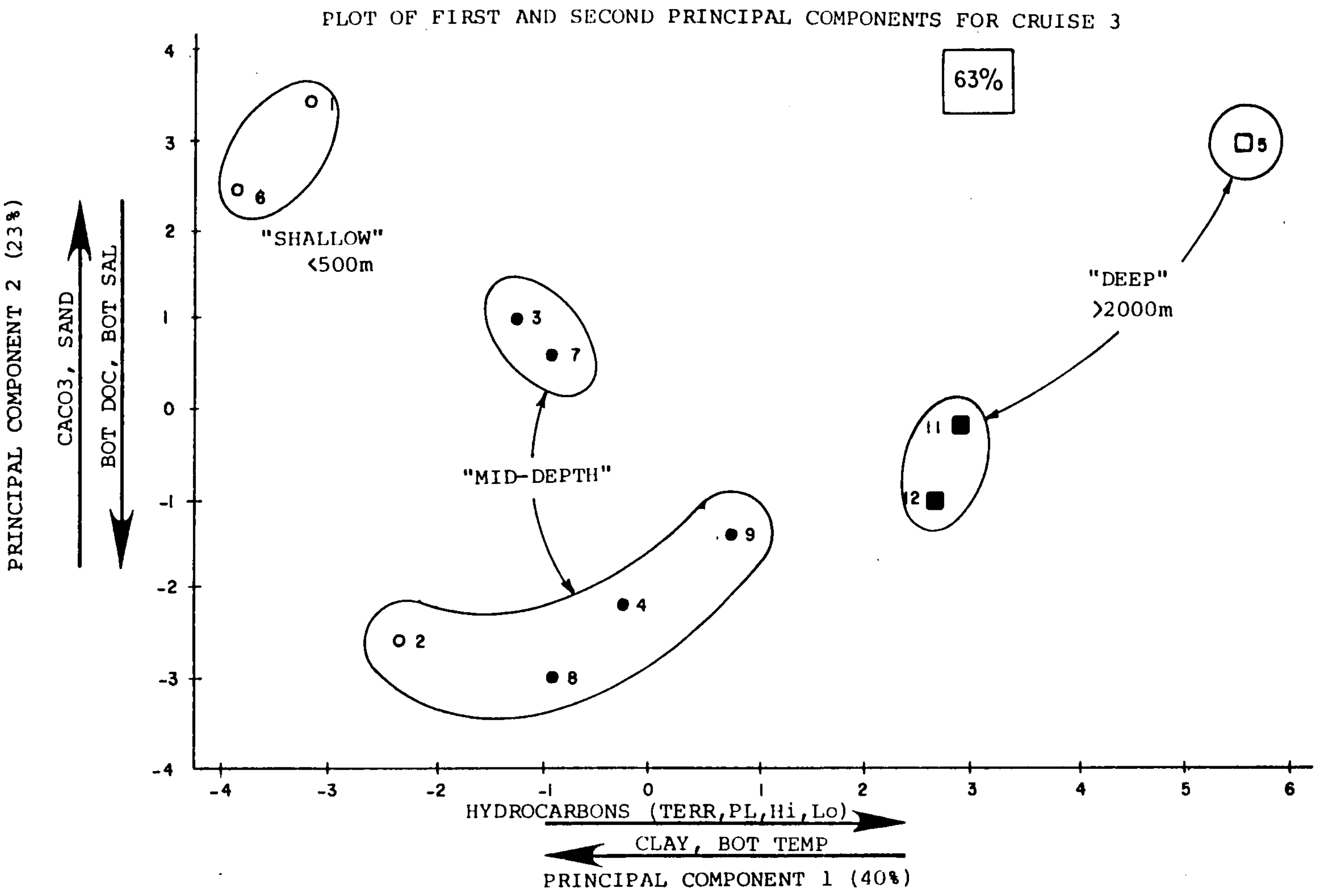

Figure 4-13. Results of biological cluster analysis for central transect stations sampled on Cruise III superimposed by overlaying group designation symbol (see Fig. 4-12) on the results of the corresponding PCA analysis (see Fig. 2-16 in Chapter 2).

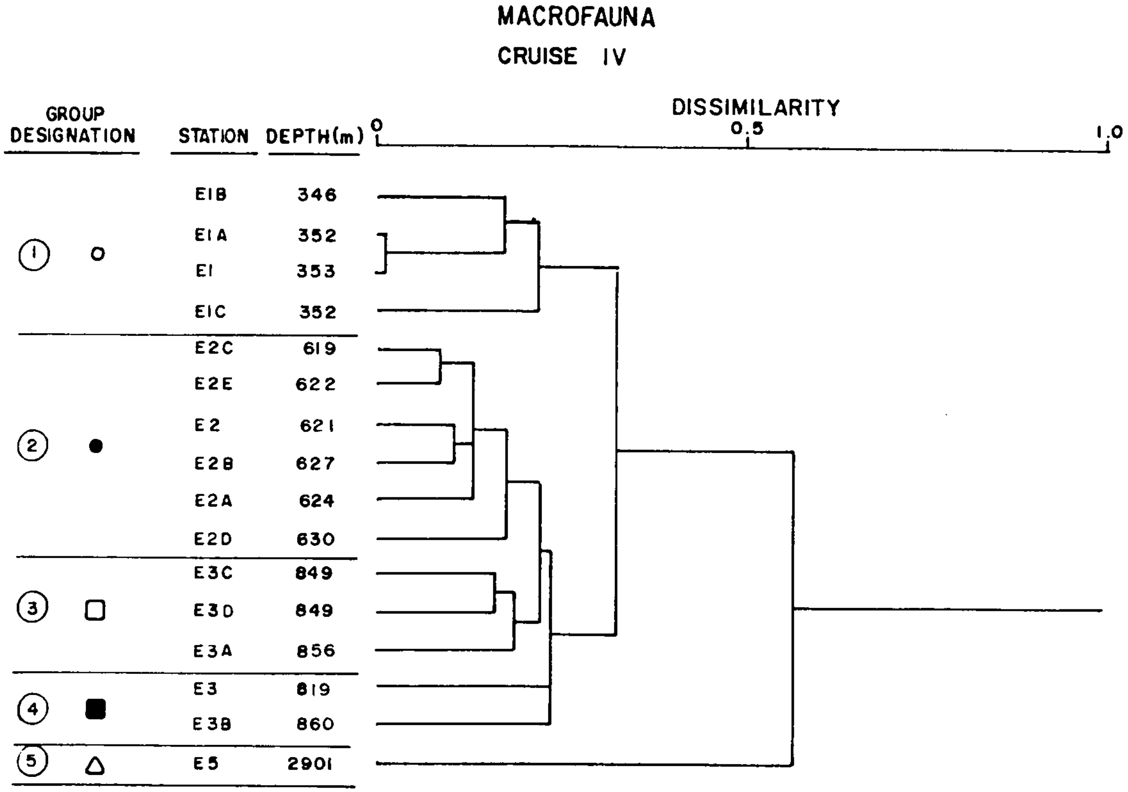

Figure 4-14. Results of cluster analysis for stations sampled on Cruise IV along isobaths in the eastern Gulf of Mexico, spring 1985.

less than overall dissimilarity levels observed for Cruise III stations when sampling was conducted across isobaths.

Results of both the PCA and biological cluster analyses were similar in that the stations were ordered mainly by depth (Fig. 4-15). The only notable exception was that one of the 800-m deep stations (E3C) in the PCA analysis clustered with the 600-m deep stations whereas it clustered with other 800-m stations in the biological cluster analysis.

Stations sampled during Cruise V exhibited the greatest degree of dissimilarity (compare Figs. 4-10, 4-12, 4-14 and 4-16), perhaps due to the complexity of the contrast design. Five groups were identified, the most dissimilar of which was Group 5, the deep stations (Fig. 4-16). Within the balance of the stations, Groups 1 (WC1, WC2) and 2 (WC5) were next most dissimilar, representing depths between about 300 and 550 m. Groups 3 and 4 represented stations between 450 to 567 m and stations located along the ~750-m deep contours, respectively. As suggested, the groups were largely depth oriented (Fig. 4-16), with the exceptions (WC2, WC5 and WC7) being related to either sediment differences or the presence or seeps (see Fig. 2-2 in Chapter 2). As with the previous results for data from Cruises III and IV, there was reasonably good agreement between the station groupings yielded by the PCA based upon environmental variables and the cluster analysis based upon biological variables (Fig. 4-17). Again, there is a high degree of ordering by depth in the results of both analyses.

Species Abundance Patterns

The abundance data for 60 of the most numerous macrofaunal species (more than 90 specimens) and for Vesicomya sp. were analyzed by ANOVA to ascertain significances in (1) regional, seasonal, and overall depth trends (ANOVA 1), (2) fine-scale depth trends on the central transect (ANOVA 2), and (3) variation along isobaths and at selected environmental features in the eastern (ANOVA 3) and west-central (ANOVA 4) regions of the Gulf of Mexico continental slope. This resulted in some 244 ANOVAs, the results of which are summarized below. Because so many tests were run, the 0.01 significnce level was used. Most of the ANOVAs exhibiting

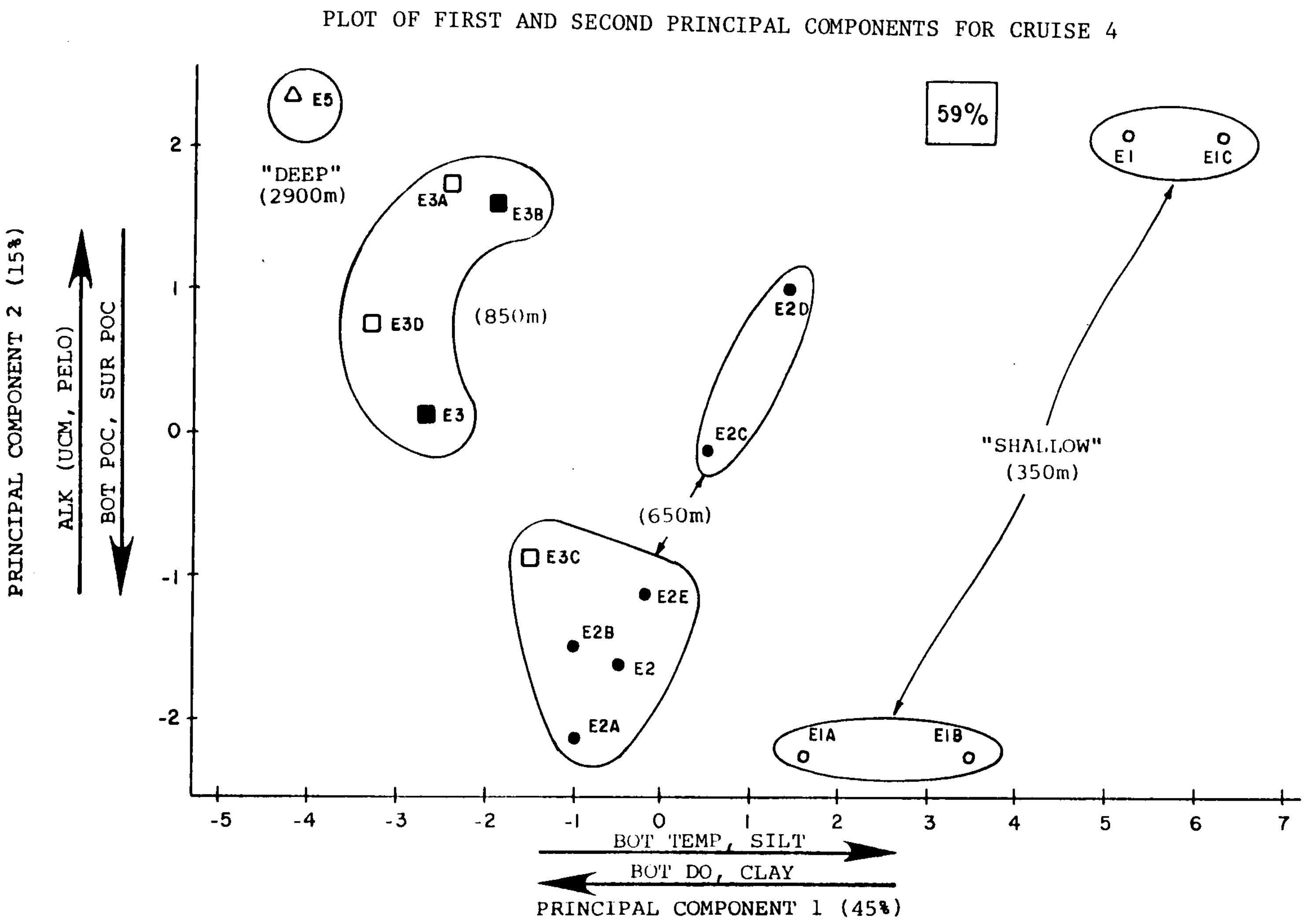

Figure 4-15. Results of biological cluster analysis for stations sampled along isobaths in the eastern Gulf of Mexico on Cruise IV superimposed by overlaying group designation symbol (see Fig. 4-14) on the results of the corresponding PCA analysis (see Fig. 2-17 in Chapter 2).

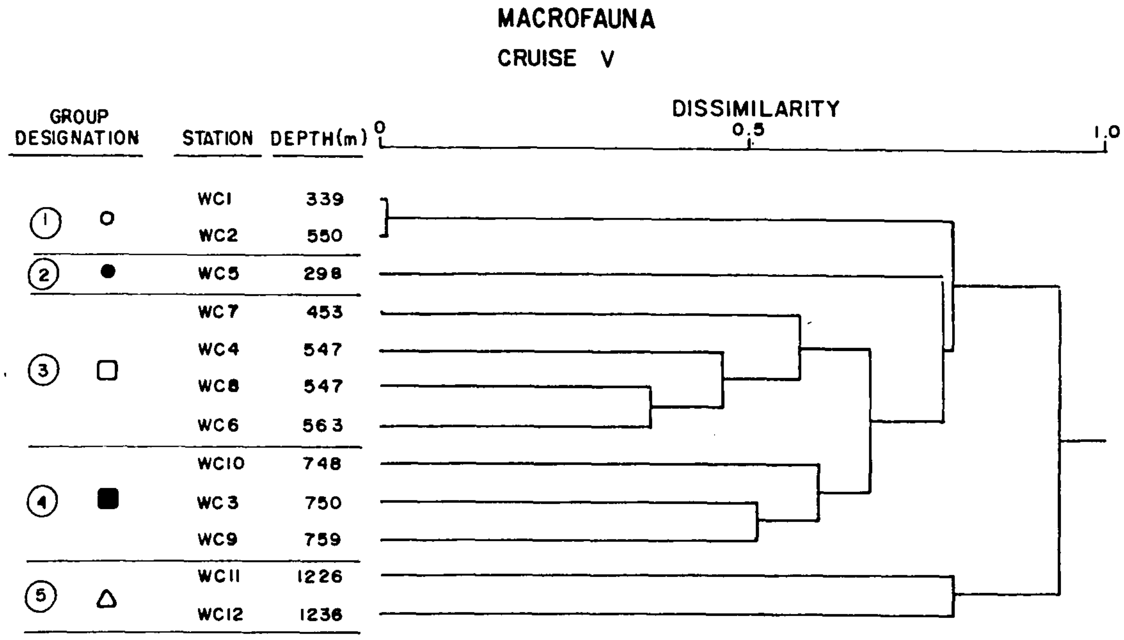

Figure 4-16. Results of cluster analysis for stations sampled on Cruise V along isobaths in the west-central Gulf of Mexico, summer 1985.

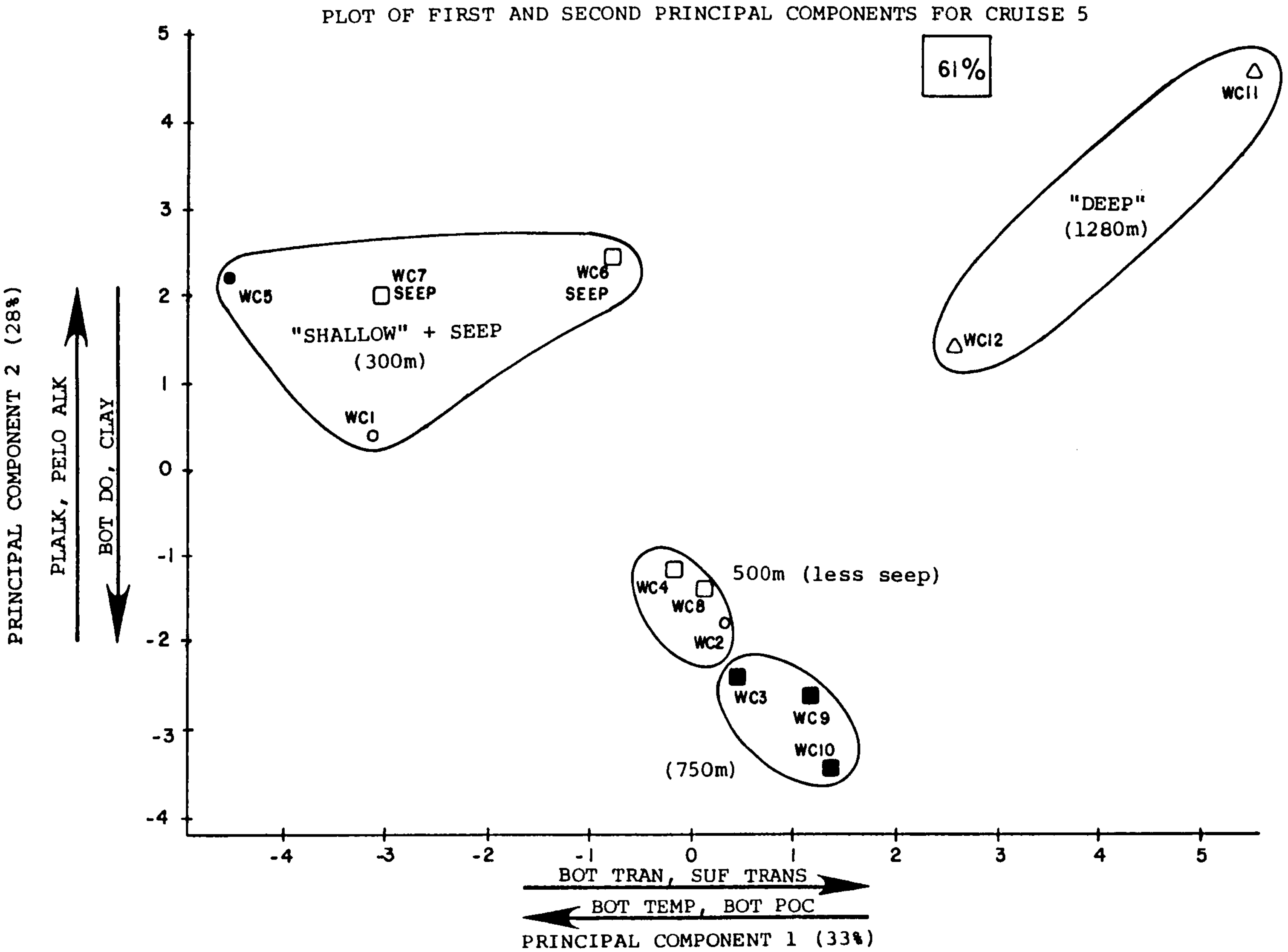

Figure 4-17. Results of biological cluster analysis for stations sampled along isobaths in the west-central Gulf of Mexico on Cruise V superimposed by overlaying group designation symbol (see Fig. 4-16) on the results of the corresponding PCA analysis (see Fig. 2-18 in Chapter 2).

significant differences had probability levels greater than 0.001 (Table 4-4).

Only 45% of the ANOVAs (111 of 244) involving 46 species showed significant differences (Table 4-4), despite the complexity of the experimental design and extreme differences in habitats sampled. The results of the significant ANOVAs, the corresponding orthogonal contrasts, and the distributional patterns (station means) for these species are presented in Appendix A, Volume III of this report. The paucity of significant differences is consistent with the overall macrofauna results--i.e., slope macrofauna are highly diverse and widespread in distribution with marked abundance by any one species (species dominance) being typically rare anywhere, except along the upper slope.

Regional, Seasonal and Annual Differences by Depth (ANOVA 1)

Species exhibiting significant differences for each of the 24 contrasts used in ANOVA 1 are listed by major group in Table 4-5. Only two species of polychaetes (Tachytrypane sp. A and Sarsonuphis hartmanae) exhibited annual differences in abundance, based upon fall 1983 and 1984 collections made on the central transect. The former was more abundant in 1983 than in 1984, whereas the latter was more abundant in 1984 than in 1983. Given that only two of the 61 taxa analyzed reflected a seasonal difference and that these showed conflicting results, we conclude that annual differences in slope macrofauna abundance patterns were not pronounced.

Five species exhibited seasonal differences in abundance between spring (1984) and fall (1983, 1984) collections made on the central transect (Table 4-5). These included three polychaetes, one tanadacean and one isopod:

Table 4-4. Species of common macrofauna exhibiting significant differences in abundance patterns. The numbers represent the observed probability level, 0.01 was used as the significance level.

	Total	ANOVAS			
	Count	1 (CR 1-3)	2 (CR 3)	3 (CR 4)	4 (CR 5)
Polychaeta (32)					
1. *Litocorsa antennata*	1209	0.0001	0.0001	0.0001	0.0001
2. *Aurospio dibranchiata*	1190	-	-	-	0.0081
3. *Tachytrypane* sp. A	571	0.0001	-	0.0005	0.0001
4. *Spiophanes berkeleyorum*	505	0.0016	0.0034	0.0086	0.0026
5. *Exogone* sp. A	467	-	0.0024	-	-
6. *Aricidea suecica*	421	-	0.0071	-	-
7. *Pholoe* "sp. C"	417	0.0020	0.0001	0.0001	0.0001
8. *Maldane* "sp. A"	402	0.0001	-	-	-
9. *Prionospio ehlersi*	380	0.0003	0.0001	0.0001	0.0001
10. *Levinsenia gracilis*	371	-	-	0.0002	0.0015
11. *Fauveliopsis* sp. B	283	-	-	-	-
12. *Sarsonuphis hartmanae*	276	0.0099	0.0007	-	-
13. *Prionospio cirrifera*	272	-	-	-	-
14. *Tharyx marioni*	231	-	-	-	-
15. *Lumbrinerides dayi*	229	0.0001	0.0098	-	-
16. *Ceratocephale oculata*	220	0.0018	-	0.0005	0.0017
17. *Paralacydonia paradoxa*	211	0.0001	-	0.0021	0.0001
18. *Leitoscoloplos* sp. A	196	0.0001	-	-	0.0048
19. *Tharyx annulosus*?	191	-	0.0022	0.0067	-
20. *Paramphinome jeffreysii*	188	-	-	-	-
21. *Terebellides stroemi*	173	-	-	-	-
22. *Diplocirrus capensis*	168	0.0100	0.0074	-	-
23. *Pionosyllis* "sp. H"	161	-	-	-	-
24. *Terebellides atlantis*	153	-	-	-	-
25. *Paramphinome* sp. A	130	-	-	-	-
26. *Spiophanes bombyx*	118	-	0.0008	-	-
27. *Diplocirrus* "sp. A"	116	-	-	0.0013	-
28. *Cirrophorus lyra*	116	-	-	-	-
29. *Lumbrineris verrilli*	113	-	-	-	-
30. *Exogone* sp. B	104	-	-	-	-
31. *Euchone incolor*	101	-	-	-	-
32. *Levinsenia uncinata*	91	-	-	-	-
Bivalvia (7)					
1. *Eulamellibranchia* sp. F	319	0.0033	0.0001	0.0001	0.0001
2. ?*Vesicomya* sp.	262	0.0001	0.0001	0.0001	-
3. *Malletia* sp. B	239	0.0005	0.0001	-	-
4. *Crenella* sp. A	225	0.0001	0.0001	0.0003	0.0001
5. *Nucula* sp. A	208	0.0027	-	0.0019	0.0002
6. *Eulamellibranchia* sp. B	105	-	-	0.0001	-
7. *Yoldiella* sp. A	105	0.0001	0.0001	-	-

Table 4-4 (cont'd)

	Total Count	ANOVAS			
		1 (CR 1-3)	2 (CR 3)	3 (CR 4)	4 (CR 5)
Myodocopan Ostracods (5)					
1. *Euphilomedes* sp. A	332	0.0001	-	0.0001	0.0026
2. *Angulorostrum* sp. A	279	0.0001	-	0.0001	0.0001
3. *Philomedes* sp. A	203	0.0001	-	0.0001	0.0001
4. *Pseudophilomedes* sp. A	127	-	-	0.0001	0.0040
5. *Harbansus* sp. A	98	0.0001	0.0005	0.0001	0.0005
Tanaidacea (5)					
1. *Pseudotanais* sp. 1	299	0.0021	-	0.0014	0.0001
2. *Mesotanais* sp. 1	181	0.0001	-	0.0001	0.0001
3. *Leptognathia* sp. 15	173	-	0.0021	-	0.0088
4. Apseudidae sp. A	154	0.0001	0.0001	0.0001	0.0001
5. *Tanaella* sp. 1	119	-	-	0.0010	0.0099
Isopoda (5)					
1. *Ischnomesus* sp. 208	231	0.0001	0.0008	0.0001	0.0001
2. *Gnathia* sp. 201	240	-	-	-	-
3. *Prochelator* sp. 202	118	0.0001	0.0001	-	-
4. *Prochelator* sp. 408	97	-	-	0.0020	-
5. *Macrostylus* sp. 256	94	0.0001	0.0015	-	0.0001
Bryozoa (3)					
1. ?*Nolella monniotae*	1772	-	-	0.0001	0.0014
2. *Euginoma cavillieri*	289	-	0.0001	0.0001	-
3. *Setosellina elegantula*	109	-	-	0.0004	-
Amphipoda (2)					
1. *Pardisynopia* sp. 1	145	-	-	0.0050	0.0017
2. Phoxocephalidae sp. 1	143	-	0.0001	-	-
Nemertea (2)					
1. Nemertea sp. CL4	130	-	-	-	-
2. Nemertea sp. D	193	-	-	0.0050	0.0001

Table 4-5. Orthogonal contrasts for ANOVA 1 and macrofaunal species exhibiting significant (0.01 level) differences for each contrast. Numbers represent species as listed in Table 4-4. A plus (+) means the first factor being contrasted was higher than the second factor and a minus (-) means the second factor was highest.

MAJOR GROUP: ANOVA 1 Contrasts	Polychaetes	Bivalves	Mydocopan Ostracods	Tanaidaceans	Isopods
Regional Contrasts					
(1) Eastern vs. western gulf	$7^+,16^+$	3^+	2^+	4^-	-
(6) Central vs. western	$1^-,3^+,8^+,9^+,15^-$	-	-	-	$1^-,3^+$
Seasonal Contrasts					
(11) Spring vs. fall (central)	$3^+,16^+,18^+$	-	-	4^+	5^+
Year Contrasts					
(16) Fall 1983 vs. fall 1984 (central)	$3^+,12^-$	-	-	-	-
Eastern Gulf Depth Contrasts					
(2) Shelf/slope transition zone vs. slope	$1^+,3^+,15^-$	1^+	2^+	-	-
(3) Archibenthal vs. abyssal	$1^+,7^+,12^+,15^+,16^+,18^-$	$3^+,5^+,7^-$		-	-
(4) Horizon A vs. horizon B (archibenthal)	$1^+,7^-$	5^-	-	-	-
(5) Upper abyssal vs. mesoabyssal	18^+	$2^+,7^+$	2^+	-	-
Western Gulf Depth Contrasts					
(7) Shelf/slope transition zone vs. slope	1^+	-	-	-	-
(8) Archibenthal vs. abyssal	$1^+,7^+$	-	-	-	-
(9) Horizon A vs. horizon B (archibenthal)	1^+	-	-	-	-
(10) Upper abyssal vs. mesoabyssal	-	-	-	-	-
Central Gulf Depth Contrasts/Spring 1984					
(12) Shelf/slope transition zone vs. slope	-	4^-	-	4^-	$3^+,5^-$
(13) Archibenthal vs. abyssal	$1^+,3^+,4^+,16^+,17^+,18^+$	$3^+,7^-$	$1^+,3^+,5^+$	$2^+,4^+$	$1^+,5^-$
(14) Horizon A vs. horizon B (archibenthal)	$1^+,3^+,18^-$	$1^+,4^-$	$1^+,3^+$	4^+	-
(15) Upper abyssal vs. mesoabyssal	-	$4^+,7^+$	2^+	-	-
Central Gulf Depth Contrasts/Fall 1983					
(17) Shelf/slope transition vs. slope	$3^+,9^+$	-	-	-	3^+
(18) Archibenthal vs. abyssal	$9^+,15^-,17^+$	2^+	$1^+,3^+,5^+$	4^+	-
(19) Horizon A vs. horizon B (archibenthal)	$1^+,3^+,9^+,17^+$	2^-	$1^+,3^+,5^-$	4^+	-
(20) Upper abyssal vs. mesoabyssal	$8^+,15^-$	-	-	-	5^-
Central Gulf Depth Contrasts/Fall 1984					
(21) Shelf/slope transition vs. slope	-	-	-	-	-
(22) Archibenthal vs. abyssal	$1^+,4^+,17^+$	$2^-,7^-$	-	-	-
(23) Horizon A vs. horizon B (archibenthal)	-	$4^-,7^-$	-	-	-
(24) Upper abyssal vs. mesoabyssal	-	$4^+,7^+$	-	-	5^+

	More Abundant In Fall	More Abundant In Spring
Polychaetes		
(3) Tachytrypane sp. A		x
(16) Ceratocephale oculata		x
(18) Leitoscoloplos sp. A		x
Tanadacea		
(4) Apseudidea sp. A		x
Isopoda		
(5) Macrostylus sp. 256		x

All were more abundant in spring than in fall, perhaps reflecting increased carbon input in the central transect area from Mississippi River.

Significant differences between the eastern and western Gulf regions (central and west transect combined) were indicated for five species:

	More Abundant Eastern Gulf	More Abundant Western Gulf
Polychaetes		
(7) Pholoe sp. C	x	
(16) Ceratocephale oculata	x	
Bivalve		
(3) Malletia sp. B	x	
Myodocopan Ostracod		
(2) Angulorostrum sp. A	x	
Tanadacean		
(4) Apseudidae sp. A		x

Apseudidae Sp. A was not collected in the eastern Gulf but the other four species were more abundant in the eastern as compared to the western Gulf.

Five polychaetes and two species of isopods reflected significant differences in abundance between the central and western transects within the western Gulf region:

	More Abundant Central	More Abundant Western
Polychaetes		
(1) Litocorsa antennata		x
(3) Tachytrypane sp. A	x	
(8) Maldane sp. A	x	
(9) Prionospio ehlersi	x	
(15) Lumbrinerdes dayi		x
Isopods		
(1) Ischnomesus sp. 208		x
(3) Prochelator sp. 202	x	

Three of the five polychaetes and one of the isopods were more abundant along the central transect than along the western transect.

All of the remaining contrasts from ANOVA 1 examine depth differences for specific transects within a season. On the eastern Gulf transect, five species showed significant differences in abundance between the Shelf/Slope Transition Zone versus deeper areas of the slope combined. Only one of these species (the polychaete Ceratocephale oculata, number 15 on Table 4-5) exhibited greater abundance at depth on the slope than in the region of the shelf break, and even this species was more abundant in the Archibenthal zone than in the Abyssal Zone. Of the nine species showing significant differences for contrast (3) in Table 4-5, all but Leitoscoloplos sp. A (polychaete 18) and Yoldiella sp. A (bivalve 7) were more abundant in the Archibenthal Zone than in the Abyssal zone. Within the Archibenthal Zone, polychaete 1 (Litocorsa antennata) was more abundant in Horizon A than in Horizon B and the reverse pattern was seen for polychaete 7 (Pholoe sp. C) and bivalve 5 (Nucula sp. A). For contrast 5, each of the four species exhibiting significant differences were more abundant in the Upper Abyssal Zone as compared to the

Mesoabyssal Zone. In general, the results of the sequential contrasts show the same trend as reflected by the overall macrofauna data--an overall decline in abundance with depth below depths of 1000 m.

Only two species of polychaetes (*Litocorsa antennata* and *Pholoe* sp. C) exhibited significant depth contrasts in abundance on the western transect. The patterns exhibited were the same as described above for the same species which also occurred on the eastern transect. *Litocorsa antennata* declined in abundance between 350 and 850-m depths and was absent deeper. *Pholoe* sp. C exhibited peak abundance in the Archibenthal Zone with no differences observed between the two sampled depths (620 and 850 m).

Three sets of contrasts were available for the central transect, one during spring 1984, one in fall 1983 and the last in fall 1984 (contrasts 12-24, Table 4-5). For polychaetes, all but one species (*Lumbrinerides dayi*) were more abundant at depths of 850 and shallower than at deeper depths. *Lumbrinerides dayi* was more abundant at the 2,600-m deep station than at the 1,400-m deep station. The myodocopan ostracods and the tanaidaceans reflected a pattern similar to the polychaetes in that the significant abundance differences suggested a shallow distribution; i.e., greatest abundance occurred at depths between 350 and 850 m with the peak usually occurring at 620 m.

Five species of bivalves exhibited significant differences on the central transect. Of these, two (species 2, *Vesicomya* sp. and species 7, *Yoldiella* sp. A), had higher abundance in the Abyssal Zone (>1,000 m) versus the shallower depths on at least one occasion. Within the Abyssal Zone, the greatest abundance of each of these species was at the 1,400 m depth as compared to the 2,600 m depth. When *Vesicomya* sp. occurred at depths above 1000 m, they were usually more abumndant at 850 than at 620 m. Peak abundance of this genus within the macrofauna occurred at depths between 850 and 1,400 m.

Megafaunal-sized *Vesicomya* sp. have been collected or photographed at depths ranging between 420-890 m (see Chapter 6), where they exhibit very clumped and restricted distributions in the vicinity of petroleum seeps. The young (or small forms) are much more widespread, occurring in all regions of the Gulf (Fig. 4-18). If these two size groups of this genus both represent the same chemosynthetic species, dispersal of young may be

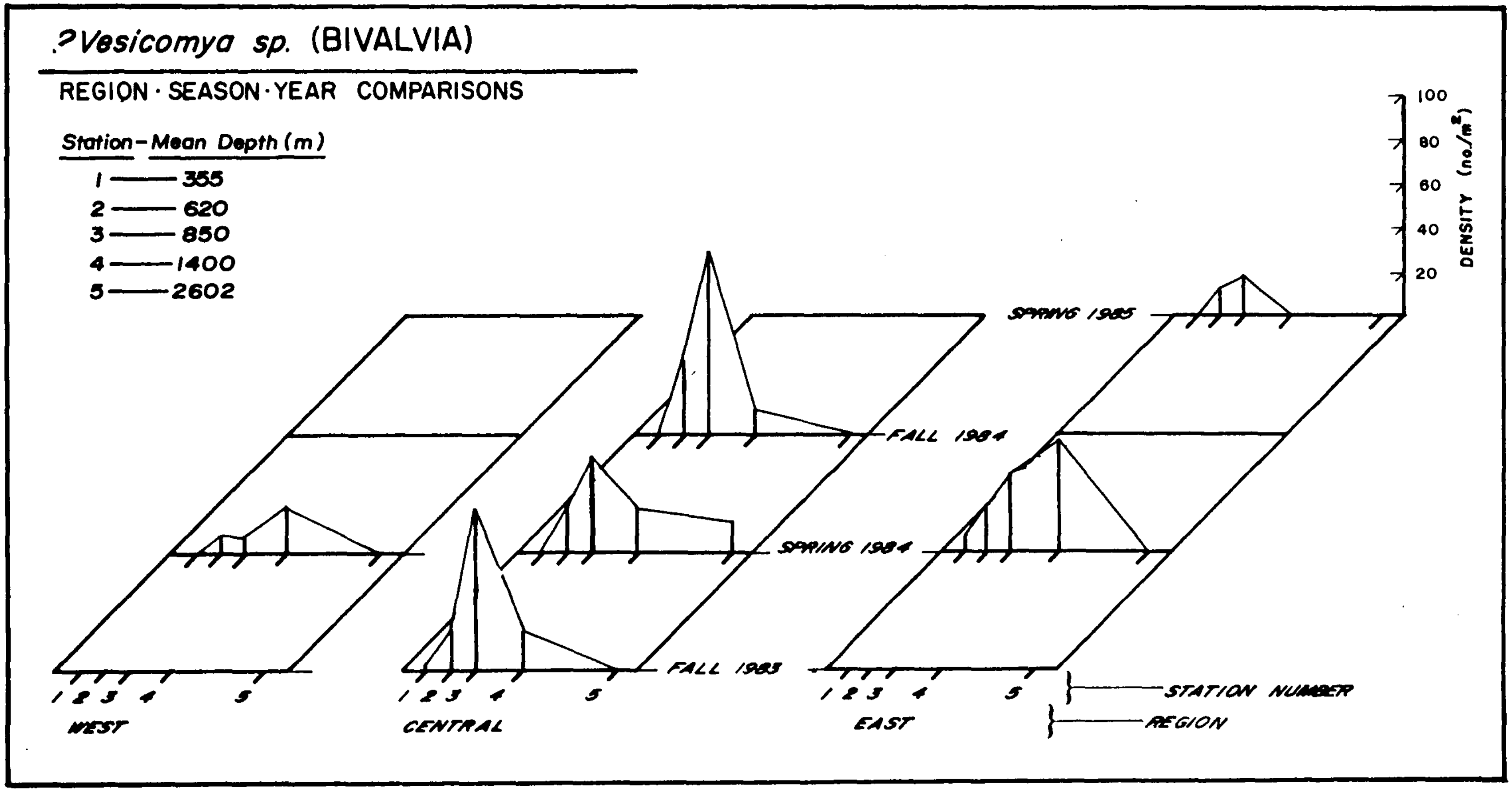

Figure 4-18. Distribution of macrofaunal-sized Vesicomya sp. on the continental slope of the Gulf of Mexico.

widespread with only those which settle in petroleum seeps growing to maturity.

Three species of isopods exhibited significant differences in abundance on the central transect two of which were indicated to be shallow forms (Ischnomesus sp. 208 and Prochelator sp. 202) and the other (Macrostylus sp. 256) a deep form.

Depth Differences (ANOVA 2)

The results of the ANOVA designed to test for fine-scale variation across isobaths on the central transect (Table 4-6) yielded results similar to the depth differences observed in ANOVA 1 (see Table 4-5). Six species of polychaetes reflected significant abundance differences between depths less than 1,000 m. Of these, four were more abundant shallow and two were more abundant in deep water. Also, six species of polychaetes showed differences in abundance between the Shelf/Slope Transition Zone and Archibenthal Zones. Here, however, four of the six polychaete species were more abundant in the Archibenthal Zone (sample depths were 693 and 881 m) than at depths of 357 to 497 m. Only one polychaete (species 12, Sarsonuphis hartmanae) suggested decreased abundance within the zone of the oxygen minimum layer (contrast 4, Table 4-6).

Three species of polychaetes exhibited differences in abundance between Horizons A and B within the Archibenthal Zone with two of these (Pholoe sp. C and Tharyx annulosus) being more abundant at 881 m than at 693 m. For the balance of the polychaete contrasts, the abundance patterns reflected a tendency of higher abundance at 1000 to 1,200 m depths than at depths below 2,000 m.

Five species of bivalves exhibited significant differences of abundance in ANOVA 2. Of these, Eulamellibranchia sp. F was indicated to be an upper slope form; Vesicomya sp. reflected high abundance between 693 and 1,430 m (except for Station C8 at 1,200 m) with peak abundance occurring in the Archibenthal Horizon B Zone (881 m, Fig. 4-19); Malletia sp. B was most abundant about 1,000 m; Crenella sp. A was most abundant between 881 and 1,021 m; and Yoldiella sp. A was most abundant in depths of 1,000 to 1,200 m. Most of the common bivalves exhibited relatively narrow depth ranges except for Vesicomya sp. which was widespread.

Table 4-6. Orthogonal contrasts for ANOVA 2 and macrofaunal species exhibiting significant (0.01 level) differences for each contrast. Numbers represent species as listed in Table 4-4. A plus (+) means the first factor being contrasted was higher than the second factor and a minus (-) means the second factor was highest.

MAJOR GROUP:	ANOVA 2 Contrasts	Polychaetes	Bivalves	Myodocopan Ostracods	Tanaidaceans	Isopods	Bryozoans	Amphipods
(1)	Shallow (<1000 m) depths vs. abyssal depths (>1000 m)	$1^{+},5^{-},7^{+},9^{+},12^{+},15^{-}$	$1^{+},7^{-}$	-	4^{+}	3^{+}	-	-
(2)	Shelf/slope transition vs. archibenthal	$1^{-},6^{+},7^{-},9^{+},22^{-},26^{-}$	-	$3^{-},4^{-}$	3^{+}	-	-	-
(3)	Station C1 vs. C6 (oxygen minimum layer)	12^{+}	1^{-}	-	-	-	-	-
(4)	Horizon A vs. horizon B (archibenthal)	$1^{+},7^{-},19^{-}$	$2^{-},4^{-}$	-	4^{+}	-	-	-
(5)	Upper abyssal zone vs. mesoabyssal zone	$4^{+},19^{+}$	$4^{+},7^{+}$	-	-	-	2^{+}	2^{+}
(6)	Station C5 (marked declivity) vs. C12 (mesoabyssal zone)	-	-	-	-	-	-	-
(7)	Station C11 (~2000 m) vs. stations between 1000 and 1500 m	5^{-}	$4^{-},7^{-}$	-	-	-	2^{+}	-
(8)	Stations 1000- to 1200-m deep vs. stations 1450-m deep	26^{+}	$3^{+},7^{+}$	5^{+}	3^{+}	1^{+}	-	2^{+}
(9)	Station C7 (1000-m deep) vs. C8 (1200-m deep)	26^{+}	$2^{+},3^{+}$	5^{+}	-	1^{+}	-	2^{+}
(10)	Station C9 vs. C4 (variation at 1450 m)	-	-	-	-	5^{+}	-	-

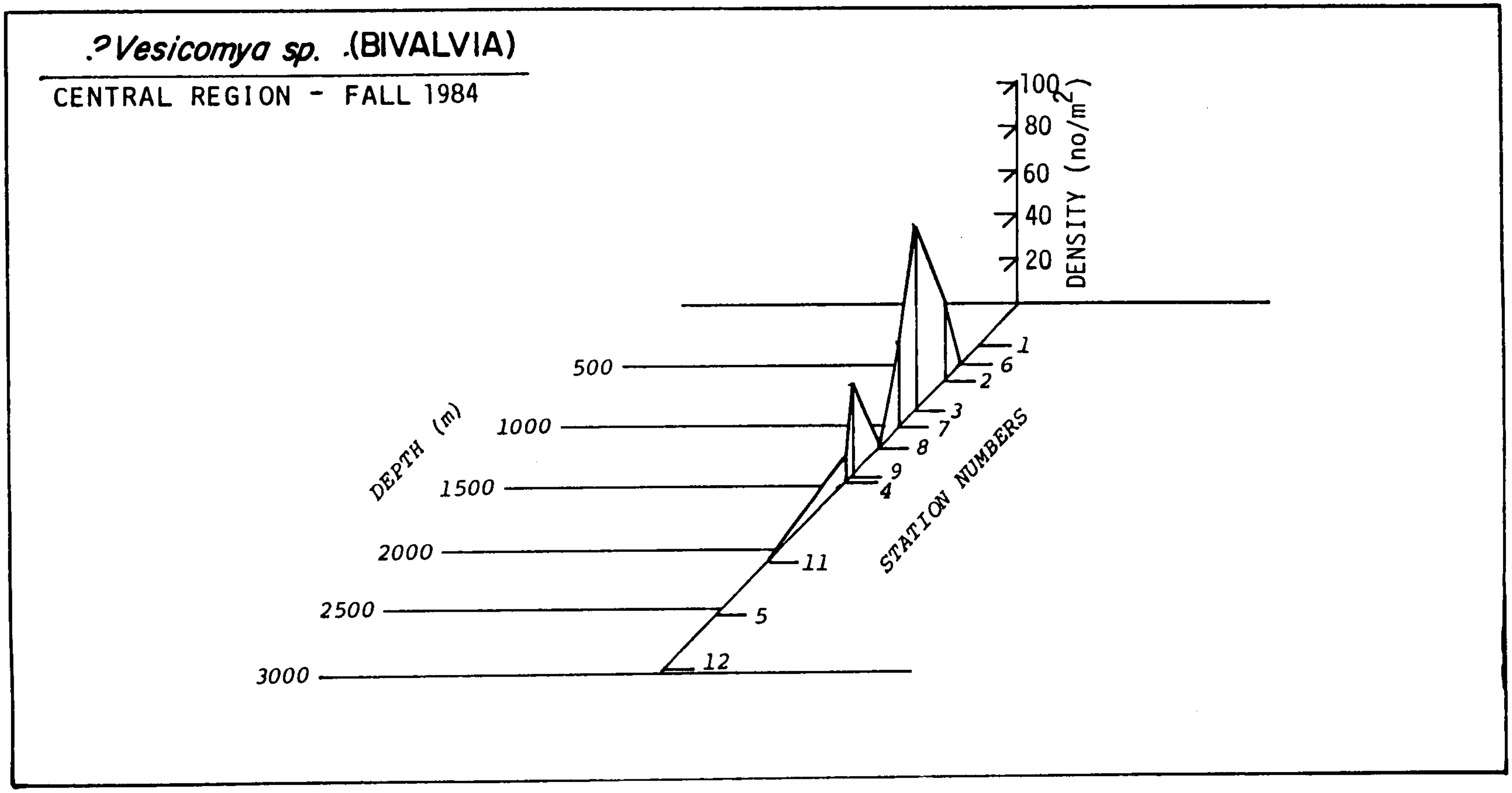

Figure 4-19. Distribution of macrofaunal-sized Vesicomya sp. on the central Gulf of Mexico transect, fall 1984.

Only one of the common myodocopan ostracods (Harbansus sp. A) reflected significant differences in abundance and this was due to a single large collection taken at C7 (1,021 m). The tanaidaceans showing significant differences were both most abundant between 881 and 1,021 m. The isopods were represented by one shallow (Prochelator sp. 202) and two deeper-water forms (Ischnomesus sp. 208 and Macrostylus sp. 256). Only one species each of bryozoans and amphipods reflected significant depth differences (Euginoma cavillieri amd Phoxocephalidae sp. 1, respectively). The bryozoan was most abundant at a depth of about 2,000 m whereas the amphipod was most abundant at depths of about 1,000 to 1,200 m.

Variation Along Isobaths (Eastern Gulf, ANOVA 3)

A total of 68 significant differences in abundance were identified in the orthogonal contrasts for ANOVA 3 (Table 4-7). Of these 66% (45 of 68) were related to differences in abundance between isobaths with only 34% representing differences along isobaths. Within the 23 cases of significant differences along an isobath, eight were related to sediment type differences. Thus, when all other factors were considered equal only 15 (22%) of the observed differences represented instances where abundance levels along an isobath varied significantly. Clearly, in the eastern Gulf, depth variation in abundance greatly exceeded variation in abundance observed along isobaths.

Representatives of the genus Vesicomya sp. were present at intermediate depths and were most abundant along the 850-m depth contour (Fig. 4-20). Significant variation was observed along both transects (Table 4-7, Fig. 4-20). we are unaware of any observations of megafaunal-sized vesicomyids at these depths in the eastern Gulf.

Variation Along Isobaths (Western Gulf, ANOVA 4)

Seventy-seven contrasts for ANOVA 4 were significant at the 0.01 level (Table 4-8). Approximately half of these (38) indicated variation among depths as opposed to along isobaths. Further, seven were associated with sediment differences, two with topographic feature contrasts and 13 with petroleum seep comparisons. Thus, only 24% of the significant

Table 4-7. Orthogonal contrasts for ANOVA 3 and macrofaunal species exhibiting significant (0.01 level) differences for each contrast. Numbers represent species as listed in Table 4-4. A plus (+) means the first factor being contrasted was higher than the second factor and a minus (-) means the second factor was highest.

ANOVA 2 Contrasts	Polychaetes	Bivalves	Myodocopan Isopods	Tanaidaceans	Isopods	Bryozoans	Amphipods
(1) Shelf/slope transition vs. archibenthal and abyssal zones	$1^+,3^+,9^+,10^+,16^+,17^-$	$1^+,2^-,4^-,6^-$	$1^-,2^+,3^-,5^-$	1^+	$1^-,4^-$	2^-	1^-
(2) Silty clay (EIA) vs. sand-silt-clay (E1, EB, EC), shallow (350 m)	$7^-,9^+$	-	-	-	-	1^-	-
(3) Station E1 vs. E1B, E1C (variation along 350-m isobath)	-	-	5^+	-	-	-	-
(4) Station E1B vs. E1C (variation along 350-m isobath)	-	-	-	-	-	-	-
(5) Mesoabyssal zone vs. archibenthal zone	$1^-,7^-$	$2^-,5^-,6^-$	3^-	$1^-,2^-$	$1^-,4^-$	1^-	-
(6) Horizon A vs. horizon B, archibenthal zone	$1^+,4^+,10^+,17^+$	$1^+,2^-,5^-$	$1^+,3^+,4^+$	$2^+,4^+$	4^+	$1^+,3^-$	-
(7) Stations E2, E2B, E2C, vs. E2A, E2D, E2E (variation along 624-m isobath)	-	$1^+,2^-$	-	-	-	-	-
(8) Station E2C vs. E2, E2B (variation along 625-m isobath)	19^+	-	3^-	4^-	-	-	-
(9) Station E2 vs. E2B (variation along 625-m isobath)	-	-	3^-	-	-	-	-
(10) Station E2A vs. E2D, E2E (variation along 625-m isobath)	10^-	2^-	1^+	$4^+,5^+$	-	1^-	-
(11) Sand-silt-clay (E2D) vs. silty clay (E2E) (variation along 625-m isobath)	1^-	-	-	2^-	1^-	$1^-,2^-$	-
(12) Station E3B, E3 vs. E3A, E3C, E3D (variation along 850-m isobath)	-	-	-	-	-	-	-
(13) Station E3B vs. E3 (variation along 850-m isobath)	-	-	-	-	-	-	-
(14) Station E3A vs. E3C, E3D (variation along 850-m isobath)	27^-	-	-	-	1^-	-	-
(15) Station E3C vs. E3D (variation along 850-m isobath)	-	-	-	-	1^+	-	-

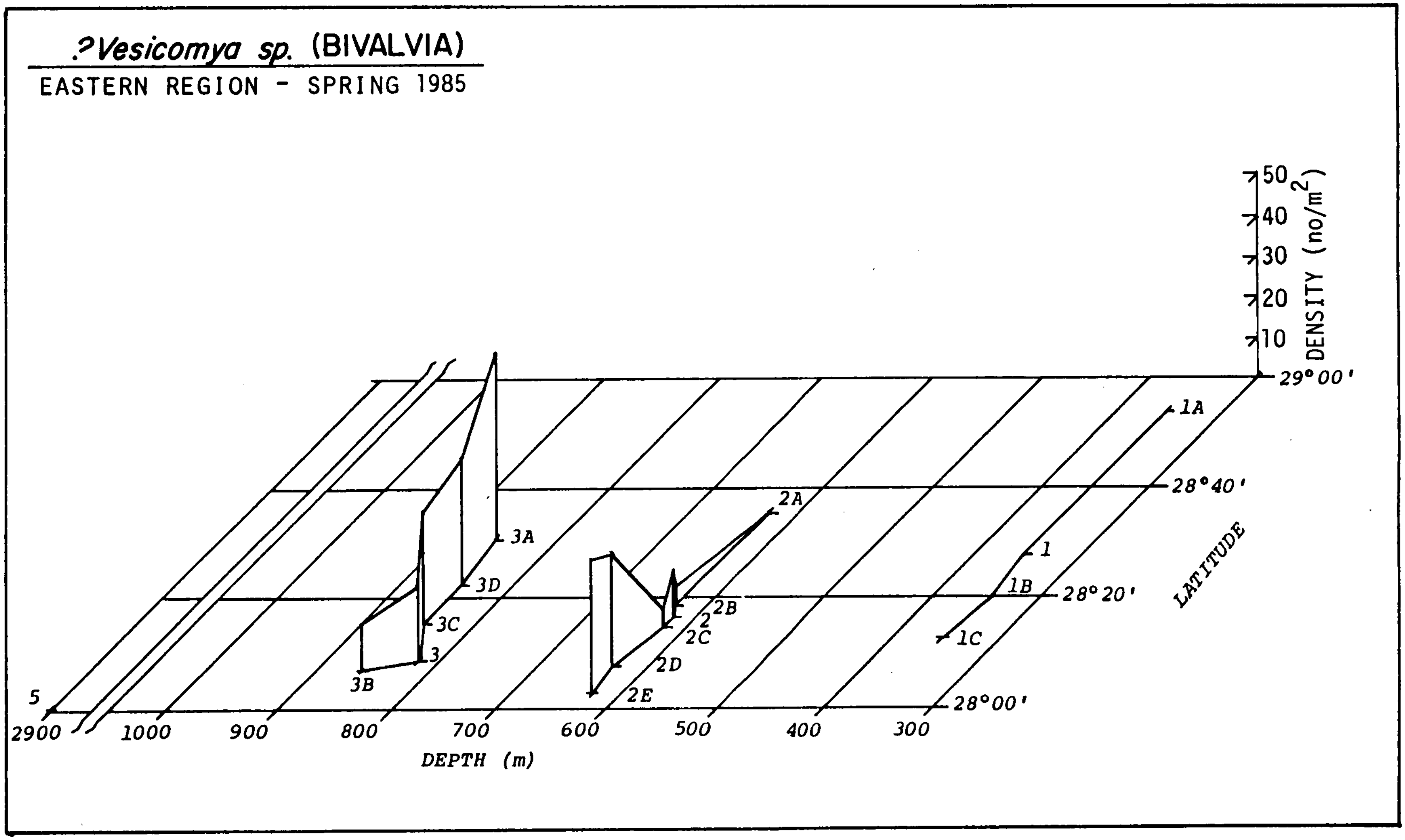

Figure 4-20. Distribution of macrofaunal-sized Vesicomya sp. along isobaths in the eastern Gulf of Mexico, spring 1985.

Table 4-8. Orthogonal contrasts for ANOVA 4 and macrofaunal species exhibiting significant (0.01 level) differences for each contrast. Numbers represent species as listed in Table 4-4. A plus (+) means the first factor being contrasted was higher than the second factor and a minus (-) means the second factor was highest.

ANOVA 4 Contrasts	Polychaetes	Bivalves	Myodocopan Ostracods	Tanaidaceans	Isopods	Bryozoans	Amphipods	Nemerteans
(1) Shelf/slope transition vs. slope	$1^+,2^+,7^-,17^-$	4^-	2^-	$1^-,4^-$	$1^-,5^-$	1^+	1^-	2^+
(2) Silty-clay sediment (WC1) vs. sandy-clay sediment (WC5)	$1^-,16^+$	5^+	2^-	2^+	-	1^-	-	2^-
(3) Archibenthal zone vs. abyssal zone	$1^+,3^+,7^+,9^+,10^+,16^+,17^+$	1^+	3^+	$1^+,4^+,5^+$	$1^+,5^-$	-	-	-
(4) Topographic high (WC11) vs. topographic low (WC12)	-	-	-	3^+	5^+	-	-	-
(5) Horizon A vs. horizon B (archibenthal)	$1^+,3^+,4^+$	-	$1^+,3^+,4^+,5^+$	$1^+,2^+,4^+$	1^+	-	-	-
(6) Station WC3 vs. WC9, WC10 (variation along 750-m isobath)	$7^+,17^-$	5^+	-	-	-	-	-	-
(7) Station WC9 vs. WC10 (variation along 750-m isobath)	7^+	-	-	-	-	-	-	-
(8) Petroleum seep sites (WC6, WC7) vs. non-seep sites	$3^-,17^-,18^+$	$1^-,5^-$	-	3^+	-	1^+	-	-
(9) Seep station WC6 vs. seep station WC7	$7^+,9^-,18^+$	4^+	$3^+,5^+$	-	-	-	-	-
(10) Station WC8 vs. W2, W4 (variation along 550-m isobath)	$3^+,7^-,9^+$	4^-	$1^+,3^+$	$4^+,5^+$	-	-	-	-
(11) Station W2 vs. W4 (variation along 550-m isobath)	-	4^+	-	$2^-,4^-$	1^-	-	1^-	-

contrasts suggested variation along isobaths, all other measured factors being more or less equal. As in the eastern Gulf, variation along isobaths in the western Gulf is markedly less than variation across isoabths.

Variation along the 550 m isobath was greater (13 significant contrasts) than observed levels of variation along the 750 m isobath (four significant contrasts, Table 4-8). This supports the earlier hypothesis that tendencies towards species dominance decrease with depth on the slope.

Seven species exhibited significant abundance differences for the contrast involving seep versus non-seep sites (Table 4-8). Of these, four were more abundant at the non-seep than at the seep sites, including both bivalve species. Of interest, Vesicomya sp. did not show significant differences in any contrast. Although the level of variation precluded any significance determinations, representatives of this genus appeared more abundant at the 550- and 750-m depths than at the 1,220-m deep stations (Fig. 4-21). It should also be noted that, although the seep collections were made in the general vicinity of known petroleum seeps, such features are small. There is no indication that our samples were taken within the area of greatest seepage based upon the observed hydrocarbon levels. Elevated hydrocarbon levels were present (as compared to background, see Chapter 2) but the concentrations did not reflect levels characteristic of those observed within seep sites.

Relation to Physical Factors

The density distributions of the 61 most common macrofaunal species (see Table 4-2) were compared with measures of 22 physical/chemical attributes of the environment (see Table 4-1). Below we present the results of these analyses for the species within the five major groups (polychaetes, bivalves, tanaidaceans, isopods and bryozoans) exhibiting significant correlations. A correlation matrix for all species and factors is included in Appendix B, Volume III of this report.

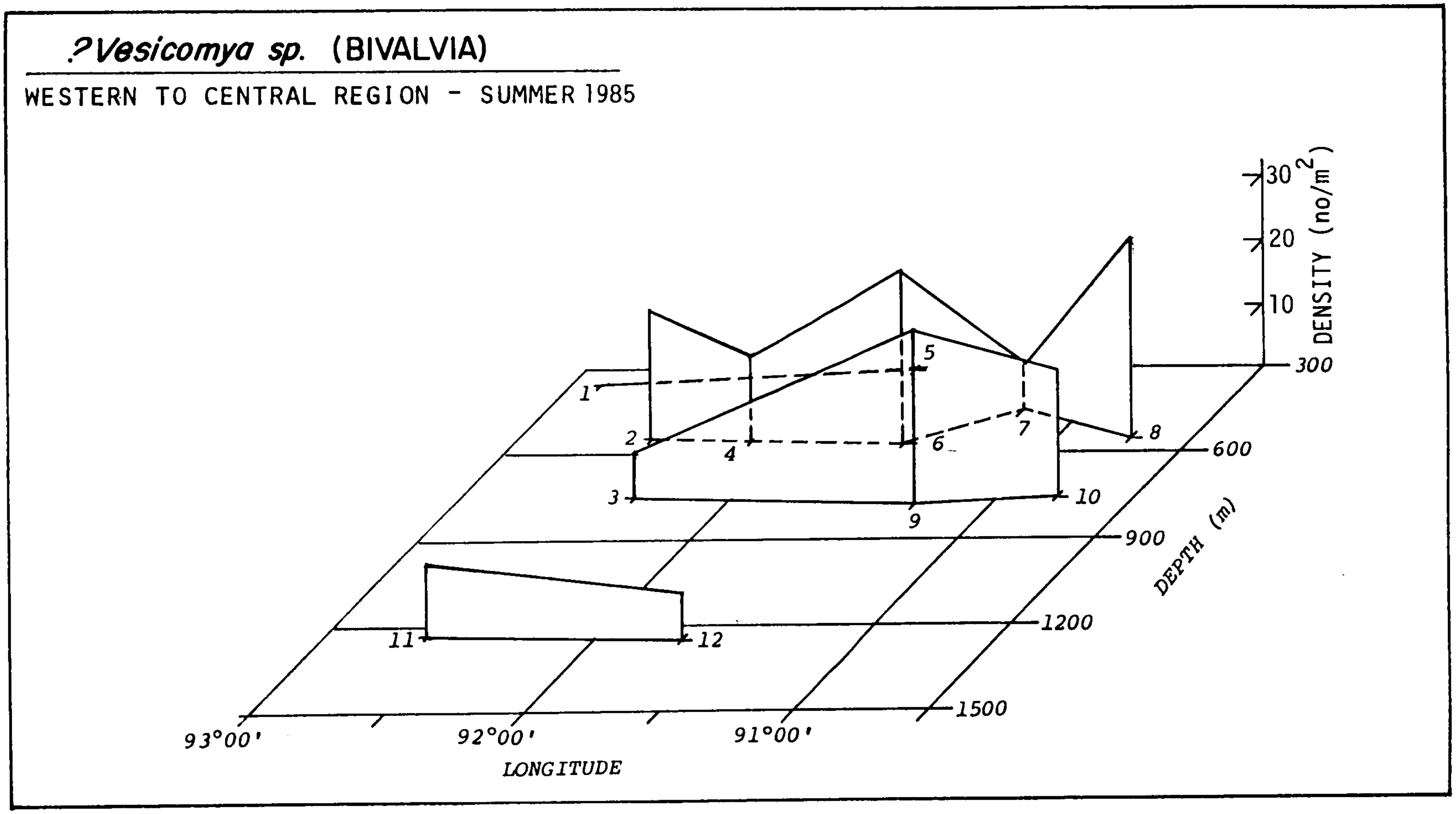

Figure 4-21. Distribution of macrofaunal-sized Vesicomya sp. along isobaths in the west-central Gulf of Mexico, summer 1985.

Polychaetes

Correlations were sought between the densities of the 32 most common polychaetes and each of 22 physical-chemical variables in sediments and water. Abundances of approximately two-thirds (21) of the species were correlated (either negatively or positively) with one or more of the variables (Table 4-9); only a very few of the more abundant species were not correlated with any variable.

More than a third of the species showed abundance correlations with levels of one or more hydrocarbons. Terrigenous sources of hydrocarbon seemed particularly important; abundances of nine species were correlated (negatively) with its levels in sediments. There was a tendency for species that responded, to respond to more than one hydrocarbon variable.

Six species responded to sediment grain size. A response to percentage of sand or clay seemed to coincide with a response to another grain size component; this is predictable because grain size categories (especially sand and clay fractions) tended to vary inversely with each other in samples.

Eight species abundances were correlated with bottom temperature and six with dissolved oxygen. Correlations with these water quality variables were expected given that both the bottom temperature and oxygen level, and the abundance of many species, vary with depth. Few correlations between species abundances and bottom or surface water salinity, transmissivity, or organic carbon levels were apparent.

There was great variability among species in their responsiveness to the physical and chemical variables. As noted above, 11 species had no significant correlations in abundance with any of the variables. Conversely, nine species responded to at least five variables each, and one (*Pholoe* Sp. C) responsed to 10 of the 22 variables.

Bivalves

Seven bivalve species were among the 61 most abundant macrofaunal species; densities of four of these were correlated with at least one physical/chemical habitat variable (Table 4-10). Hydrocarbon and other

Table 4-9. Common polychaetes found on the continental slope (in descending order of abundance) and correlations (Pearson's coefficient at the 0.01 level) between their abundance and environmental components (see Table 4-1 for definition of abbreviations of environmental components).

Species	Environmental Component	Correlation Pearson's Coefficient	Correlation Probability
Litocorsa antennata	TOTEOM	0.39735	0.0024
	ALUCM	0.34343	0.0096
	BOTTEM	0.52812	0.0001
	BOTSAL	0.46301	0.0003
	BOTDO	-0.41269	0.0016
Aurospio dibranchiata	TERRI	-0.47588	0.0002
	SAND	0.48790	0.0001
	CLAY	-0.54065	0.0001
	BOTTEM	0.53432	0.0001
	BOTDO	-0.39486	0.0026
Tachytrypane sp. A	BOTDO	-0.38838	0.0031
Spiophanes berkeleyorum	No Significant Correlations		
Exogone sp. A	BOTTEM	-0.42281	0.0012
	BOTSAL	-0.42258	0.0012
Aricidea suecica	BOTDOC	0.43594	0.0049
Pholoe sp. C	PLIALK	-0.43076	0.0009
	PELOALK	-0.44074	0.0007
	PEHIALK	-0.39648	0.0025
	TERRI	-0.56177	0.0001
	TOTEOM	-0.34241	0.0098
	ALUCM	-0.46347	0.0003
	CPI	-0.37999	0.0039
	CACO3	0.46753	0.0003
	DELC13	0.51106	0.0001
	SURTRAN	0.34532	0.0091
Maldane sp. A	No Significant Correlations		
Prionospio ehlersi	SAND	-0.35634	0.0070
	CLAY	0.38961	0.0030
	ORCAR	0.33429	0.0097
	CACO3	-0.39777	0.0024
	BOTTEM	0.40979	0.0017
	BOTDOC	0.42588	0.0061
Levinsenia gracilis	PEHIALK	-0.36379	0.0058
	ORCAR	0.34855	0.0068

Table 4-9 (cont'd)

		Correlation	
Species	Environmental Component	Pearson's Coefficient	Probability
Fauveliopsis sp. B	PEHIALK	-0.38123	0.0037
	TERRI	-0.44784	0.0005
	ALUCM	-0.35363	0.0075
	SAND	0.44956	0.0005
	CLAY	-0.47807	0.0002
	CACO3	0.52535	0.0001
	DELC13	0.42684	0.0010
	BOTDOC	-0.43760	0.0047
Sarsonuphis hartmanae	PELOALK	-0.36905	0.0051
	PEHIALK	-0.35478	0.0073
	TERRI	-0.46578	0.0003
Prionospio cirrifera	ALUCM	0.48195	0.0002
	CPI	0.43919	0.0007
	ORCAR	-0.36414	0.0046
	BOTTRAN	0.45280	0.0005
	SURTRAN	0.43974	0.0007
	CPI	0.35234	0.0086
Tharyx marioni	ORCAR	-0.33984	0.0085
Lumbrinerides dayi	TERRI	-0.35234	0.0077
	ALUCM	-0.35778	0.0068
	CLAY	-0.36249	0.0060
	CACO3	0.53777	0.0001
Ceratocephale oculata	TERRI	-0.39783	0.0024
	SILT	0.42338	0.0011
	CLAY	-0.46680	0.0003
	CACO3	0.35076	0.0080
	DELC13	0.34765	0.0087
	BOTTEM	0.42191	0.0012
	BOTDO	-0.39501	0.0026
Paralacydonia paradoxa	No Significant Correlations		
Leitoscoloplos sp. A	TERRI	-0.47300	0.0002
	TOTEOM	-0.37316	0.0046
	ALUCM	-0.42795	0.0010
	CPI	-0.35600	0.0071
	CACO3	0.48918	0.0001
	DELC13	0.38313	0.0036
	SURTRAN	-0.35350	0.0075
Tharyx annulosus?	No Significant Correlations		

Table 4-9 (cont'd)

Species	Environmental Component	Correlation Pearson's Coefficient	 Probability
Paramphinome jeffreysii	BOTTEM	0.53118	0.0001
	BOTSAL	0.46582	0.0003
	BOTDO	-0.35368	0.0075
	SURPOC	0.37348	0.0046
Terebellides stroemi	No Significant Correlations		
Diplocirrus capensis	No Significant Correlations		
Pionosyllis sp. H	TERRI	-0.38166	0.0037
Terebellides atlantis	No Significant Correlations		
Paramphinome sp. A	BOTTEM	0.36229	0.0061
Spiophanes bombyx	No Significant Correlations		
Diplocirrus sp. A	PLIALK	-0.44078	0.0007
	PELOALK	-0.46787	0.0003
	PEHIALK	-0.35117	0.0080
	TERRI	-0.49339	0.0001
	ALUCM	-0.35998	0.0064
	CACO3	0.36597	0.0055
	DELC13	0.52466	0.0001
	BOTDOC	-0.51426	0.0007
Cirrophorus lyra	No Significant Correlations		
Lumbrineris verrilli	BOTTEM	0.44687	0.0006
	BOTDO	-0.46069	0.0004
Exogone sp. B	No Significant Correlations		
Euchone incolor ?	SAND	0.51416	0.0001
	SILT	0.34782	0.0086
	CLAY	-0.59601	0.0001
	CACO3	0.48867	0.0001
	DELC13	0.39368	0.0027
Levinsenia uncinata	No Significant Correlations		

Table 4-10. Common bivalves found on the continental slope (in descending order of abundance) and correlations (Pearson's coefficient at the 0.01 level) between their abundance and environmental components.

Species	Environmental Component	Correlation Pearson's Coefficient	Probability
Eulamellibranchia sp. F	TERRI	-0.43718	0.0008
	BOTTEM	0.56089	0.0001
	BOTDO	-0.55166	0.0001
	BOTTRAN	-0.35135	0.0079
	SURPOC	0.36133	0.0062
? *Vesicomya* sp.	No Significant Correlations		
Malletia sp. B	ALUCM	-0.36722	0.0054
	CACO3	0.36719	0.0054
Crenella sp. A	No Significant Correlations		
Nucula sp. A	PLIALK	-0.41266	0.0016
	PELOALK	-0.40711	0.0018
	TERRI	-0.42250	0.0012
	ALUCM	-0.35681	0.0069
	DELC13	0.48193	0.0002
Eulamellibranchia sp. B	PLIALK	0.58615	0.0001
	PELOALK	0.58020	0.0001
	PEHIALK	0.78577	0.0001
	TERRI	0.61601	0.0001
	BOTTEM	-0.45228	0.0005
	BOTDO	0.36677	0.0054
Yoldiella sp. A	No Significant Correlations		

carbon variables in sediments and the quality of bottom water seemed to exert the most influence on bivalve abundance; sediment size and surface water quality had little to no apparent effect.

Three of the seven most common species (Eulamellibranchia spp. B and F, and Nucula sp. A) seemed relatively sensitive to several sediment and bottom water variables. Populations of three other species showed no significant correlations with habitat variables and one species was intermediate in sensitivity.

Tanaidaceans

The four tanaidacean species that were among the 61 most abundant macrofaunal species were insensitive to variability in physical and chemical habitat components. Density of only one species (Leptognatha sp. 15) was correlated with any habitat component, and this species responded to only one of 22 variables, delta ^{13}C (correlation coefficient was 0.3537, probability level was 0.0075).

Isopods

Three of the five isopod species that were among the most abundant 61 species of macrofauna varied in their abundance with physical and chemical habitat variables:

		Correlation	
Species	Environmental Component	Pearson's Coefficient	Probability
Ischnomesus sp. 208	No Significant Correlations		
Gnathia sp. 201	No Significant Correlations		
Prochelator sp. 202	ORCAR	0.35391	0.0075
	CACO3	-0.34403	0.0094
	BOTTEM	0.36507	0.0057
Prochelator sp. 408	TERRI	-0.43576	0.0008
	SURTRAN	-0.34854	0.0085
Macrostylus sp. 256	BOTTEM	-0.40539	0.0019

The two most abundant isopods exhibited no significant correlations.

Bryozoans

All three species of bryozoans that were included among the 61 most abundant species of macrofauna responded to at least one of the habitat variables included in the analyses:

	Environmental	Correlation	
		Pearson's	
Species	Component	Coefficient	Probability
?*Nolella monniotae*	TERRI	-0.42770	0.0010
	CPI	-0.35263	0.0077
	ORCAR	-0.34522	0.0092
	CACO3	0.36289	0.0060
	SURTRAN	-0.34468	0.0093
Euginoma cavillieri	SILT	0.36730	0.0054
Setosellina elegantula	DELC13	0.36394	0.0058

Two of the species responded to only one variable each whereas *Noellela monniotae* responded to a number of variables, three of which were hydrocarbon indicators.

Summary

Only 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 (Table 4-11). Most of the species responded negatively to sediment hydrocarbon levels, including those of phytoplankton or terrigenous plant origin.

Table 4-11. Numbers of common macrofaunal species (in five major groups), the densities of which were correlated with selected environmental variables on the continental slope. Only the significant correlations (Pearson's correlation test at the 0.01 level, both positive and negative values) between the environmental variables and the members of these groups among the 60 most abundant species are included.

	Taxonomic Group										
	Polychaeta		Bivalvia		Tanaidacea		Bryozoa		Isopoda		Total
Environmental Variable	+	-	+	-	+	-	+	-	+	-	+ or -
Hydrocarbons											
PL1 alkanes		2	1	1							4
PE-LO alkanes		3	1	1							5
PE-Hi alkanes		5	1								6
Terrigenous		9	1	2				1		1	14
Extractable organic matter	1	2									3
Aliphatic unresolved complex mixture	2	5		2							9
Carbon preference index	2	2						1			5
Sediment size											
Sand	3	1									4
Silt	2						1				3
Clay	1	5									6
Organic carbon	2	2						1	1		6
Calcium carbonate	7	1	1				1			1	11
Delta ^{13}C	6		1		1		1				9
Bottom temperature	7	1	1	1					1	1	12
Bottom salinity	2	1									3
Bottom dissolved oxygen		6	1	1							8
Bottom transmissivity	1			1							2
Bottom particulate organic carbon			1								1
Bottom dissolved organic carbon	2	2									4
Surface transmissivity	2	1						1	1		5
Surface particulate organic carbon	1										1
Surface dissolved organic carbon											

Sediment grain size and levels of calcium carbonate and delta ^{13}C 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 temperatures, of course, vary markedly with depth and a relatively high number of correlations would be expected to result.

SUMMARY AND DISCUSSION

The macrofauna of the continental slope of the Gulf of Mexico are abundant (average transect densities ranged from 1,500 to 3,000 individuals/m^2) 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, consits 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 (Fig. 4-22). 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

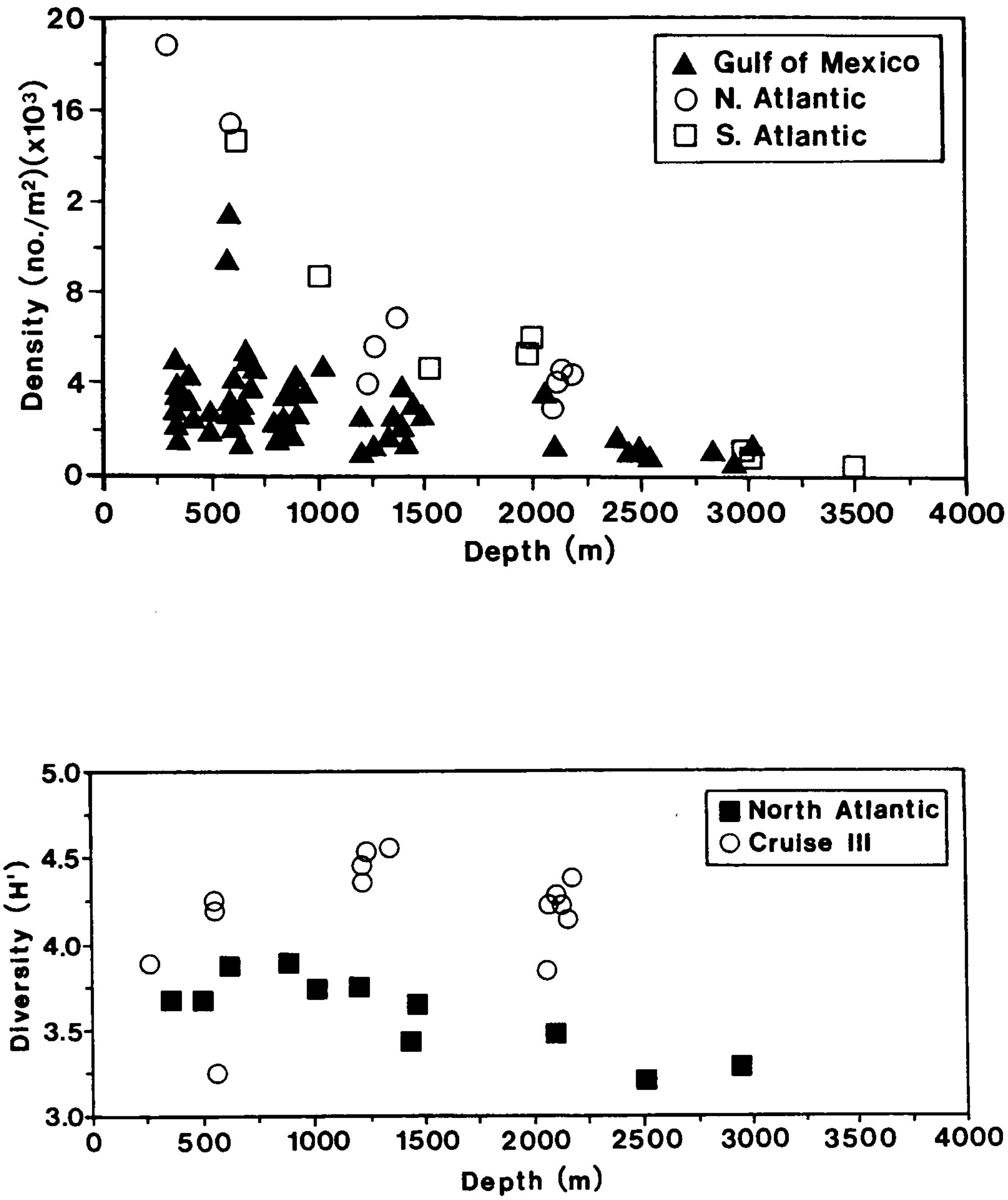

Figure 4-22. Comparison of densities and diversities of continental slope macrofauna in the Gulf of Mexico and U.S. Atlantic Ocean.

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 (see Fig. 4-12). 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 Haedrichs 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.

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CHAPTER 5. THE MEGAFAUNA OF THE CONTINENTAL SLOPE OF THE NORTHERN GULF OF MEXICO—COMMUNITY STRUCTURE AND DIVERSITY, WITH COMMENTS ON LIFE HISTORY INFORMATION

B.J. Gallaway and W.E. Pequegnat

INTRODUCTION

The megafauna data were more completely analyzed than other groups in each of the previous annual reports because the collections were smaller and less diverse. The most complete account, prior to this one, can be found in Gallaway et al. (1988). In this chapter, we summarize the previous work as necessary and place the emphasis on interpretation of the findings and certain life history features of relevance for understanding the continental slope benthic community.

The specific program objectives of the megafaunal studies were to:

(1) Describe over time and space the composition, distribution and abundnace of the megafauna of the continental slope of the northern Gulf of Mexico;

(2) Relate any trends to environmental features and compare results to other deep-sea regions; and

(3) Describe food habits and other life history information that would contribute to a better understanding of the benthic community of the slope.

The results presented herein draw largely from our trawl collections, and emphasis is placed upon the fishes and decapod crustaceans. Benthic photography studies were also conducted, but the taxonomic resolution for most species was too poor for the results to be useful in meeting the primary objectives of this task. However, one important finding of the photography efforts (see Gallaway et al., 1988 for the results of these studies), was that density estimates made by trawling greatly underestimate actual densities of slope megafauna.

STUDY AREA AND METHODS

As outlined in Chapter 1, megafaunal samples were obtained by trawling. Trawl tows were made at each station, but several were considered to be of dubious quality, especially the tow made at Station C9 on Cruise III (see Fig. 1-7). There the trawl filled with a mud lump and, even though some organisms were caught, this collection was not considered in the analyses. Collections from the other dubious tows were included because organisms were caught and there was no tangible basis for confirming our suspicions that the gear may not have sampled efficiently. In future deep-sea programs of this type, tows should be of longer duration than 1-2 hours and made using nets with larger openings than the 9-m wide nets which we used. The tows should also be replicated.

RESULTS

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).

In general, megafaunal invertebrates were four to five times more abundant than fish, and the two categories exhibited similar patterns in abundance and diversity. Both categories, 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 5-1).

Abundance Patterns

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 (Fig. 5-1). 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,

Table 5-1. Most abundant species (>1% of the total) of fishes and invertebrates collected during the Gulf of Mexico continental slope study.

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

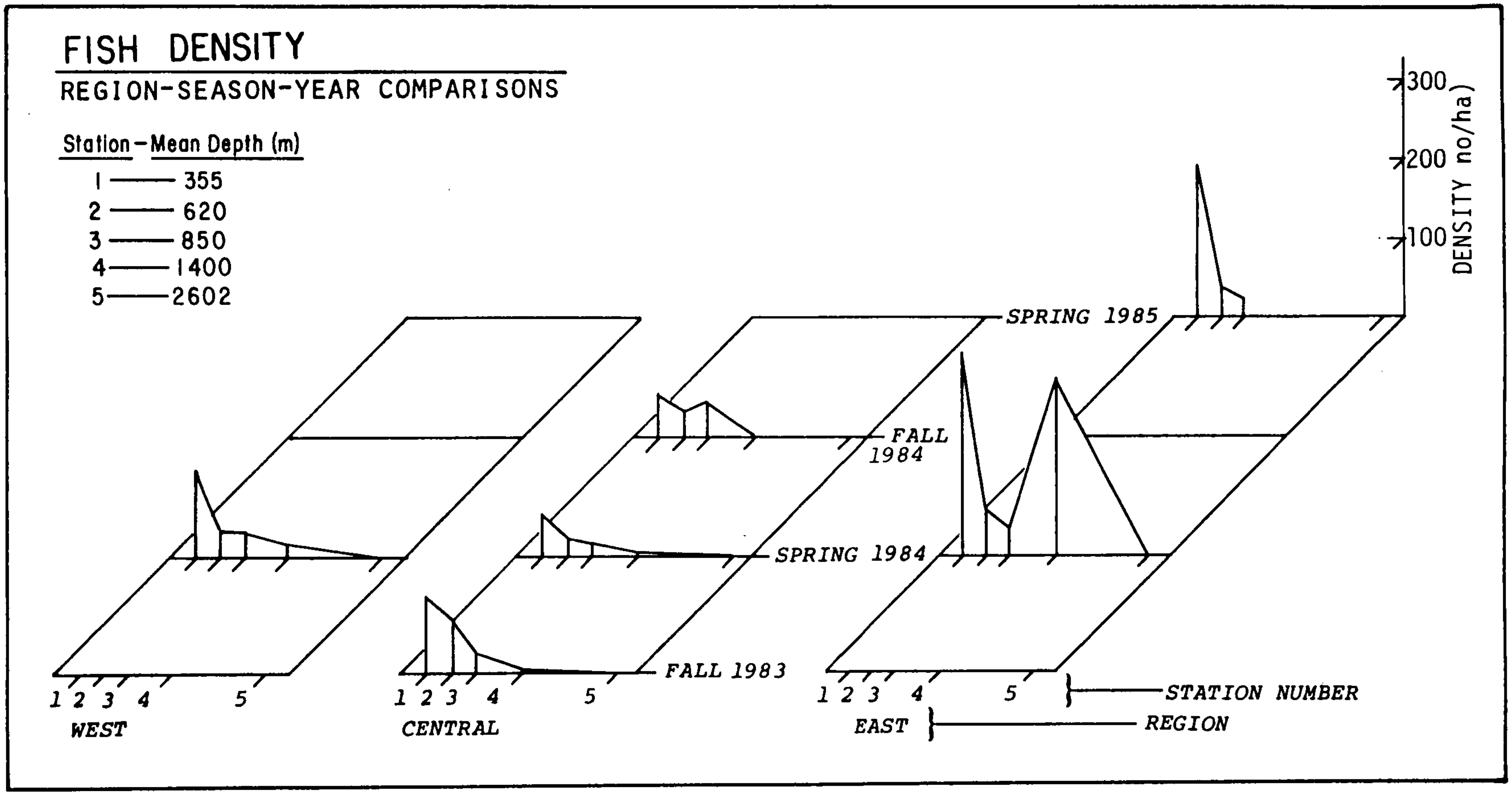

Figure 5-1. Comparative levels of fish densities by region, season, year and selected depth interval.

based upon common stations sampled on the eastern transect, there was little difference in overall fish density between the 1984 and 1985 spring collections.

The seasonal fish abundance patterns differed from that exhibited by the macrofauna. The latter group exhibited peak abundance in spring in an apparent direct response to increased carbon input. However, fish abundance did not increase until fall, suggesting a several month lag between predator response to prey abundance--or little trophic relationship between the two groups. More questions that explanations are provided by the data in hand.

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 (Fig. 5-2). 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 (Fig. 5-3). 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 (Fig. 5-4, compare to Fig. 5-3). The isobathic sampling in the west-central Gulf included a number of specific contrasts as outlined in Chapter 4. Fish densities at stations WC1 (silty clay) and WC5 (sandy clay) differed little despite being widely separated over different sediment types. On the 650-m isobath, abundance levels at WC7 and WC8 were higher than at other stations (WC2, WC4 and WC6). On

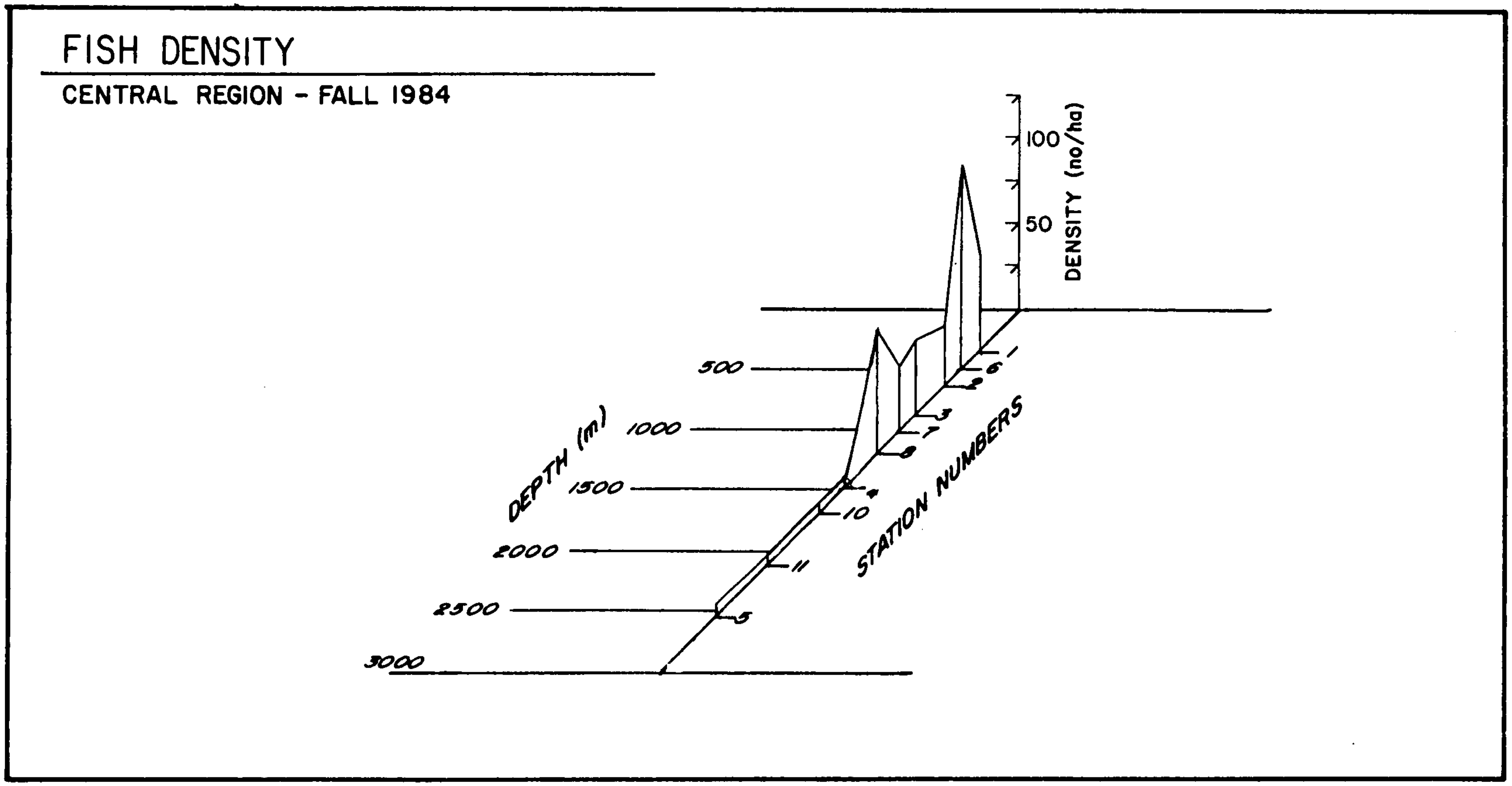

Figure 5-2. Comparative levels of fish density by depth on the central transect, fall 1984.

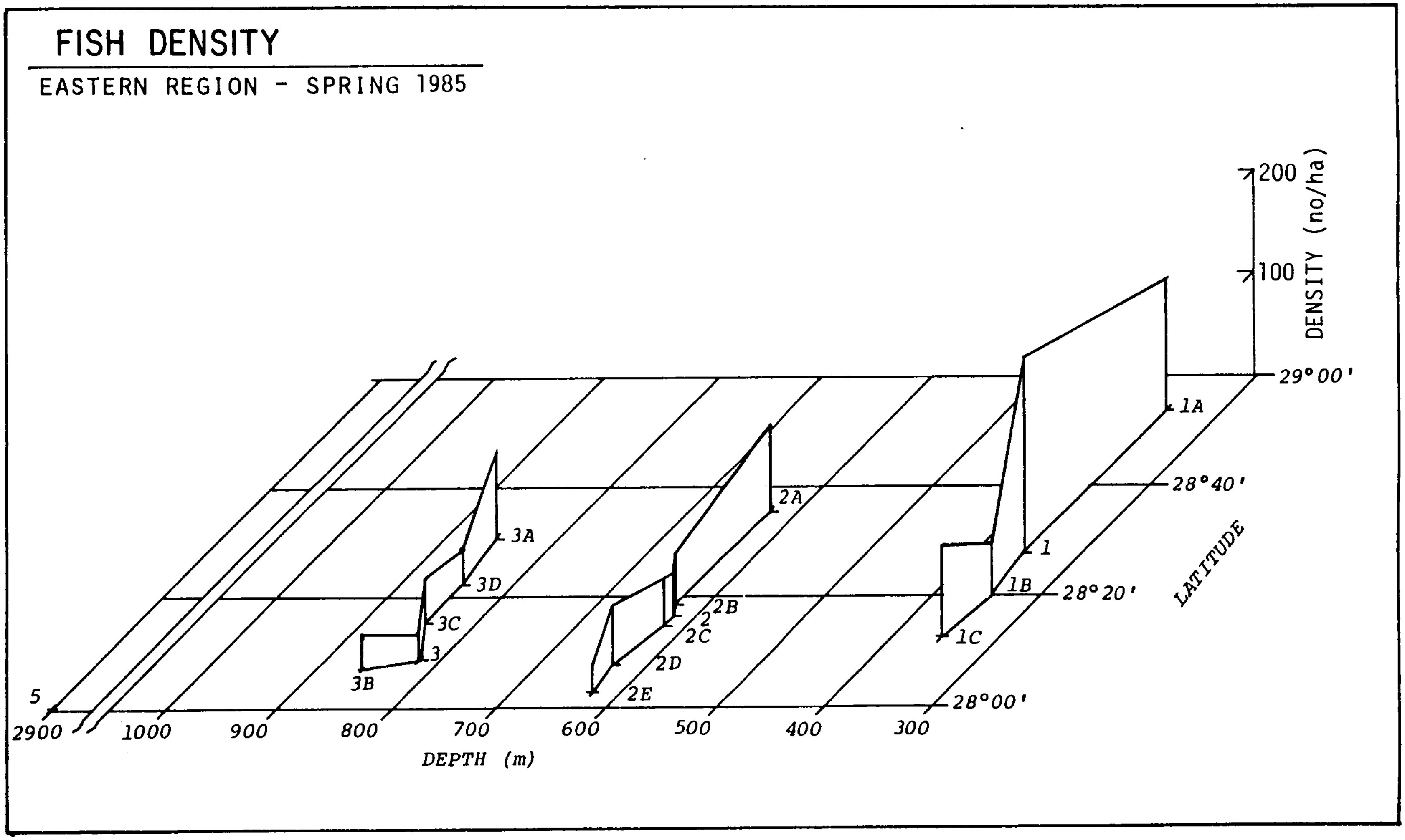

Figure 5-3. Comparative levels of fish density along selected isobaths in the eastern Gulf of Mexico during spring 1985.

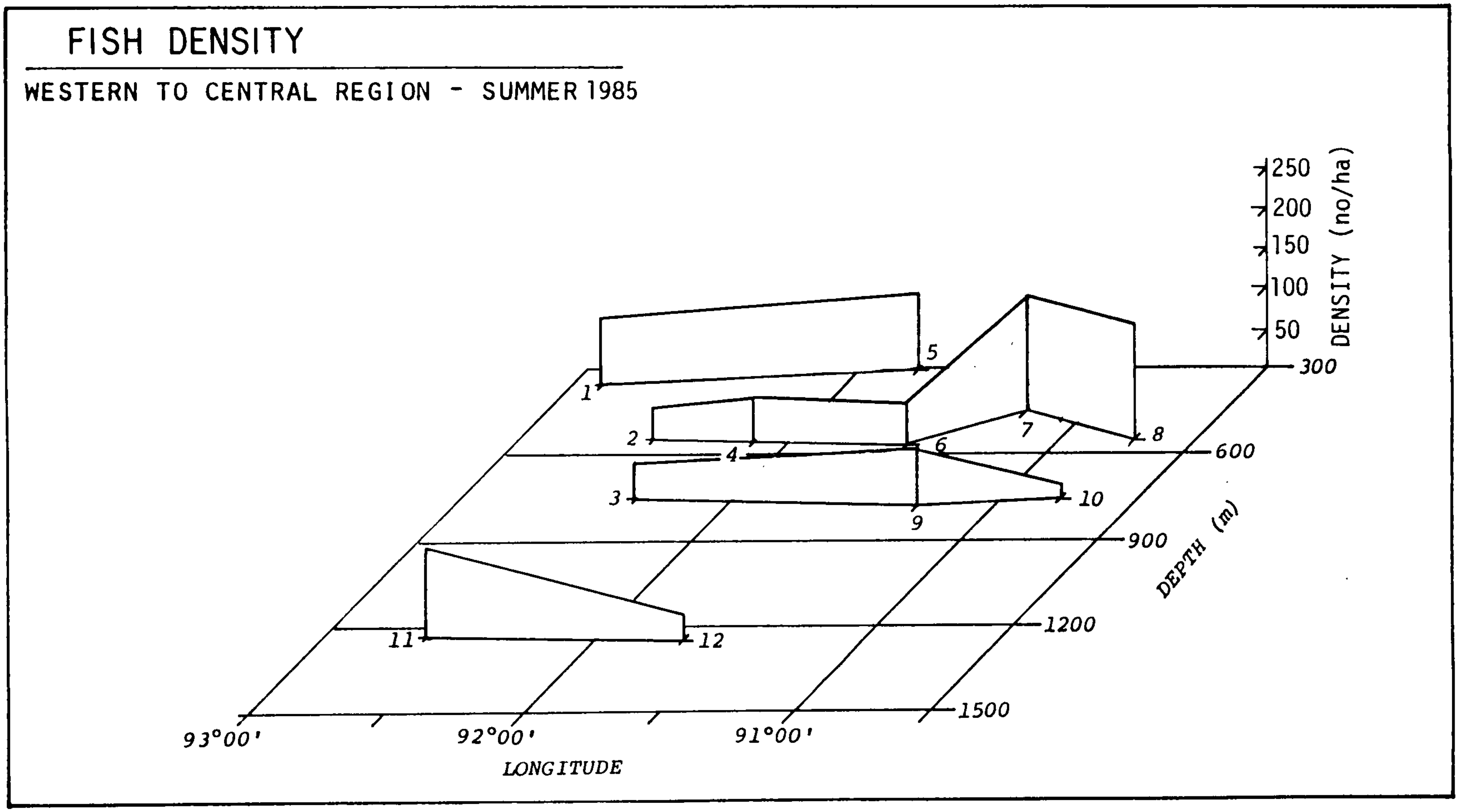

Figure 5-4. Comparative levels of fish density along isobaths between the central and western Gulf of Mexico sampling transects, summer 1985.

this transect, it had been planned that the tows at stations WC6 and WC7 would be within petroleum seeps; however, these were missed.

Stations WC3, WC9 and WC10 were all on the same sediment type and at approximately the same depth (850 m). Stations WC9 and WC10 were in closer physical proximity to one another than to Station WC3, which was located farther to the west. Fish abundance was similar at stations WC3 and WC9 but was markedly lower at Station WC10. Stations WC11 and WC12 were located at the same depth (1,220 m) but WC11, where abundance was notably higher, was a topographic high.

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 (Fig. 5-5). 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 (Fig. 5-6).

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 (Fig. 5-7). 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 (Fig. 5-8). However, in contrast to fish, invertebrate density at WC1 (silty clay) was higher than at WC5 (sandy clay) although both stations were at similar depths. Also, invertebrate density at the topographic high (WC11) was higher than density at the same depth at Station WC12.

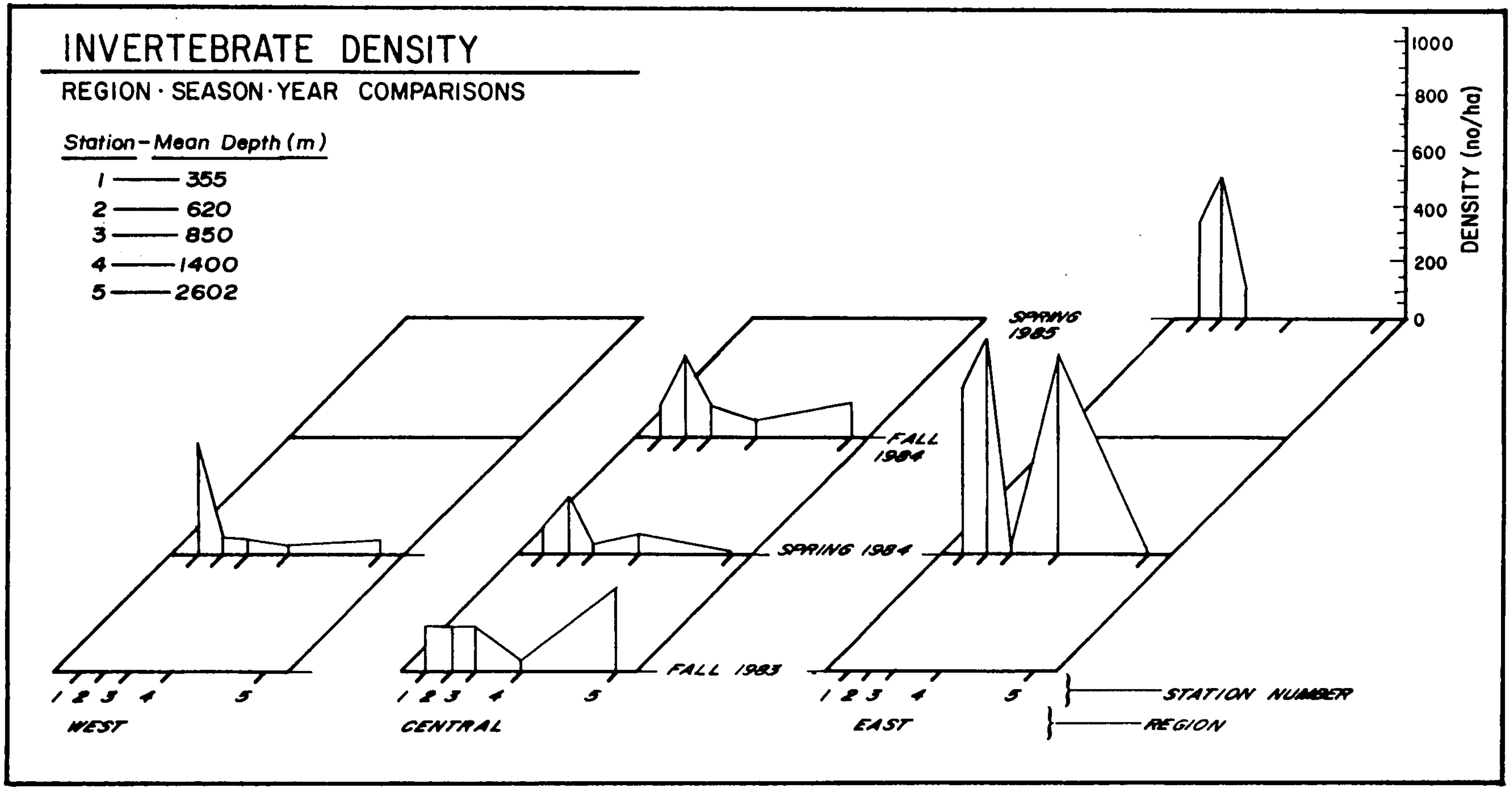

Figure 5-5. Comparative levels of megafaunal invertebrate densities by region, season, year and selected depth interval.

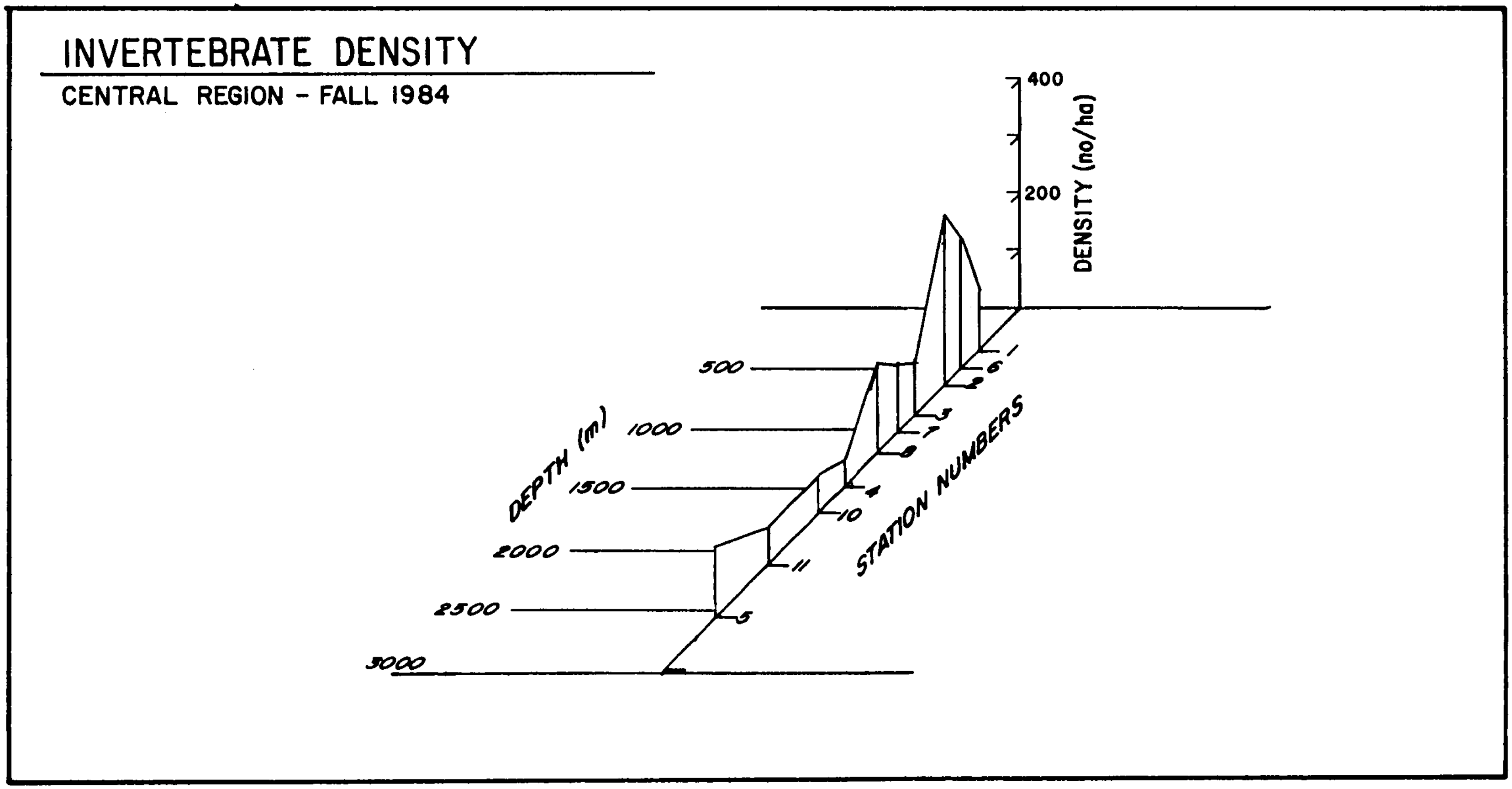

Figure 5-6. Comparative levels of megafaunal invertebrate densities on the central transect, fall 1984.

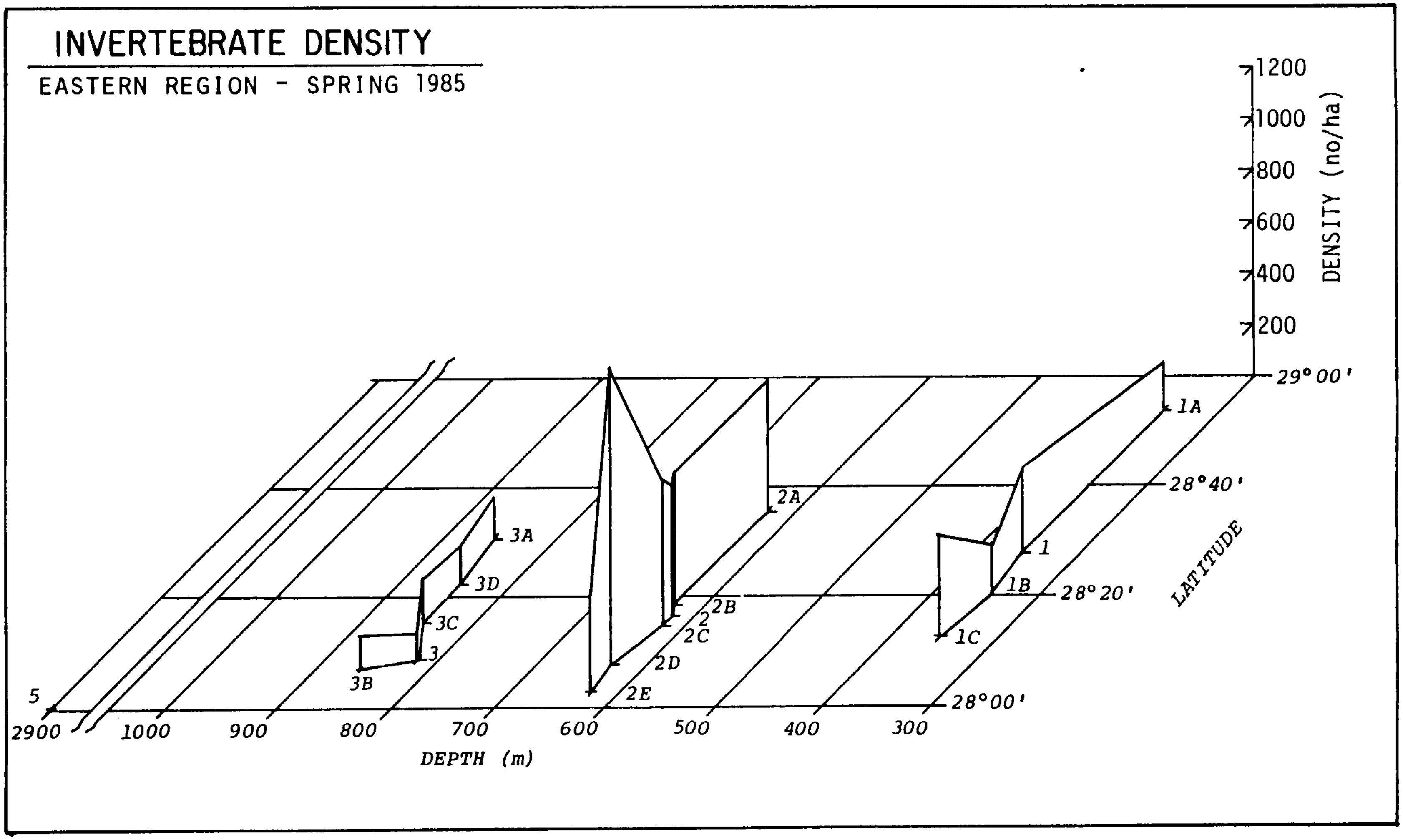

Figure 5-7. Comparative levels of megafaunal invertebrate density along selected isobaths in the eastern Gulf of Mexico during spring 1985.

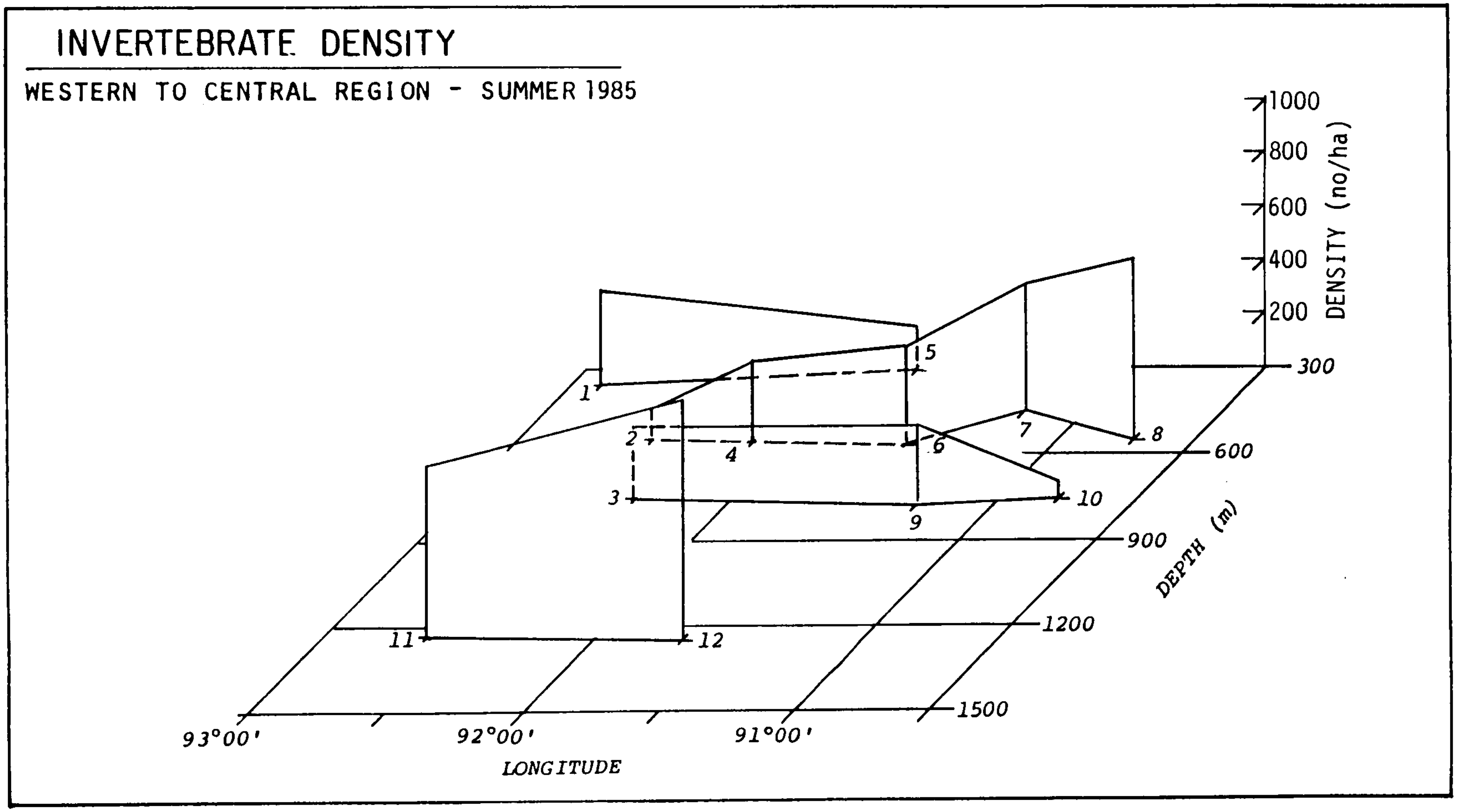

Figure 5-8. Comparative levels of megafaunal invertebrate density along isobaths between the central and western Gulf of Mexico sampling transects, summer 1985.

Diversity Patterns

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 (Fig. 5-9). Comparison of diversity levels by depth on the central transect during fall 1984 (Fig. 5-10), 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 (Figs. 5-11 and 5-12). Fish diversity in the Gulf appears remarkably similar to fish diversity in the U.S. Atlantic (Musick, 1976; Fig. 5-13).

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 (Fig. 5-14). 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 (Fig. 5-15). Likewise there was little variation in decapod diversity along or between isobaths in the eastern Gulf (Fig. 5-16).

Isobathic sampling in the west-central Gulf produced few major differences in decapod diversity except for the shallowest and deepest station pairs (Fig. 5-17). At a depth of 350 m, the station over sandy clay (WC5) had lower diversity than WC1 (silty clay). Station WC11, the topographic high at a depth of 1,220 m, was characterized by low diversity relative to the Station WC12.

Zonation Patterns and Relation to Environment

Throughout this study, emphasis has been placed upon determining the validity of the megafaunal zonation scheme hypothesized by Pequegnat

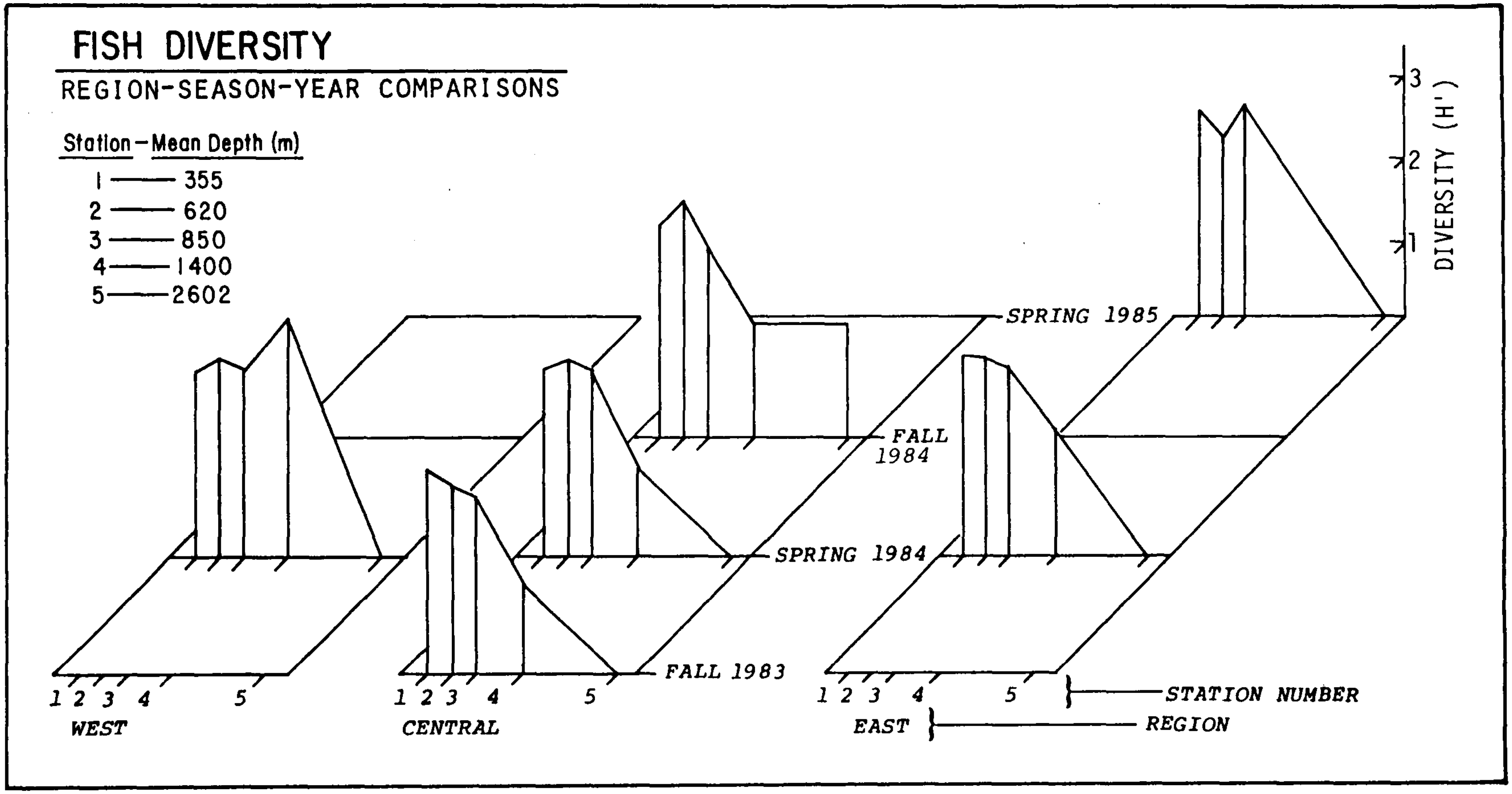

Figure 5-9. Comparative levels of fish diversity by region, season, year and selected depth interval.

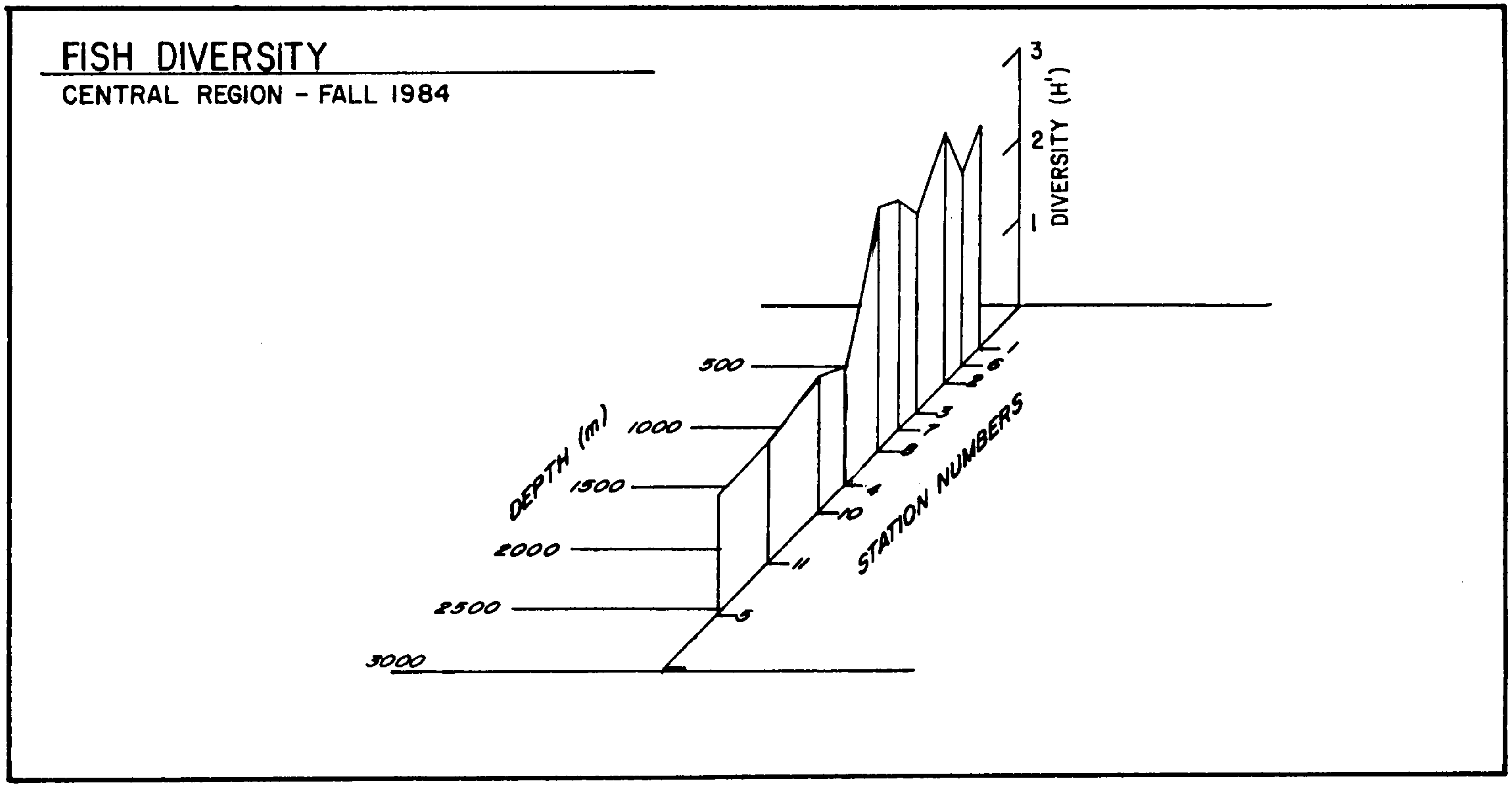

Figure 5-10. Comparative levels of fish diversity by depth on the central transect, fall 1984.

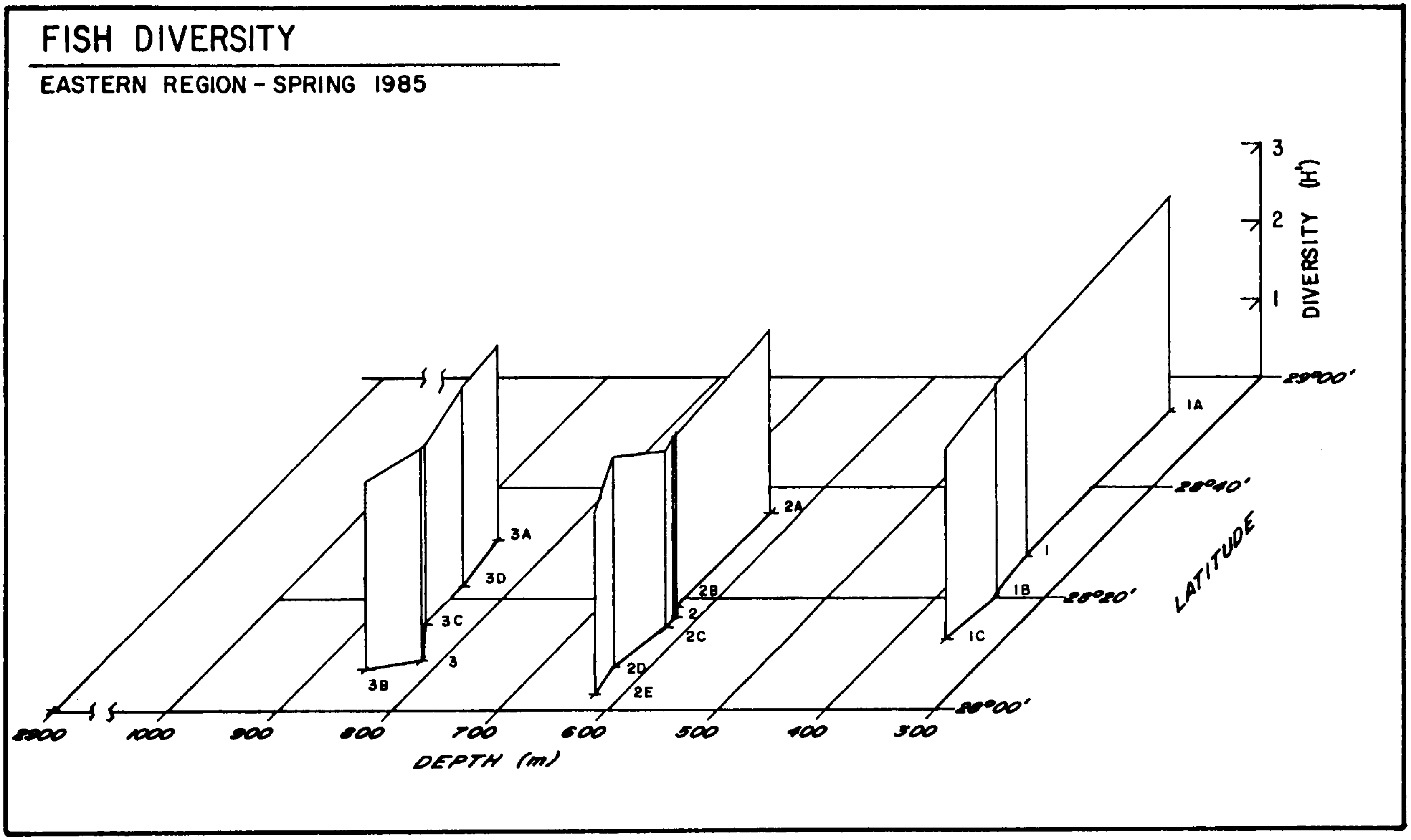

Figure 5-11. Comparative levels of fish diversity along selected isobaths in the eastern Gulf of Mexico during spring 1985.

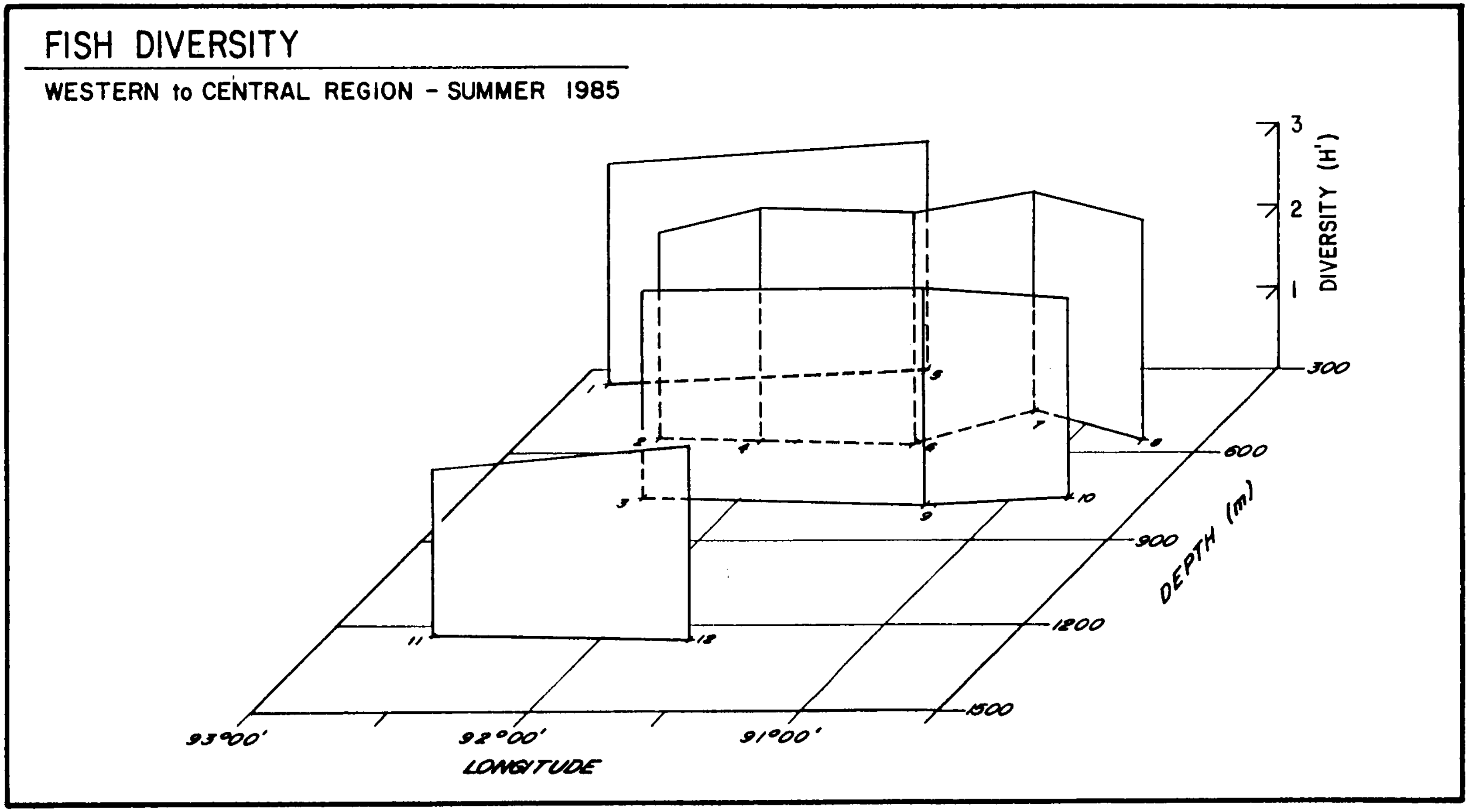

Figure 5-12. Comparative levels of fish diversity along isobaths between the central and western Gulf of Mexico sampling transects, summer 1985.

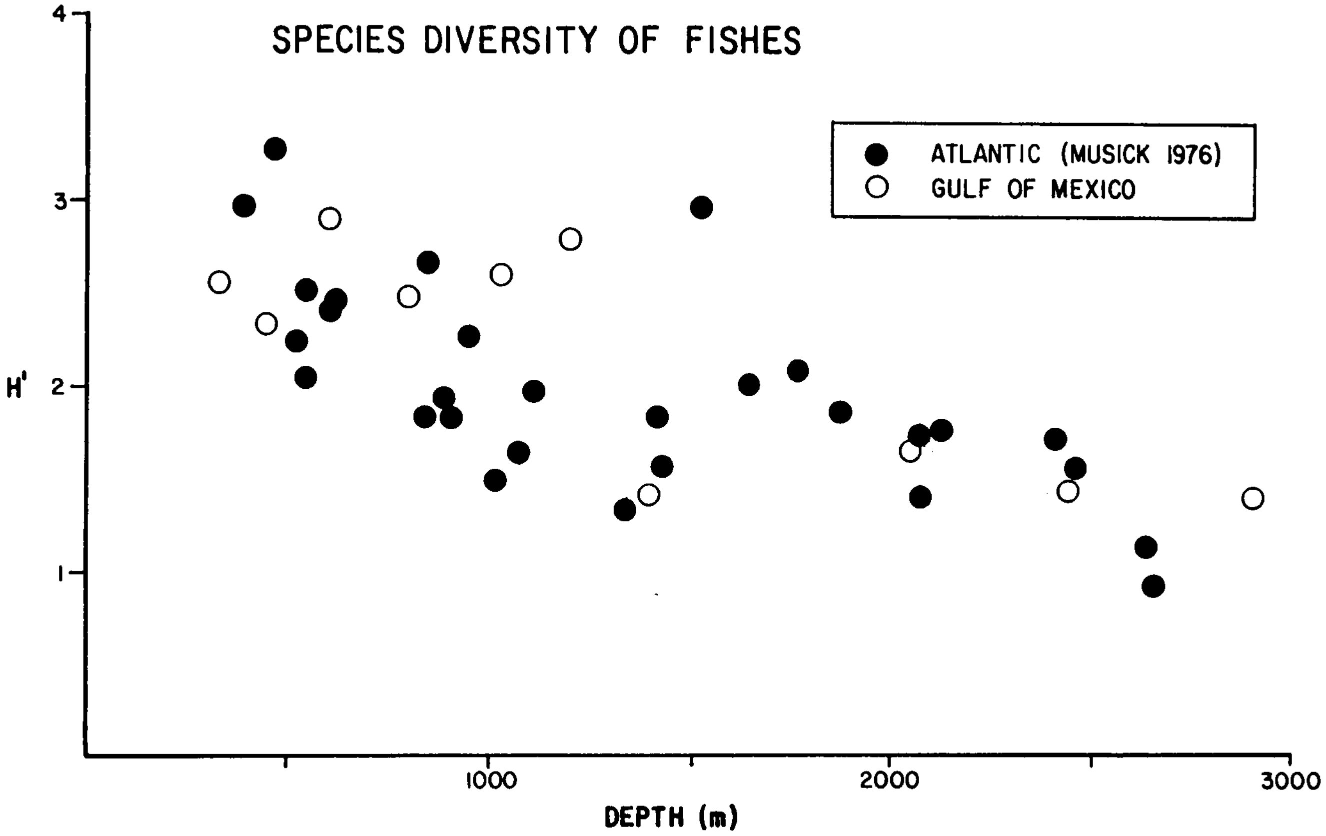

Figure 5-13. Comparison of fish diversity levels, by depth, between the Gulf of Mexico (this study) and Atlantic (Musick, 1976) continental slopes.

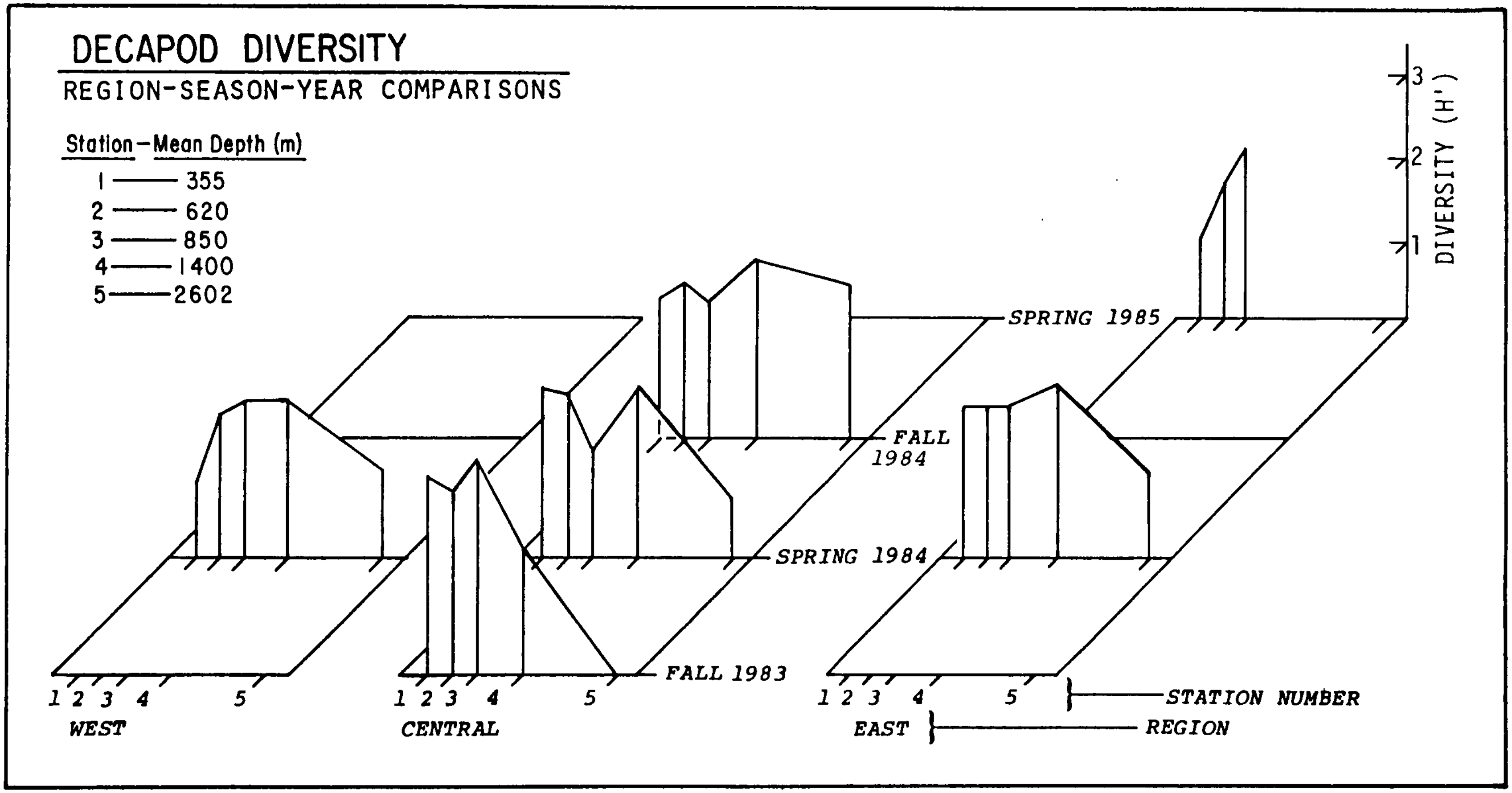

Figure 5-14. Comparative levels of decapod diversity by region, season, year and selected depth interval.

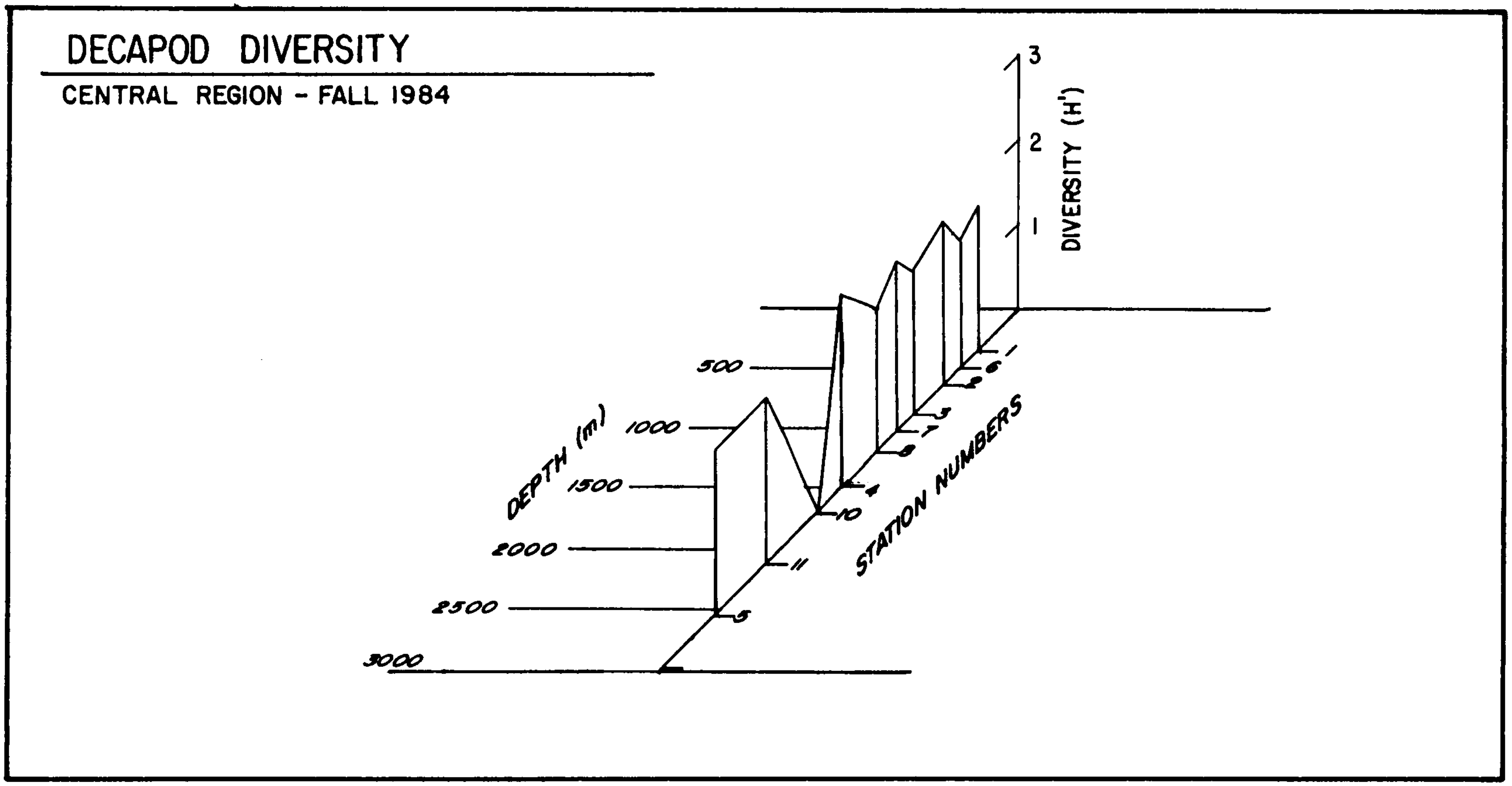

Figure 5-15. Comparative levels of decapod diversity by depth on the central transect, fall 1984.

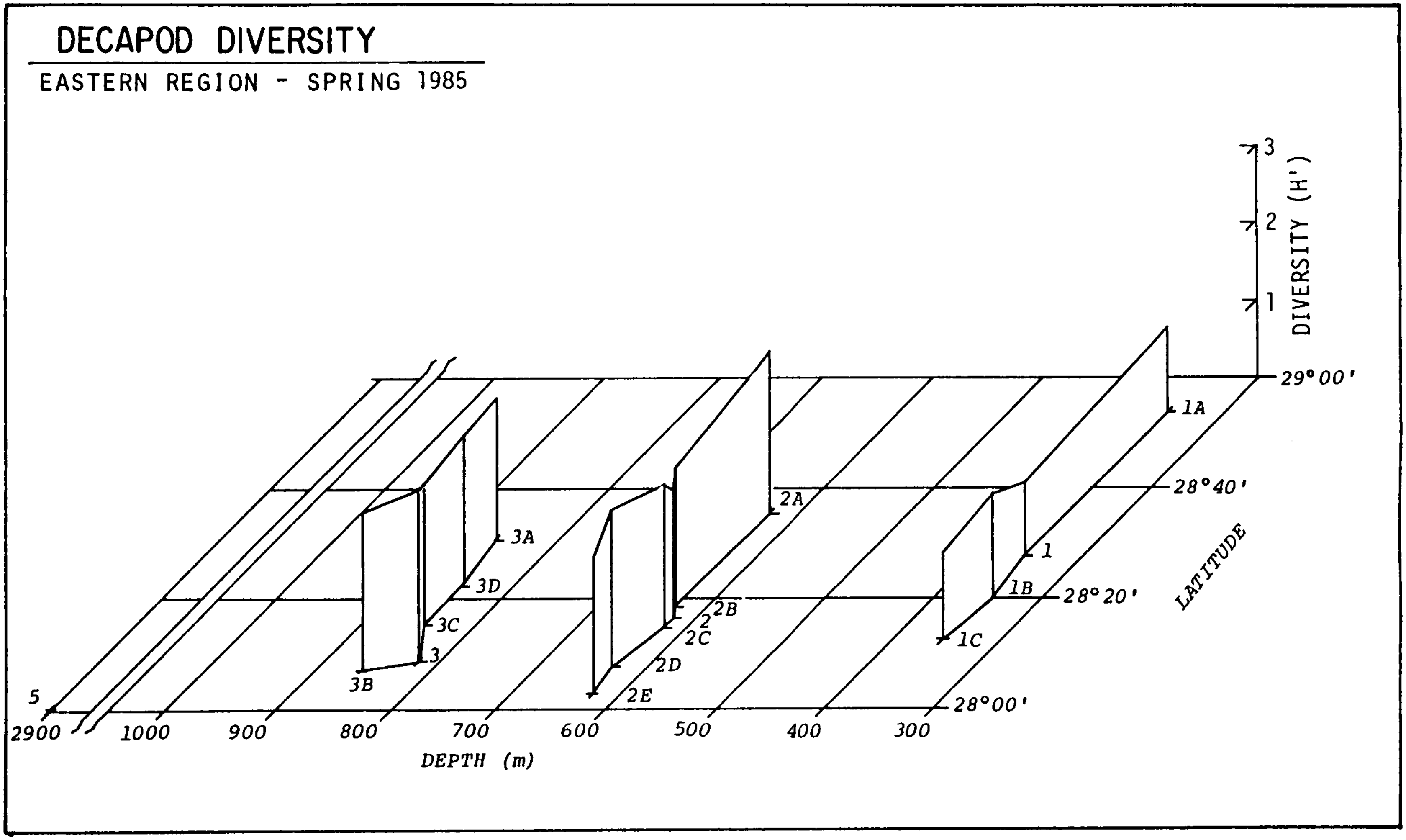

Figure 5-16. Comparative levels of decapod diversity along selected isobaths in the eastern Gulf of Mexico during spring 1985.

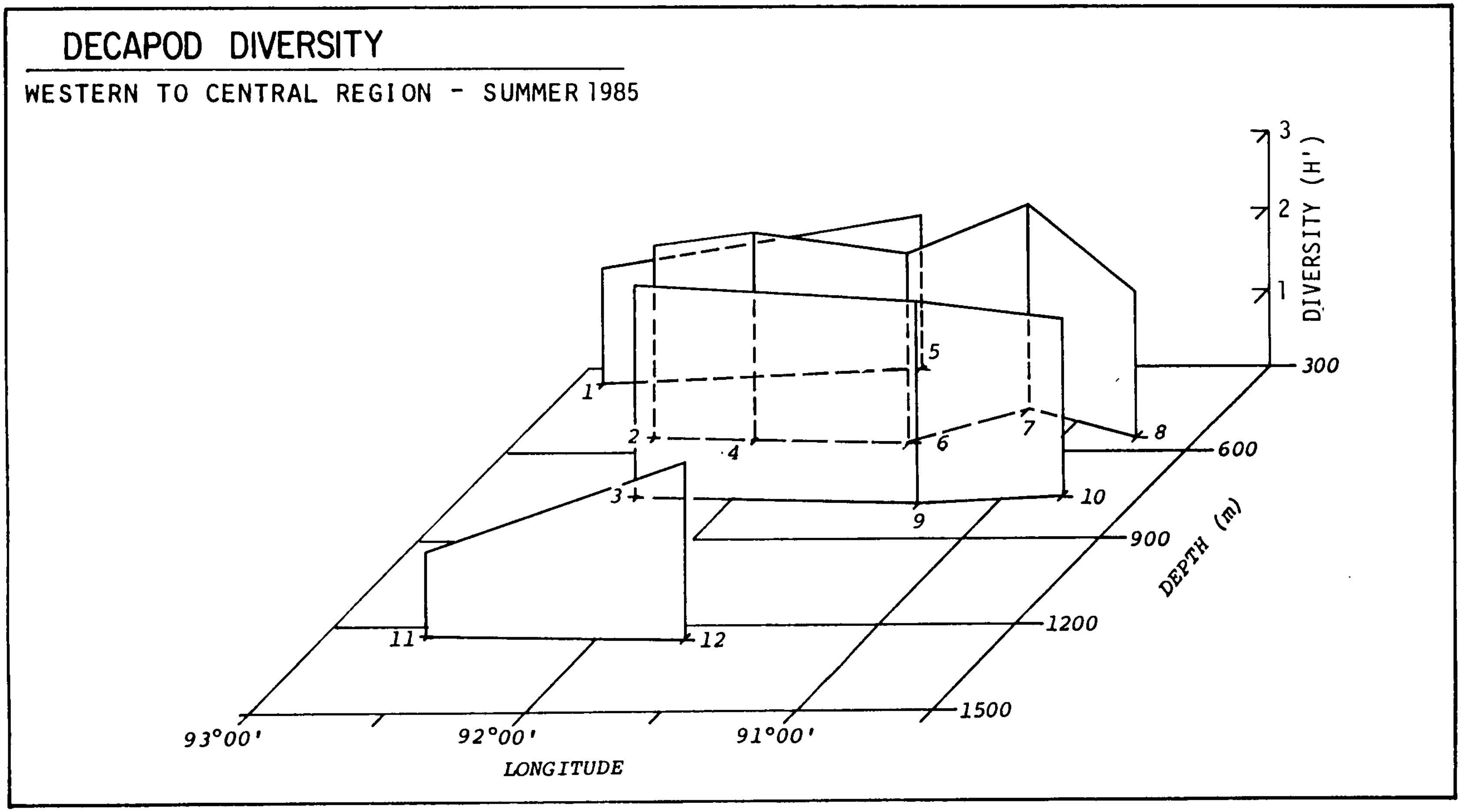

Figure 5-17. Comparative levels of decapod diversity along isobaths between the central and western Gulf of Mexico sampling transects, summer 1985.

(1983) for Gulf megafauna. The general phenomenon 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 the existence of boundaries between zones; i.e., are homogeneous zones present within sharply defined boundaries, 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 (Fig. 5-17) 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 (Fig. 5-18) 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:

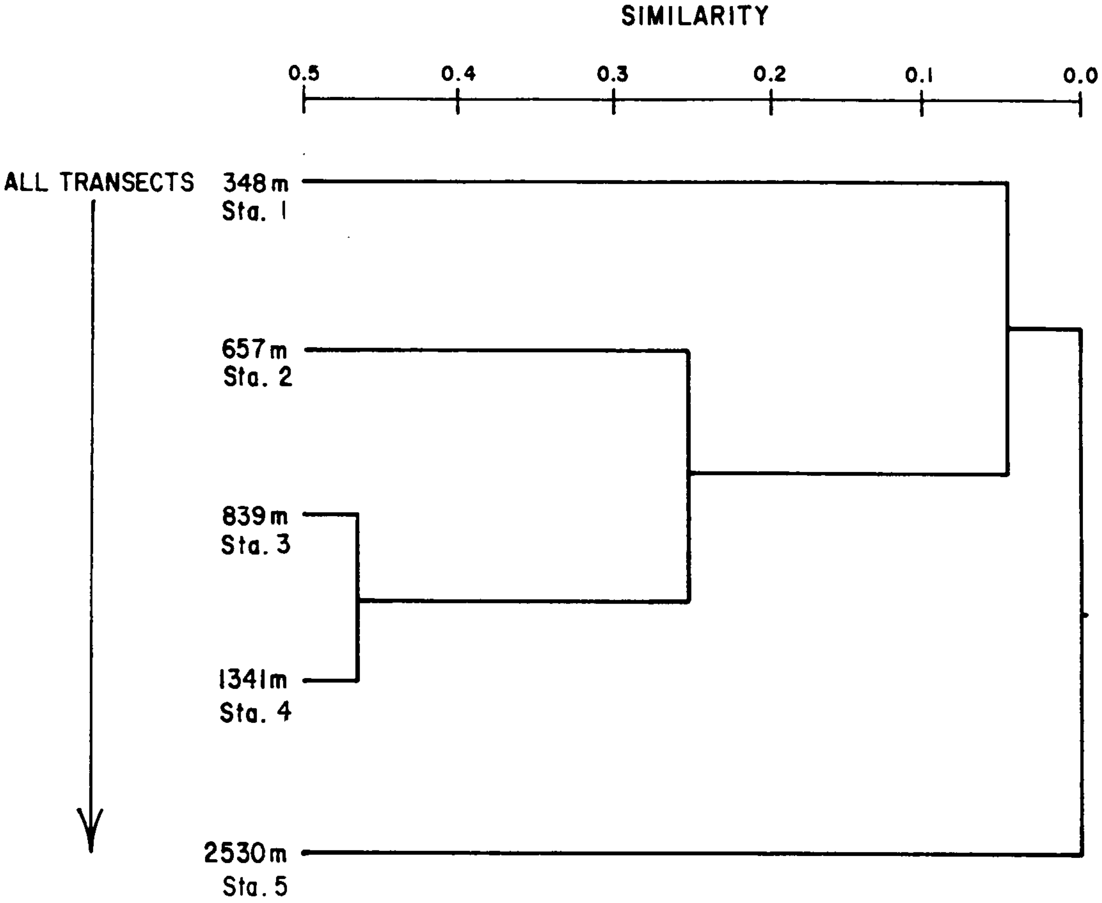

Figure 5-18. Dendrogram showing similarity by station (or depth) at all transects. Based upon clustering of the most abundant macroepifaunal species of decapods, echinoderms, and fish.

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, in fact, dominated by a reasonably small number of species. The relative abundance of a representation of the dominant species is plotted over the depth range sampled in Figure 5-19. We interpret those data to show the presence of at least two areas where groups of species having greatly restricted bathymetric distributions co-occur over a depth interval which is separated by a sharp discontinuity from the next group of co-occurring species. The first group ranges from about 500 to 800-m in depth, with peak abundance occurring between 475 and 650 m in depth. This is not a shelf assemblage (an outer shelf group of penaeids, e.g., _Penaeopis serrata_, are present at 350 m but are absent at 475 m, Fig. 5-19), but a group of upper slope forms. Included are _Benthochascon schmitti_, _Bathyplax typhla_, and _Plesionika holthuisi_.

The next group of species is most abundnat 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 (Fig. 5-19).

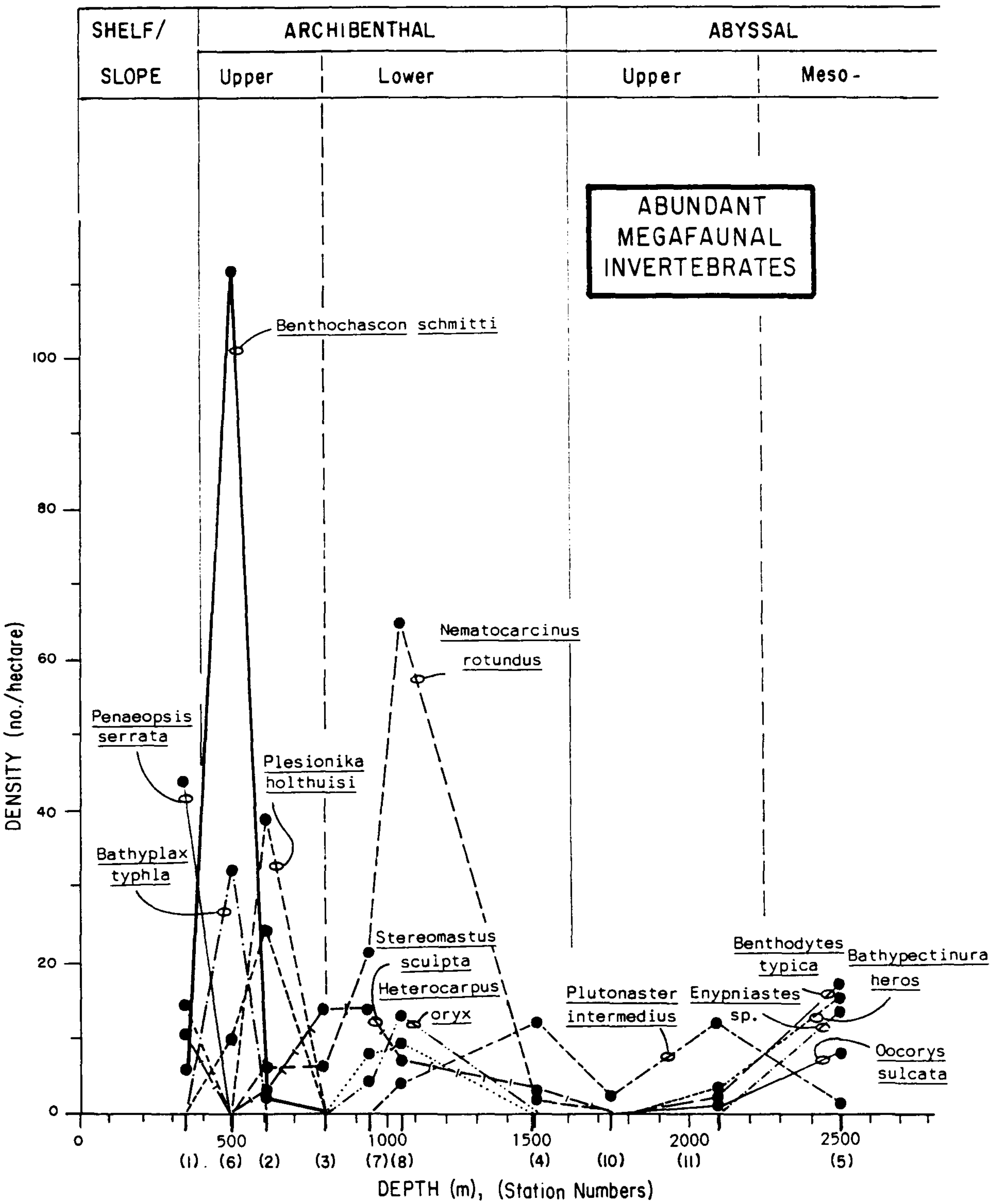

Figure 5-19. Comparative patterns of relative abundance by depth, for selected megafaunal invertebrates abundant on the central transect, fall 1984.

Minor peaks in abundance by one to two species appear 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 appears 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 (Fig. 5-19).

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 (Fig. 5-20). 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

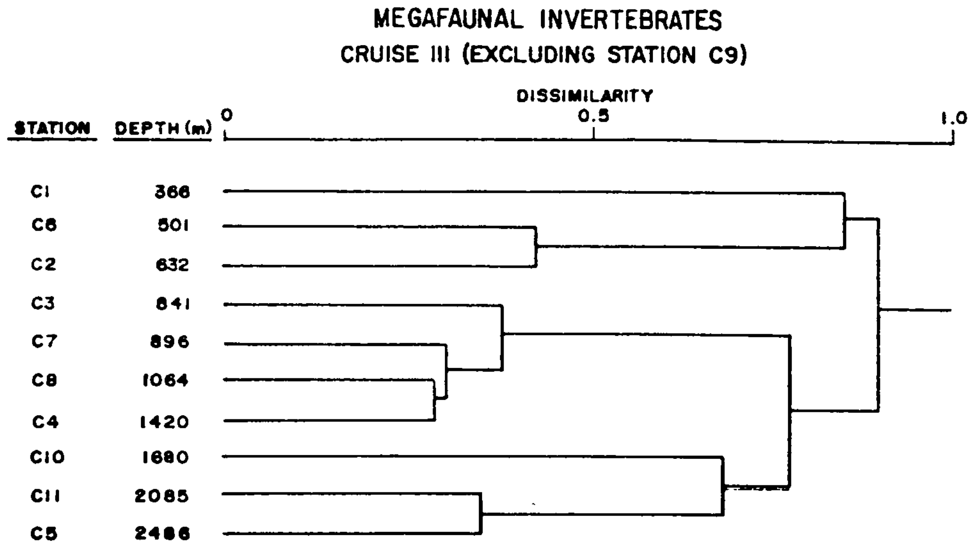

Figure 5-20. Results of cluster analyis performed on the megafaunal invertebrate data for the central transect, fall 1984.

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 (1983) zonation scheme was documented to have predictive value.

In Chapter 2 on benthic habitats, Principal Component Analysis (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 wre 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).

Life History Observations

Life history data were taken for macrofauna trawled at the 60 sampling stations. The specimens were first measured for length 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 less 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 5-2). 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 (Chloropthalmus 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

Table 5-2. Food habits for eight species of fishes collected on the Gulf of Mexico continental slope, 1983-1984.

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

depth distribution similar to Dibranchus atlanticus but fed almost exclusively on natantia (82%), based upon the contents of 13 somtachs.

Specimens of Gadomus longifillis 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 longifillis fed mainly on natantia and copepods.

The biochemistry work on this project, conducted to supplement the food habit studies (see Chapter 2), 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.

SUMMARY

Biomass levels of megafauna on the continental slope were higher in the eastern Gulf than in the western Gulf, and markedly higher at depths above 1,250 m than at deeper points on the slope. Two biomass peaks were noted for megafauna on the Upper Slope, one at about 500 to 600 m, the other at about 1,000 to 1,100 m. These two areas proved to have characteristic assemblages dominated by decapod crustaceans and demersal fishes.

The data suggest that the concept of five faunal zones represented on the slope is appropriate, at least for management purposes. Actually, there are three zones (Shelf/Slope, Archibenthal and Abyssal) but the latter two are each subdivisible into two depth ranges that have management significance. The Shelf/Slope and Archibenthal Zones are characterized by the greatest biomass of megafauna having resource potential (namely, decapod crustacea such as Penaeopsis serrata). Peak abundance in the Archibenthal Zone occurred at depths of from 500 to 800 m, corresponding to depths where chemosynthetic communities have been found to be prevalent.

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CHAPTER 6. CHEMOSYNTHETIC COMMUNITIES ON THE CONTINENTAL SLOPE OF THE NORTHERN GULF OF MEXICO--AN OVERVIEW

J.M. Brooks, M.C. Kennicutt II, and R.R. Bidigare

INTRODUCTION

The northern Gulf of Mexico continental slope has been the site of a number of recent discoveries that have dramatically altered our understanding of chemical, biological and geological processes on the continental slope. The Geochemical and Environmental Research Group (GERG) at Texas A&M University reported the first occurrence of thermogenic gas hydrates in oil-stained cores in deep ocean sediments in 1984 (Brooks et al., 1984). Trawling in these areas has captured tube worms and bivalves containing chemosynthetic, bacterial endosymbionts (Kennicutt et al., 1985; Brooks et al., 1986a; 1987a,b). These discoveries significantly expand the geographic area of the deep ocean where one might expect to encounter dense populations of vent-type taxa. Subsequent studies on the upper Gulf of Mexico continental slope using submersibles and surface ships have:

(1) Identified chemosynthetic organisms or their remains (tube worms, mussels and/or clams) at 17 northwestern Gulf of Mexico continental slope sites;

(2) Confirmed, based on enzyme activities, elemental sulfur content and electron microscopy; that tube worms and clams from these sites contain chemoautotrophic, bacterial endosymbionts (Childress et al., 1986; Brooks et al., 1987b);

(3) Found a mussel that is capable of utilizing methane as its sole carbon and energy source (the first demonstrated symbiosis between a methanotrophic bacteria and an animal; Childress et al., 1986);

(4) Identified shallow seismic "wipe-out" zones as high probability sites for chemosynthetic ecosystems;

(5) Shown that active oil and gas seepage is associated with all of the chemosynthetic ecosystems discovered on the Gulf of Mexico slope to date;

(6) Demonstrated that carbon, nitrogen and sulfur isotopes are useful in differentiating heterotrophic, sulfur-based and methane-based ecosystems (Brooks et al., 1987b);

(7) Confirmed the transfer of chemosynthetic carbon to background heterotrophic organisms;

(8) Discovered ten gas hydrate and several active oil seepage locations in the Gulf of Mexico; and

(9) Determined that shell beds are actively being produced in and around areas of petroleum seepage.

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, Fig. 6-1) 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 CO_2 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]. Under conditions of temperature and

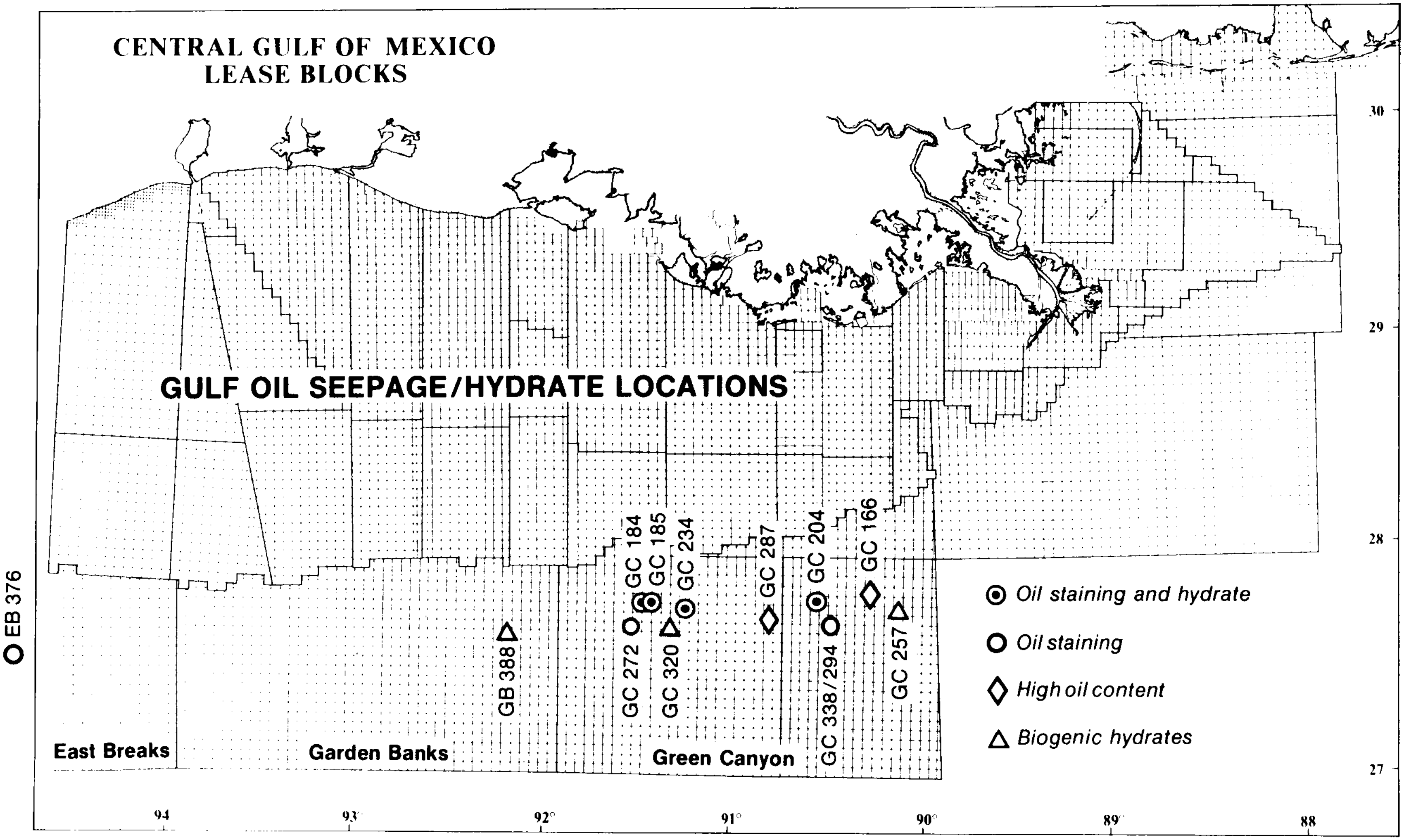


Figure 6-1. Known sites of oil seepage and gas hydrates in the Gulf of Mexico as identified by the Geochemical and Environmental Research Group at Texas A&M University. Most of these sites are associated with chemosynthetic ecosystems and all are associated with shallow seismic "wipe-out" zones.

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 (Fig. 6-1). 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 (Fig. 6-2) indicate that the sediments in these regions contain oil, hydrate and/or gas.

The first trawl was taken at ca. 27°40'N and 91°31'W for 60 minutes over a 3.5 nautical mile (nmi) long track between 600 and 700 m water depth (Fig. 6-3). Approximately 800 kg of bivalves and gastropod shells

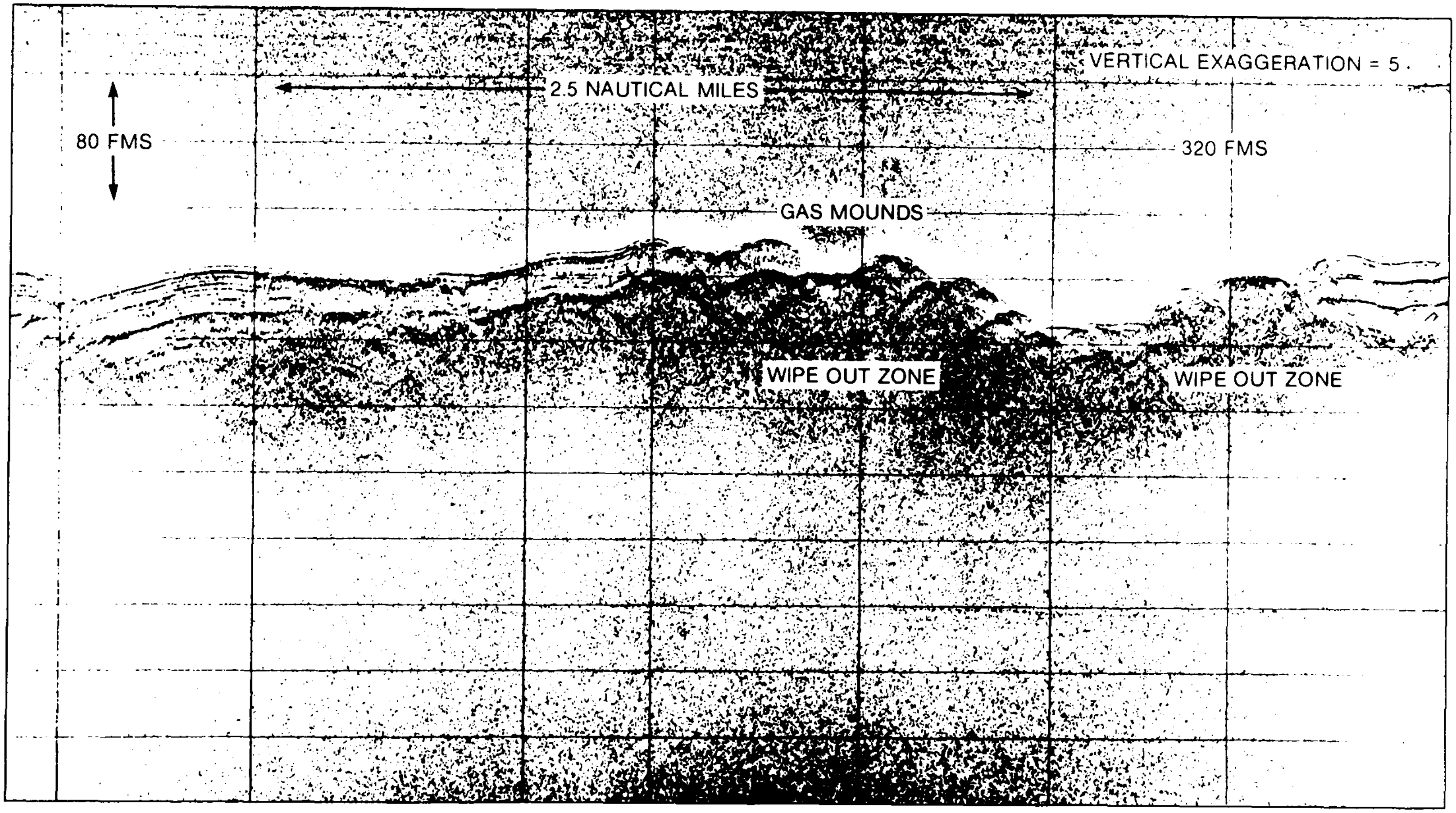


Figure 6-2. Typical seismic "wipe-out" zone in the Gulf of Mexico. These areas are characterized by oil seepage, gas hydrates and/or gas-charged sediments.

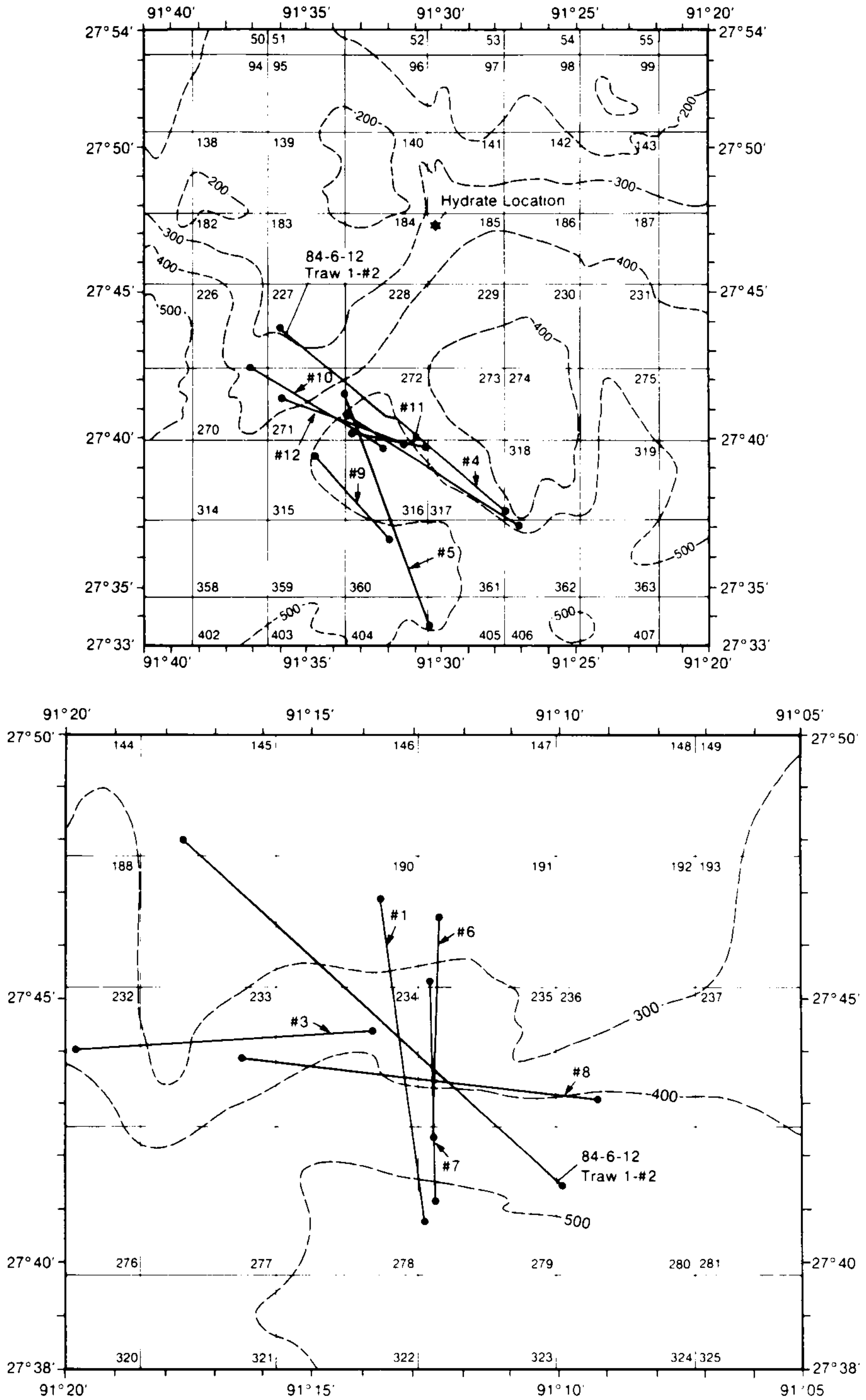


Figure 6-3. Location of trawl lines in Green Canyon lease blocks from <u>R/V Gyre</u> Cruises 84-G-12 and 85-G-5. Chemosynthetic organisms were collected in 12 of 15 trawls. All trawls were performed during 85-G-5, unless specifically labeled as 84-G-12.

were recovered. The catch contained both living and disarticulated bivalves ranging in size from 5 to 10 cm in length. The second trawl taken near 27°45'N and 91°14'W contained vestimentiferan tube worms up to 2.0 m in length and 1 cm in diameter, as well as gastropods and an assortment of other organisms (Kennicutt et al., 1985).

Carbon isotopic analyses performed on bivalves, gastropods and tube worms were used 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 factionation occurs as carbon is transferred through marine food webs. Marine, photosynthetically-derived carbon generally has carbon isotopic (delta ^{13}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 (Fig. 6-3). 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. 6-3). The Offshore Operators Committee, in conjunction with the Minerals Management Service, supplied GERG with 33 locations on the continental slope (see Fig. 6-4) where shallow seismic profiles from hazard surveys indicate "wipe-out" zones. GERG took 39

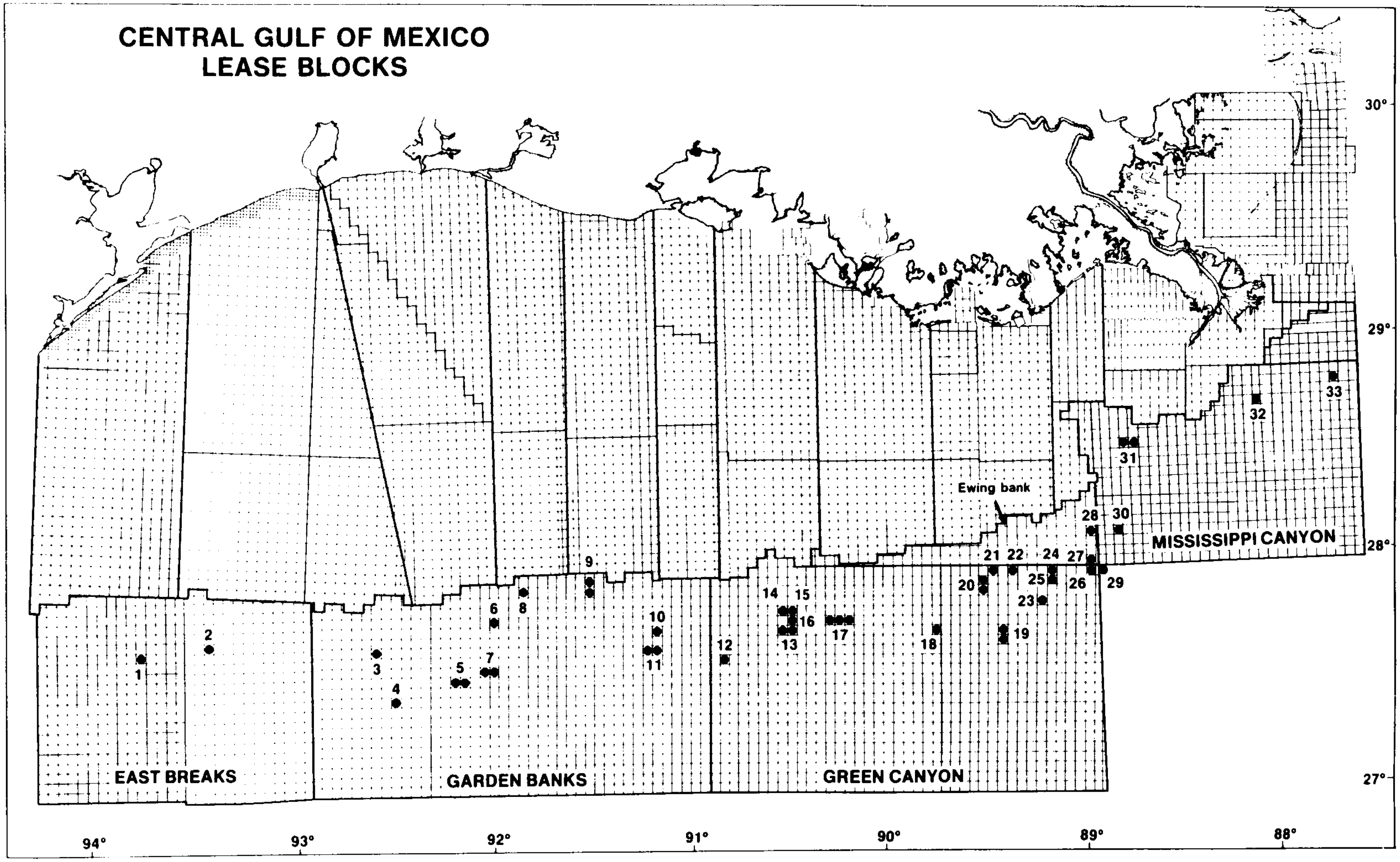


Figure 6-4. Locations of the 33 study sites on the Louisiana/Upper Texas continental slope. Thirty-nine trawls were performed during R/V Gyre cruise 86-G-1/2 in water depths between 180 and 900 m.

trawls and piston cores in these areas (see Figs. 6-5 and 6-6 for hazard maps and 3.5 kHz shallow seismic "wipe-out" zones in the trawl areas).

The results of the latter field study demonstrated that chemosynthetic organisms (either their remains or living tube worms, mussels and/or clams) are present in the Green Canyon (13 sites), Garden Banks (six sites), Ewing Bank (1 site) and East Breaks (1 site) lease areas. This significantly expands 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 be 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 (GC) 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 documented the community on "Bush Hill" (see Fig. 6-7 for location). 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 these 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 for the first time.

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

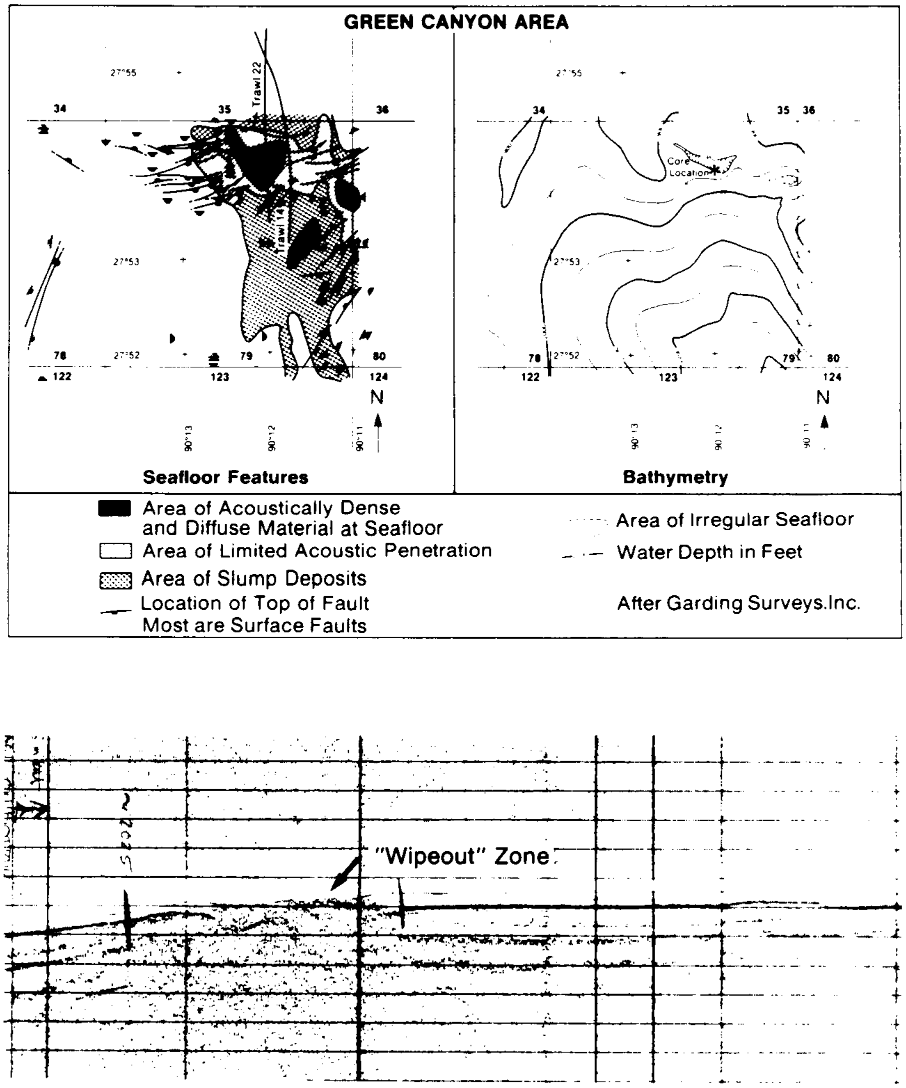


Figure 6-5. Shallow seafloor features, bathymetry and 3.5 kHz subbottom profile for the trawl line performed in Green Canyon Block 79.

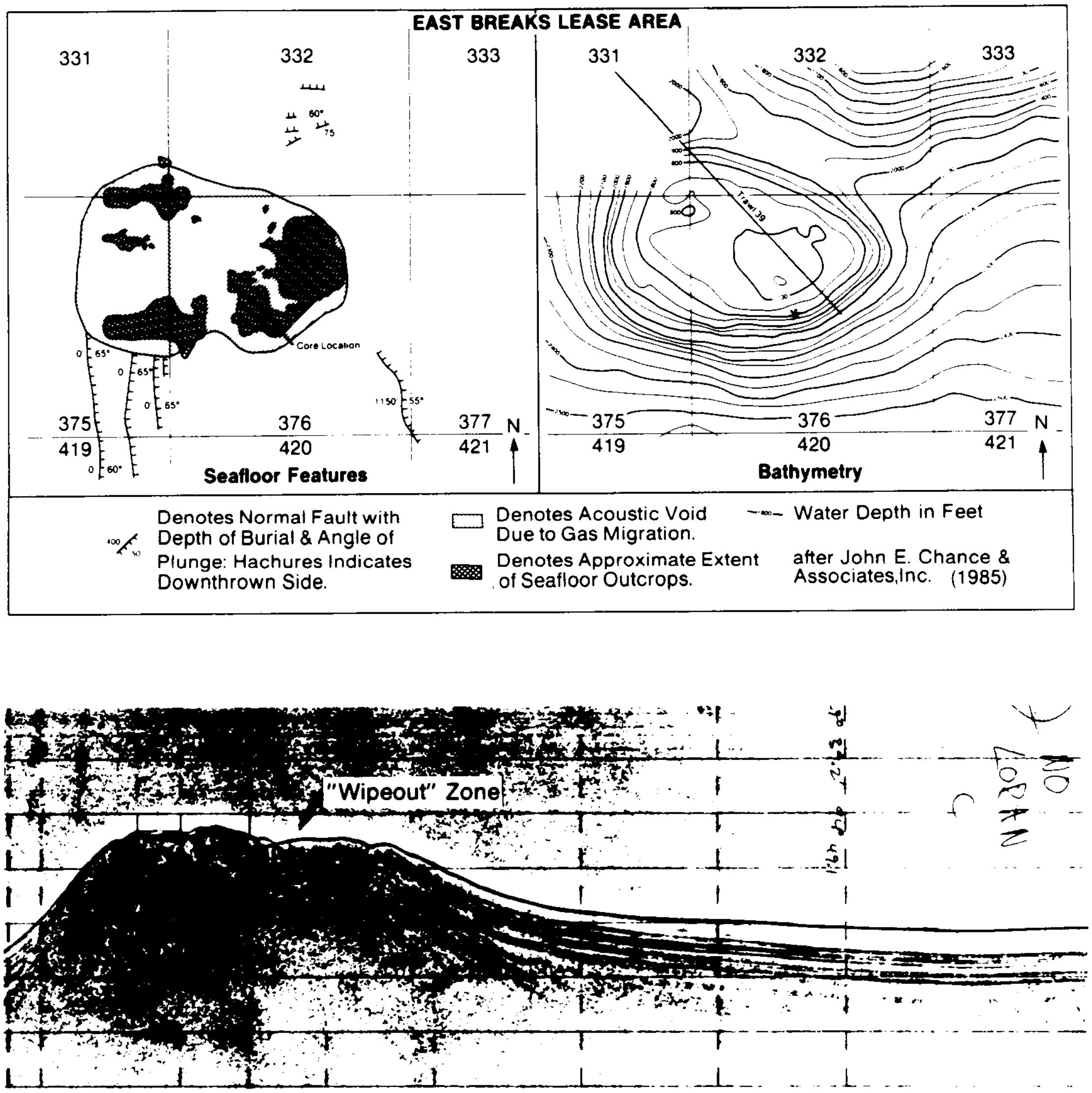


Figure 6-6. Shallow seafloor features, bathymetry and 3.5 kHz subbottom profile for the trawl line performed in East Breaks Block 376.

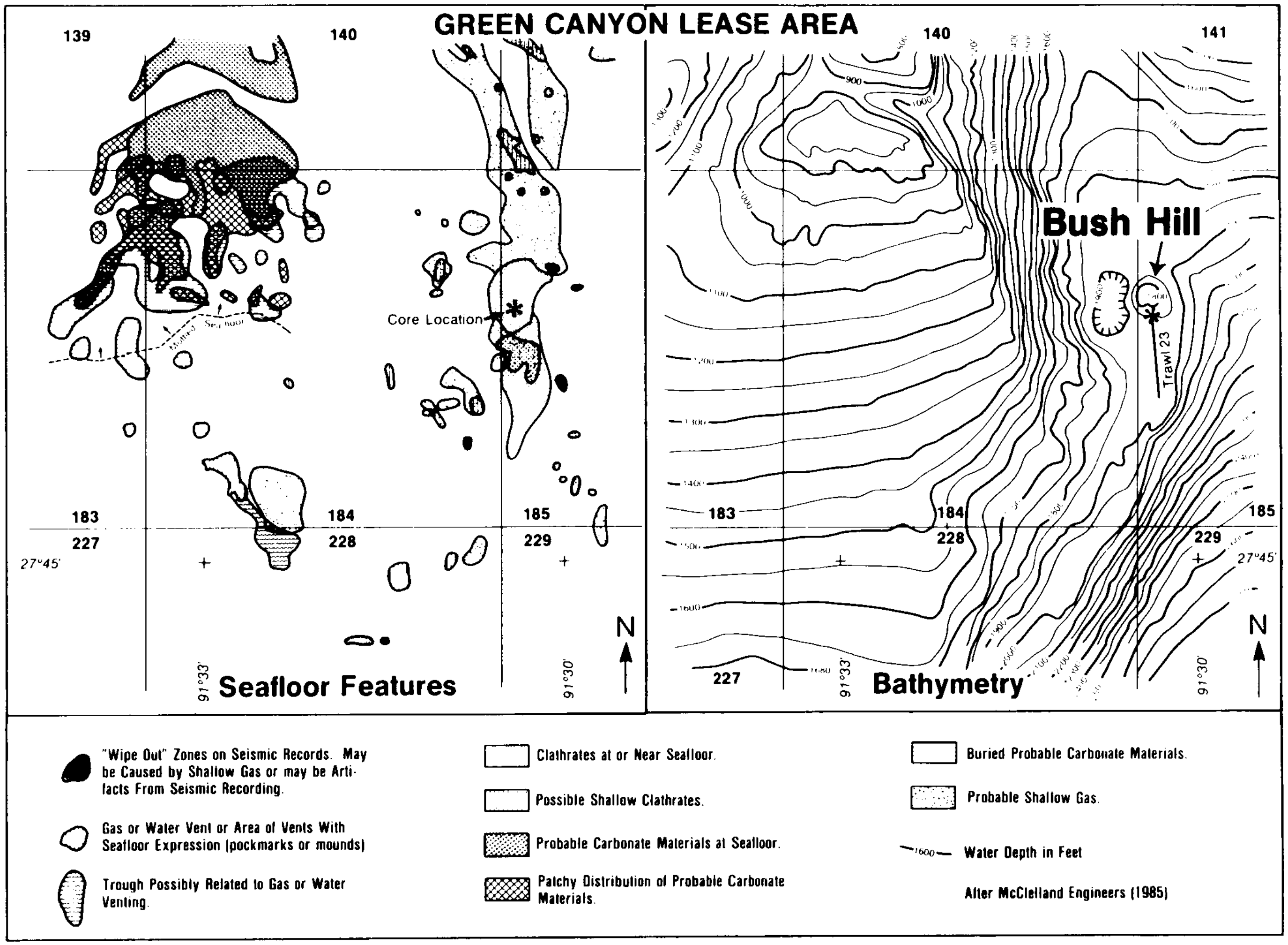


Figure 6-7. Bathymetry and seafloor features map for the Green Canyon Block 184/185 lease area (map supplied by Conoco, Inc.).

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.

SPATIAL DISTRIBUTIONS

The most comprehensive study of chemosynthetic community distributions on the northern Gulf of Mexico continental slope was undertaken by GERG on Cruises 86-G-1/2. Thirty-nine 10-m otter trawls were taken at 33 locations. Some locations were trawled twice. The sites were in water depths ranging from 80-900 m and spanned an area from Mississippi Canyon to East Breaks lease areas (Fig. 6-4). Sites were chosen that contained shallow seismic "wipe-out" zones. These sites were selected by members of the Offshore Operators Committee from an extensive examination of shallow hazard surveys. Seismic "wipe-out" zones generally contain gas-charged, gas hydrated and/or oil-stained sediments on the Gulf of Mexico continental slope (Brooks et al., 1986b). Typical hazard surveys and associated 3.5 kHz subbottom transects containing seismic "wipe-out" zones are shown in Figures 6-5 and 6-6. Thirty of 39 trawl transects crossed shallow seismic "wipe-out" zones.

The presence of a "wipe-out" zone during trawling and the occurrence of oil-staining, gas pockets and/or a hydrogen sulfide odor (H_2S) in the core samples are summarized for each site in Figure 6-8. A "wipe-out" zone, oil-staining, gas pockets, and an H_2S odor were observed at 24, 9, 12 and 18 sites, respectively. The collection of chemosynthetic bivalves and tube worms in trawl catches (either living organisms or their remains) is also summarized in Figure 6-8. Tube worms (Vestimentiferans and/or pogonophorans), clams (Calyptogena and/or Vesicomya), and mussels were recovered in 18, 12 and 5 trawls, respectively.

Stable carbon isotopic analysis of organism tissues from trawl catches were performed to confirm the nutritional nature (chemosynthetic or heterotrophic) of the organisms (Brooks et al., 1987b). Many trawl samples contained tissues exhibiting isotopically light carbon indicative of chemosynthesis including:

Stations	Depth (m)	(1) Calyptogena ponderosa	(2) Vesicomya cordata	(3) Mussel Beds	(4) Vestimentiferan Tube Worms	(5) Pogonophoran Tube Worms	(6) Wipe-Out Zones	(7) Oil-Stained Cores	(8) Gas Pockets In Cores	(9) Hydrogen Sulfide In Cores	(10) Isotopically Light Tissues	Totals
		INDICATORS										
EB1	512	+	+		+	+	+	+	+	+	+	9
EB2	420						+					1
GB3	402					+	+		+	+	+	5
GB4	620					+				+	+	3
GB5	540				+	+	+			+	+	5
GB6	-											0
GB7	650		+		+	+	+	+			+	6
GB8	180											0
GB9	320											0
GB10	410		+				+			+	+	4
GB11	665	+	+		+	+	+			+	+	7
GC12	549					+	+			+	+	4
GC13	680	+	+	+	+	+	+	+	+	+	+	10
GC14	-	+	+	+	+	+	+	+	+	+	+	10
GC15	530			+	+	+	+	+	+	+	+	8
GC16	-				+	+	+	+	+	+	+	7
GC17	540	+	+	+	+	+	+	+	+	+	+	10
GC18	805	+	+				+		+	+	+	6
GC19	895	+	+				+	+	+	+	+	7
GC20	512		+								+	2
GC21	393				+		+				+	3
GC22	-				+	+	+				+	4
GC23	658			+	+	+	+		+	+	+	7
GC24	555						+					1
GC25	600		+		+	+	+	+	+	+	+	8
GC26	610				+		+		+	+	+	5
EB27	512				+		+			+	+	4
EB28	402						+					1
AV29	750		+				+					2
MC30	594											0
MC31	512											0
MC32	570											0
MC33	805											0
TOTALS		7	12	5	15	15	24	9	12	18	22	139

Figure 6-8. Summary of the occurrence of biological, physical and chemical indicators of hydrocarbon seepage and chemosynthetic communities.

Green Canyon Blocks:	29, 31, 40, 72/116, 79, 140, 166, 184, 185, 233/234, 272, 273.299, 287 and 398 (13 sites)
Garden Banks Blocks:	300, 359, 388, 458/459, 499, 581 (6 sites)
Ewing Bank Block:	1010 (1 site)
East Breaks Block:	376 (1 site)

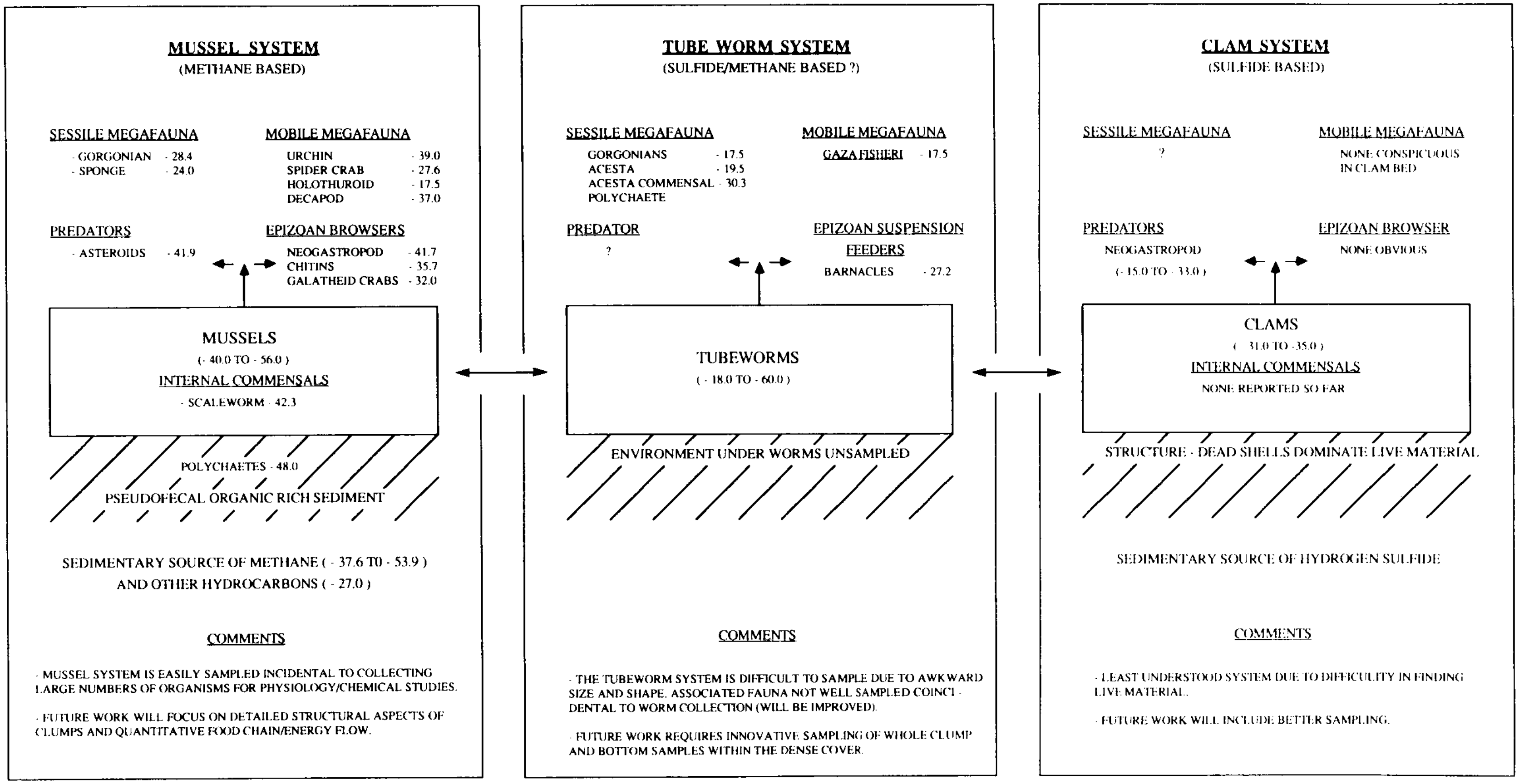
These trawl collections confirm a wide distribution of chemosynthetic ecosystms in the Gulf of Mexico.

On a smaller scale, the submersible studies documented high densities of clams and/or mussels in continuous lines, apparently associated with the leakage of hydrocarbons along faults in several lease blocks (GC-272, 185, and 234 among others). The clam and mussel communities generally did not overlap. Many of the mussel and clam beds were up to ~0.25 to 1.0 miles in length and 100 meters wide, with mussels frequently stacked several individuals deep. Submersible observations of tube worm communities have been made in GC-185, 234, 29 and 31 among others.

The spatial distributions of hydrocarbon seep faunal assemblages are very complex. While it is increasingly clear that methane and petroleum seepage supports and regulates these communities, the controls on individual assemblage distributions over topographically complex landscapes are not clear. Fine scale spatial distributions on "Bush Hill" are discussed in Chapter 7.

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 brachipod-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. 6-9). 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 6-10.



- MUSSEL SYSTEM IS EASILY SAMPLED INCIDENTAL TO COLLECTING LARGE NUMBERS OF ORGANISMS FOR PHYSIOLOGY/CHEMICAL STUDIES.

- FUTURE WORK WILL FOCUS ON DETAILED STRUCTURAL ASPECTS OF CLUMPS AND QUANTITATIVE FOOD CHAIN/ENERGY FLOW.

- THE TUBEWORM SYSTEM IS DIFFICULT TO SAMPLE DUE TO AWKWARD SIZE AND SHAPE. ASSOCIATED FAUNA NOT WELL SAMPLED COINCIDENTAL TO WORM COLLECTION (WILL BE IMPROVED).

- FUTURE WORK REQUIRES INNOVATIVE SAMPLING OF WHOLE CLUMP AND BOTTOM SAMPLES WITHIN THE DENSE COVER.

- LEAST UNDERSTOOD SYSTEM DUE TO DIFFICULITY IN FINDING LIVE MATERIAL.

- FUTURE WORK WILL INCLUDE BETTER SAMPLING.

Figure 6-9. Relationships between chemosynthetic assemblage types and the associated epifaunal browsers, sessile suspension feeders and predators. Initial isotopic measurements on the 1987 Sea-Link cruise samples show relationships between system components.

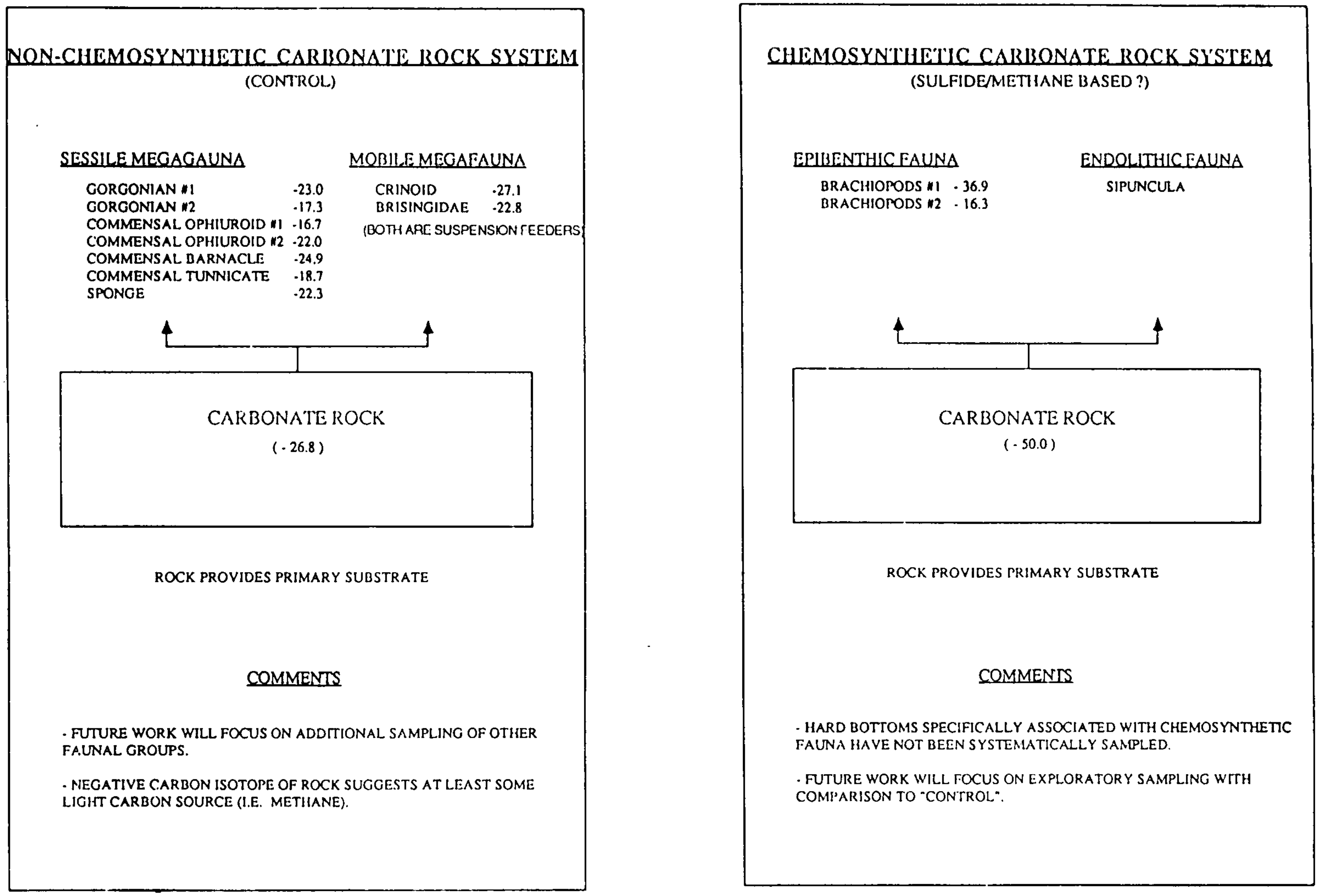


Figure 6-10. Relationships between chemosynthetic and non-chemosynthetic carbonate rock assemblage types and the associated browsers and sessile suspension feeders. Initial isotopic measurements on the Sea-Link cruise samples show relationship between system components.

Observations made during the June 1987 Johnson Sea-Link-I dives demonstrated that the spatial variations of the various assemblages is greater than anticipated from earlier work. In some instances, some of these assemblages overlapped in space, and initial isotopic data suggests some shared dependence upon chemosynthetic sources. The brachipod-solitary coral assemblage is cryptic, being found under rock ledges.

ASSOCIATION WITH ENVIRONMENTAL FACTORS

Some information on the association of the chemosynthetic animals with environmental factors is shown in Figure 6-10 and are described in greater detail below. The following subsections summarize the environmental factors present at these sites (after Kennicutt et al., 1988b).

Extractable Organic Matter

Organic matter that can be extracted by an organic solvent (i.e., hexane, methylene chloride, etc.) can be biological (lipids) as well as thermogenic (petroleum) in origin. Therefore, extractable organic matter (EOM) content is comprised of a mixture of biologically produced indigenous compounds and petroleum related compounds. In general marine sediments contain less than 50 ppm of extractable organic matter of biological origin, though this value can be quite variable (Kennicutt et al., 1987a). In cases of high hydrocarbon contamination, the extractable organic matter will be elevated due to the incorporation of solvent soluble petroleum components. Total extractable organic matter ranged from 21 (EB-339 and GB-581) to 5,800 (GC-185) ppm (Figs. 6-11 and 6-12).

Gas Chromatography

Representative gas chromatograms for sediment extracts containing large and trace amounts of upward migrated thermogenic hydrocarbons are shown in Figure 6-13A and B, respectively. Sediments containing upward migrated hydrocarbons are characterized by an unresolved complex mixture (UCM), C_{15} to C_{32} normal alkanes, and isoprenoids. This mature

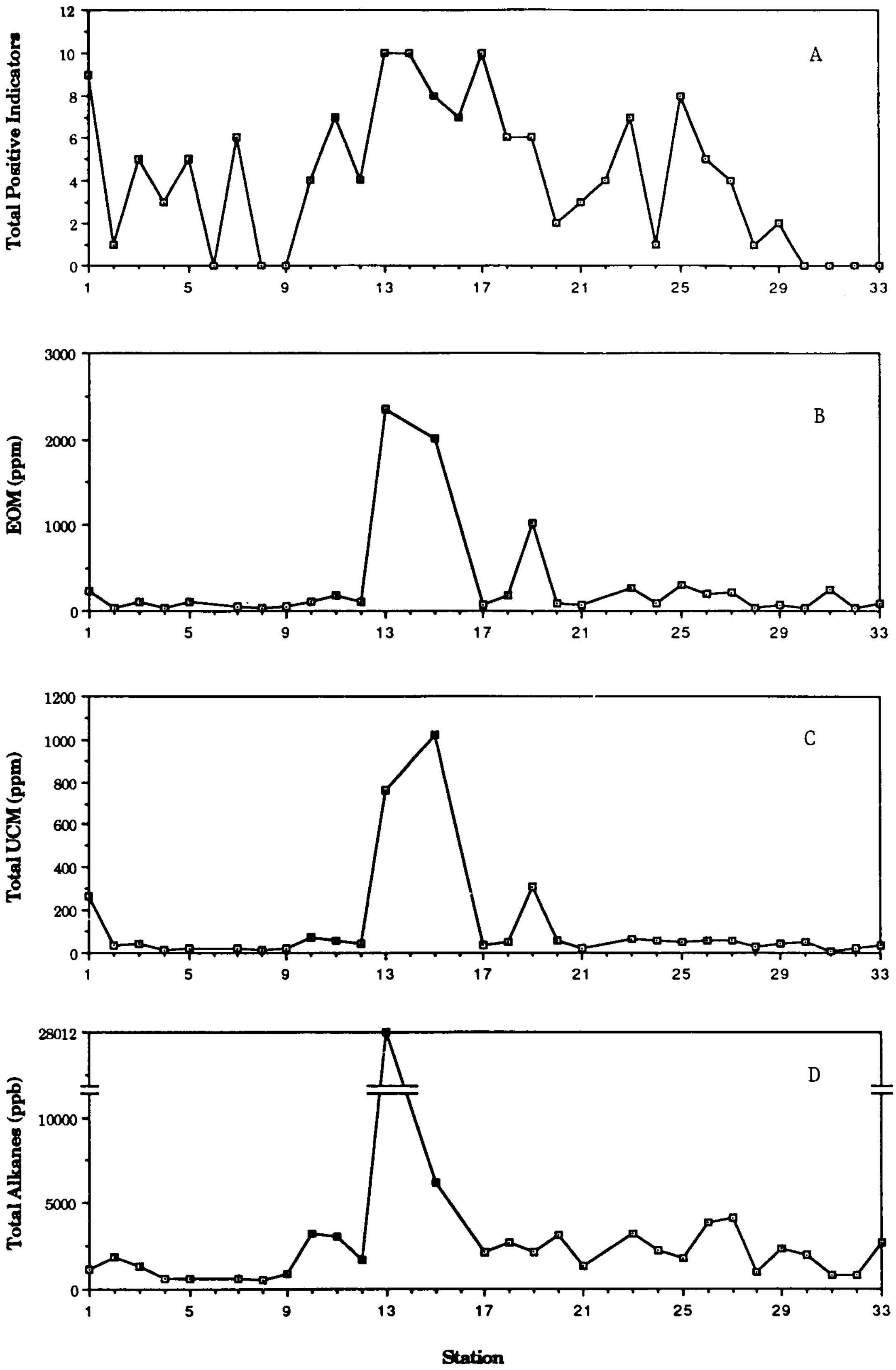


Figure 6-11. The geographical distributions of the: (A) chemosynthetic community indicators (see Fig. 6-8), (B) EOM, (C) total unresolved complex mixture, and (D) total n-alkane concentrations (15 to 32 carbons). See Figure 6-4 for station numbers.

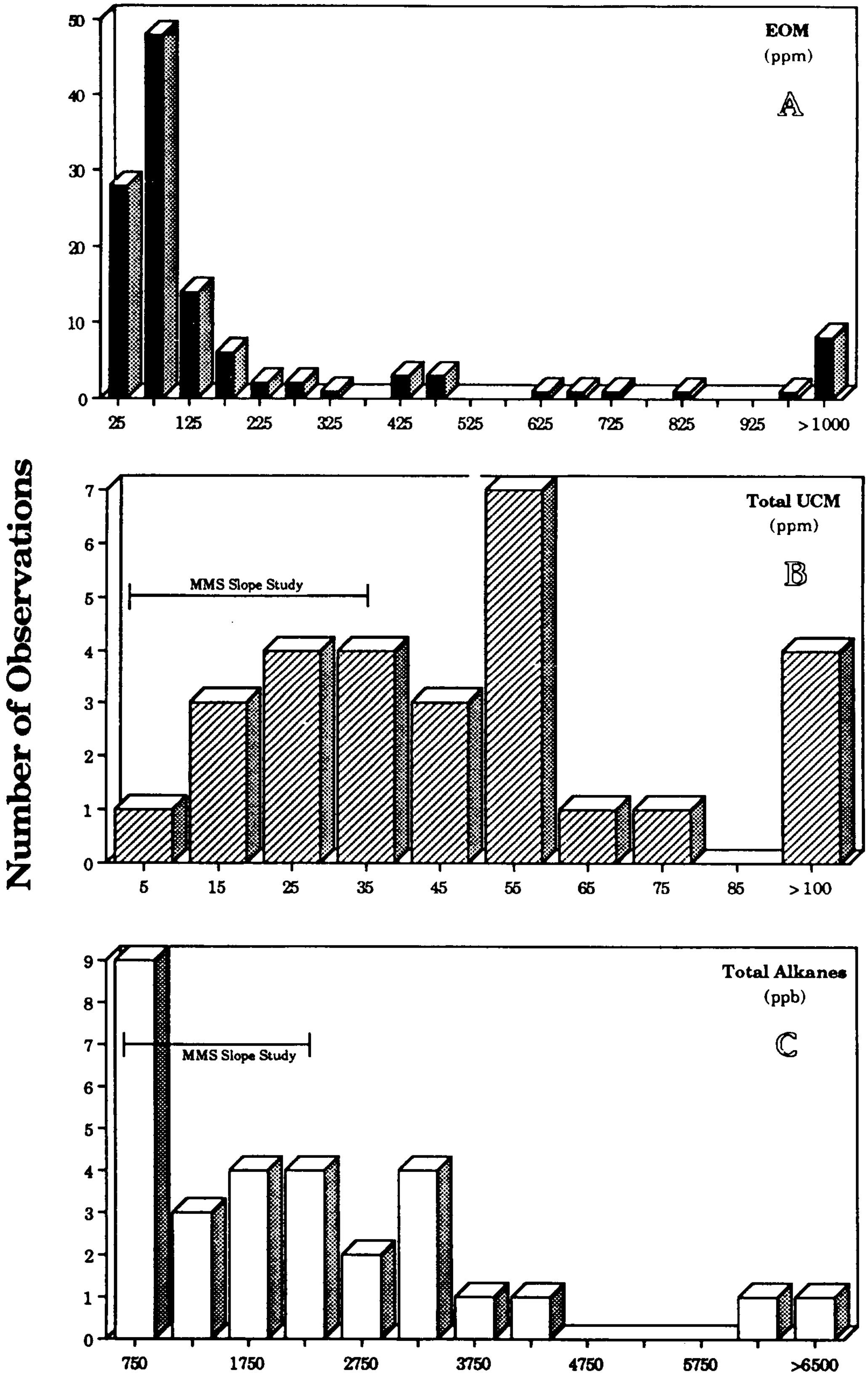


Figure 6-12. The distribution of selected hydrocarbon parameters for 30 piston cores taken at sites shown in Figure 6-4. The range of values are compared to those from the MMS slope study.

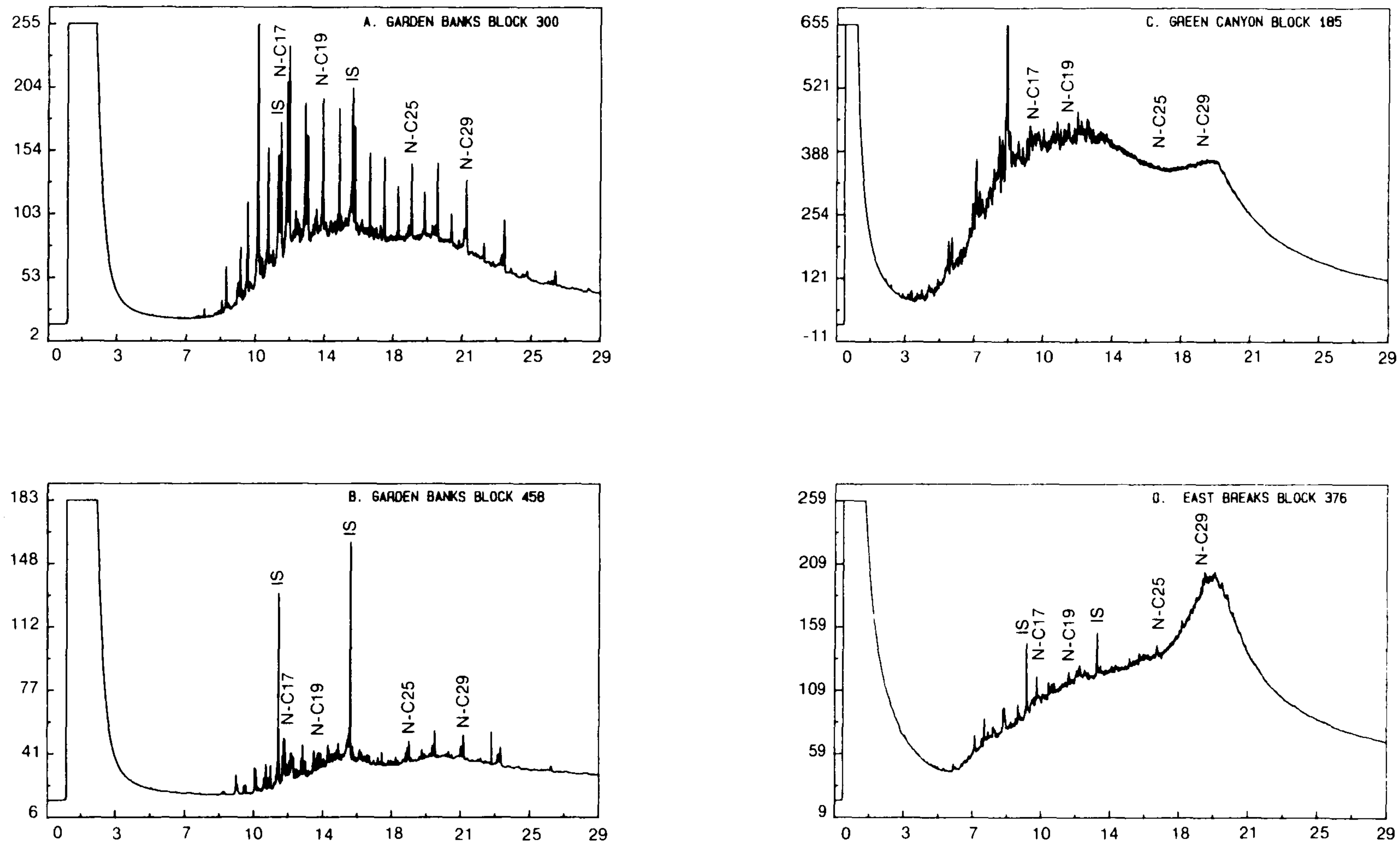


Figure 6-13. Representative gas chromatograms of sediment extracts from selected sites shown in Figure 6-4.

hydrocrabon pattern is overprinted with odd carbon number, normal alkanes with 23 or more carbons which are presumably derived from terrigenous organic matter (Kennicutt et al., 1987b). Samples containing high levels of petroleum are often extensively biodegraded and only contain an unresolved complex mixture (UCM) (Figs. 6-13C and D). High concentrations of n-alkanes in the C_{15} to C_{20} range suggest an upward migrated hydrocarbon source since hydrocarbons in this molecular weight range do not generally survive depositional transport through the environment (i.e., pollution, Kennicutt et al., 1987c). This interpretation is supported by the depth of occurrence of the hydrocarbons in the sediments as well as an increase in concentration with increasing depth within the core. Deep penetration (>2 m) of the sediment column insures that the sample is below the pollution horizon, thus the petroleum hydrocarbons detected are migrating upward from deep in the subsurface and are not being deposited from the overlying water column. Total UCM concentratins at the 34 locations varied from 8-1,033 ppm, with most locations exceeding the presumed low level background of 5 to 10 ppm (Figs. 6-11 and 6-12). These concentrations suggest that most, if not all, locations have petroleum hydrocarbons associated with them. Total n-alkane (n-C_{15} to N-C_{32}) concentrations ranged from 504-31,350 ppb (Figs. 6-11 and 6-12).

Total Scanning Fluorescence (TSF)

Fluorescence is an analytical technique that is selectively sensitive to compounds with conjugated double bonds, i.e., aromatic hydrocarbons. TSF spectra provide a semiquantitative estimate of total aromatic compounds (fluorescence intensity) as well as an estimate of the ring-number distribution of the fluorescent compounds. In general, the fluorescence excitation-emission maximum increases in wave length with increasing number of aromatic rings. Thus, sediment extracts contaminated with migrated oil contain predominantly three-ring and larger aromatic compounds emitting higher wave length fluorescence. Fluorescence spectra are not extensively altered as the direct result of biodegradation or water washing, though severe degradation can alter aromatic distributions (Kennicutt, 1988; Kennicutt et al., 1988a). Aromatics,in general, are moderately resistant to degradative removal and this resistance increases with ring number. Fluorescence analyses confirm the presence of aromatic hydrocarbons related to petroleum at all of the sites sampled for the chemosynthetic organisms distribution study.

Oil Seepage Evaluation

A ranking system based on TSF and GC has been devised to evaluate the degree of oil seepage present at a given location (Brooks et al., 1986c). On this scale, zero represents no seepage while 15 is indicative of substantial macroseepage. The presence or absence of oil is elevated on the basis of the fluorescence intensity, the ratio (R) of fluorscence at 360/270 to 320/270 (EM /Ex) and the amount and composition of the gas chromatographic signature of the sediment extract. Evaluation of the gas chromatographic data is based on the fact that oils contain a complete suite of n-alkanes, pristane, and phytane; whereas the in situ, recent organic matter of sediments contains only a relatively few specific aliphatic compounds (primarily odd carbon number normal alkanes with 23 to 32 carbons, Kennicutt et al., 1987b).

The presence of oil is evaluated on a scale of 0 to 15 and individual rankings are calculated as the sum of the three parameters discussed above (each based on a 0-5 scale). The degree of oil seepage is ranked as follows:

12-15	Very High
8-12	Medium/High
4-8	Low
0-4	Very low

Based on this evaluation scheme significant oil seepage was present at most locations (Fig. 6-14).

Most locations sampled contained medium to high levels of petroleum seepage. Based on the oil seepage evaluation described above, no chemosynthetic organisms were recovered at those areas which had a combined ranking of ten or less (MC 44/445, MC 282, EB 878, GB 581, EB 339). In contrast, at 15 of 18 areas with a seepage evaluation of 13 or more, chemosynthetic organisms were retrieved and at all locations

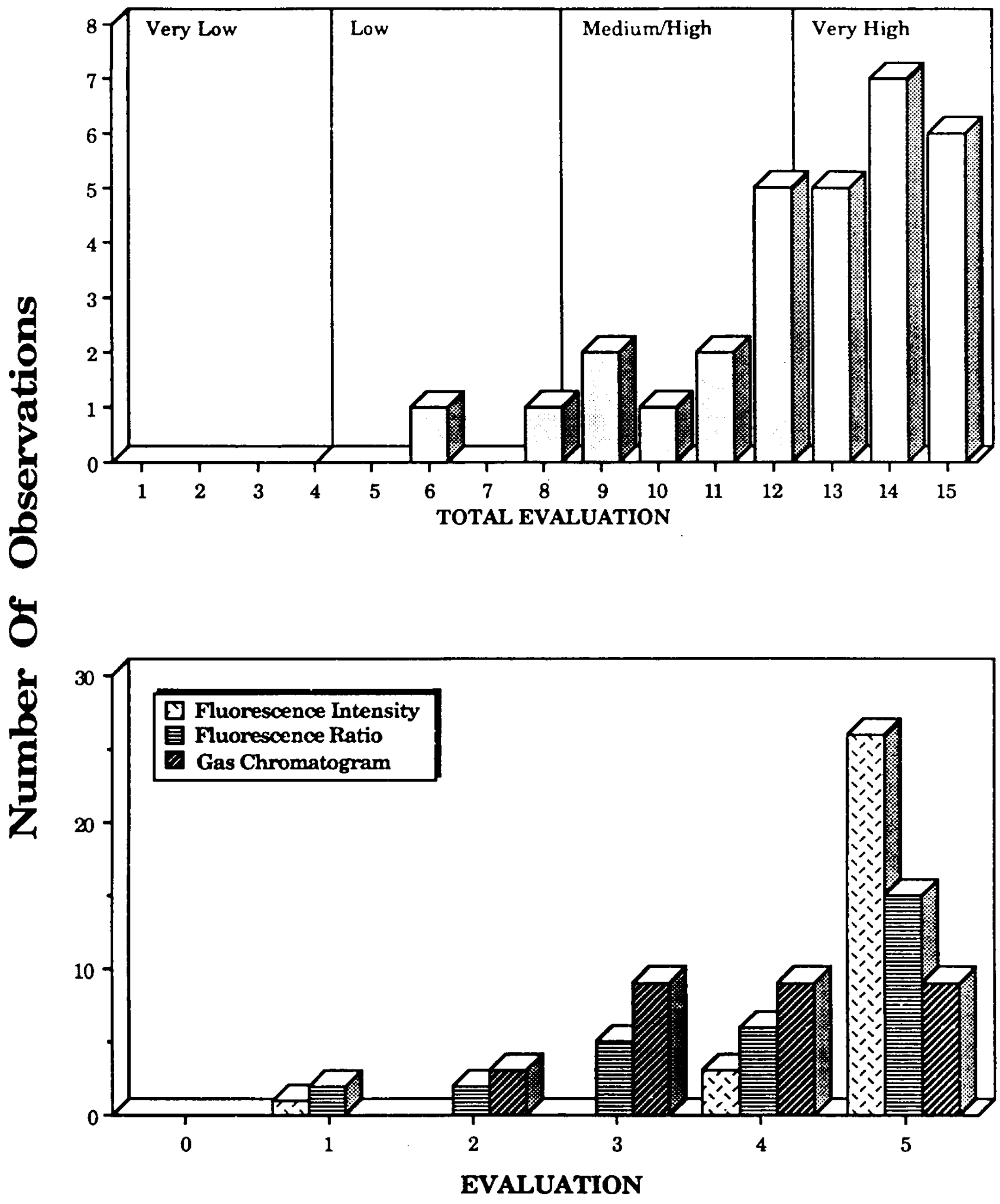


Figure 6-14. Summary of the oil seepage evaluations calculated for the piston cores retrieved at the trawl sites shown in Figure 6-4.

evaluated at 15, two or more chemosynthetic species were retrieved. These data strongly suggest a direct coupling between the chemical environment associated with hydrocarbon seepage (H_2S, CH_4, and oil) and the chemosynthetic processes on the Gulf of Mexico continental slope.

The sampling on Cruise 86-G-1/2 (Kennicutt et al., 1988b) was also designed to determine if chemosynthetic organimsms are only found in "wipe-out" zones that are associated with oil seepage. Piston cores were taken at each of the sites to determine the amount of migrated hydrocarbons present in the sediments associated with these "wipe-out" zones. Seven of the 39 piston cores were oil-stained. All of the trawl samples recovered at locations where visibly, oil-stained cores were recovered contained at least one species of chemosynthetic organism and generally represented the most abundant catches of chemosynthetic organisms. Elevated levels of hydrocarbons were present in all cores from areas where chemosynthetic organisms were retrieved suggesting that the system is predominantly driven by oil and gas seepage (H_2S derived either from sulfate reduction or associated with the seeping oil).

Investigations of Calyptogena and Vesicomya assemblages off Louisiana have shown distinct aggregation patterns on at least two spatial scales (Rosman et al., 1987) indicating that aggregation processes may occur at localized features within the seep communities. On the September 1986 Johnson Sea-Link I dives, chemical parameters reflect the importance of environmental factors in controlling the differences between tube worm and mussel assemblages. High mussel density was significantly correlated to methane levels in the water column. Tube worm distributions show no significant correlation with methane concentrations, but do with extractable organic material in the sediments; a pattern not shared by mussels. In both cases (mussels-methane and tube worms--extractable organic compounds), the significant correlation is localized to a radius of less than 7.5 m. The association of chemical parameters and biological distributions for "Bush Hill" is discussed in Chapter 7.

Mussels have been collected from a variety of sites of varying petroleum seepage, along with sediment samples, and preserved for hydrocarbon analysis. Hydrocarbon loads in the mussels appear to be variable with respect to location and tissue, as would be expected in animals living over a wide range of hydrocarbon exposure levels. Some mussels have exhibited significantly higher hydrocarbon levels in the gills, particularly in the naphthalene range, than in the rest of the body while in others a more even distribution was observed (Table 6-1).

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., 1987b). The majority of the bivalves (Calyptogena ponderosa, Vesicomyia 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, Myltilidae) at these sites derives its carbon, energy and nutritional needs from a symbiotic relationship with methane oxidizing bacteria in it's gills (Childress et al., 1986; Brooks et al., 1987b). 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 (Table 6-2 after Brooks et al., 1987b).

Three bivalves and two vestimentiferans recovered at these sites appear to harbor sulfur-oxidizing chemoautotrophic symbionts (Table 6-2). The enzyme activities, presence of elemental sulfur in the symbion-

Table 6-1. Polynuclear aromatic hydrocarbon (PAH) concentrations in mussel tissues (gill and body) collected near hydrocarbon seep sites.

Compound	Mussel	
	Body	Gill
Naphthalene	*	277.6
2-Methyl Naphthalene	*	162.2
1-Methyl Naphthalene	*	388
Biphenyl	*	*
Dimethyl Naphthalene #1	*	*
Dimethyl Naphthalene #2	*	63.6
Dimethyl Naphthalene #3	*	225.7
Dimethyl Naphthalene #4	*	118.4
Dimethyl Naphthalene #5	*	136.2
Dimethyl Naphthalene #6	*	*
Acenaphthene	*	53.4
Fluorene	*	*
Phenanthrene	59.1	26.1
Anthracene	*	*
3-Methyl Phenanthrene	52.6	33.6
2-Methyl Phenanthrene	52.6	38.9
9-Methyl Phenanthrene	52.6	35.7
1-Methyl Phenanthrene	52.6	*
Fluoranthene	*	*
Pyrene	33	*
Benz(a)anthracene	*	*
Chrysene	*	*
Benzo(e)pyrene	*	*
Benzo(a)pyrene	*	
Perylene	23.3	132.6
Dibenz(a,h)anthracene	*	*

* Concentration less than 20 ppb

Table 6-2. Enzyme activities, elemental sulfur (S^o) content, stable carbon isotope ratio ($\delta^{13}C$), presence of symbiotic bacteria (S.B.), and methane consumption (CH_4) in individual Louisiana slope seep organisms. Assays were conducted on symbiont-containing tissues (bivalve gills and vestimentiferan trophosome). One unit of enzyme activity will convert 1 μmhol of substrate to product. RuBP, ribulose-bisphosphate carboxylase; ATP, ATP sulfurylase; APS, adenosine-5'-phosphosulfate reductase; methanol, methanol dehydrogenase; sulfide, sulfide oxidase; ND, not detected; N, no; Y, yes; NT, not tested; WW, wet weight; and EM, electron microscopy.

Animal	Identification No.	Enzyme activity (unit/g WW/min)					S° (% WW)	$\delta^{13}C$	S.B. (EM)	CH_4*
		RuBP	ATP	APS	Methanol	Sulfide				
					Mollusca					
Lucinidae										
Pseudomiltha sp.									Y	N
	14-1	0.43	12.86	0.83	ND	2.1	0.02	−33.5		
	14-2	0.41	2.47	0.66	ND	1.94	0.06	−33.6		
	14-3	0.44	15.43	1.36	ND	2.04	ND	−32.5		
	14-14	NT	NT	NT		NT	0.5	−37.7		
Mytilidae										
Undescribed									Y	Y
	24-1	0.011	ND	ND	0.66	0.7	ND	−51.8		
	24-2	0.017	ND	ND	0.53	0.75	ND	−52.0		
	25-1	0.027	ND	ND	0.4	1.09	ND	−52.6		
Vesicomyidae										
V. cordata†									Y	NT
	18-1	0.003	29.58	ND	ND	NT	ND	−39.8		
C. ponderosa									Y	NT
	CAT-1	NT	NT	NT	NT	NT	0.4	−37.9		
	CAT-2	NT	NT	NT	NT	NT	8.3	−36.9		
	CAT-3	NT	NT	NT	NT	NT	ND	−39.1		
					Vestimentifera					
Lamellibrachiidae										
Lamellibrachia sp.									Y	N
	25-3	0.24	4.24	0.70	ND	1.77	4.5	−36.6		
	25-4	4.03	1.03	NT	ND	3.15	6.1	−36.8		
	25-5	4.97	0.51	0.78	ND	5.47	2.6	−37.4		
Undescribed family										
Undescribed									Y	N
	24-1	3.57	0.32	ND	ND	NT	0.1	−36.4		
	25-1	3.73	1.03	1.54	ND	5.32	NT	−39.9		
	25-2	5.40	1.90	ND	ND	2.98	1.9	−41.0		
	25-3	NT	NT	ND	NT	2.37	0.4	−37.0		

*Methane consumption from incubation of gill or trophosome tissue measured gas chromatographically (8). †The *V. cordata* died before dissection.

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 Calyptogena 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 (Table 6-3). 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 (delta $^{14}C = +100 \pm 20$ ppt; delta $^{13}C = -18$ to -20 ppt; see background fauna in Table 6-3). 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 (delta $^{14}C = -100$ ppt; delta $^{13}C = 0$ ppt) or from 'dead' CO_2 dDelta $^{14}C = -1000$). '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 fromn 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; 1986b). 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

Table 6-3. Stable carbon, nitrogen, and sulfur isotopic ratios and radiocarbon measurements of Louisiana slope seep organisms. Numbers in parentheses indicate the number of animals represented by the range. Locations are 9-square-nautical-mile Mineral Management Service lease areas and blocks (GC, Green Canyon; GB, Garden Banks; EB, Ewing Bank; and MC, Mississippi Canyon). All measurements are on animal soft tissue.

Animal	Location	$\delta^{13}C$ (per mil)	$\delta^{15}N$ (per mil)	$\delta^{34}S$ (per mil)	$\Delta^{14}C$ (per mil)
		Symbiont-containing animals (chemosynthetic)			
Bivalves					
Mussel (Mytilidae undescribed)	GC-272	−50.1 to −45.5 (9)	−12.9 to +3.0 (10)	+13.4, +7.5 (2)	−829 (1)
Clam (*C. ponderosa*)	GC-272, GC-234	−34.8, −35.0 (2)	+1.1 to +7.1 (3)	−0.1 to +2.1 (3)	
Clam (*V. cordata*)	GC-116	−36.3 (1)	−0.9 (1)		+254 (1)
Clam (*Pseudomiltha* sp.)	GC-79	−36.0 to −31.8 (3)	−3.5 to +6.1 (3)	−11.5 to +1.3 (4)	−753 (1)
Vestimentiferans					
Tube worm (Escarpia-like)	GC-272, GB-458	−40.9 to −30.4 (3)	+2.9, +5.4 (2)	−3.5 (1)	−205, −949(2)
Tube worm (*Lamellibrachia* sp.)	GC-33	−43.2 (1)	+2.7 (1)	−2.7 (1)	−586 (1)
		Heterotrophic deep-sea animals			
Neogastropods	MC-839, EB-1010, GC-33	−32.8 to −14.8 (5)	+2.8 to +13.0 (4)	0.0 to +18.7 (4)	−210, −544 (2)
Shrimp	GB-300	−19.5 to −18.6 (2)	+13.3 (1)	+13.3 (1)	+123 (1)
Clam (*Acesta*)	GC-272	−18.7 (1)	+8.9 (1)	+16.1 (1)	+96 (1)

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 (Table 6-4), 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' (Table 6-4). In contrast to the hydrothermal vent and Florida Escarpment sites, many of the mussels, tube worms and clams reported from the Gulf seeps (Table 6-3) 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).

The carbon isotopic content of these seep organisms reflect the isotopic fractionation that occurs during the synthesis of organic tissues and the food source of the animals (Williams et al., 1981; Gearing et al., 1984). The carbon isotopic compositions of 246 organisms from trawl samples collected on the Louisiana/Upper Texas slope is presented in Figure 6-15 (33 sites). The most striking feature of the figure is the three isotopically distinct groups of bivalves. The mussel tissues all have delta ^{13}C values <-40 ppt. The delta ^{13}C values betweenm -30 and -42 ppt represent clams with sulfur bacterial symbionts. These values are similar to those of the hydrothermal vent clams which appear to derive their energy from hydrogen sulfide (Williams et al., 1981; Rau, 1981; Rau and Hedges, 1979). Bivalve delta ^{13}C values typical of deep-sea fauna (-14 to -18 ppt) are assumed to be heterotrophic.

The light carbon isotopic values of the mussels are diagnostic of the methane symbiosis between the bacteria and the mussel (Childress et al., 1986). On Johnson Sea-Link-I dives 1877 and 1978, we collected mussels

Table 6-4. Stable carbon and radiocarbon measurements of seep and vent taxa from the deep sea. Numbers of individuals, without parentheses, refer to carbon isotopic measurements; numbers in parentheses refer to radiocarbon analyses. TR, values in this report.

Sample description	Number of individuals	$\Delta^{14}C$ (per mil)	$\delta^{13}C$ (per mil)
Louisiana hydrocarbon seep sites			
Clam tissue (*C. ponderosa*)	4		−31.2 to −35.3
Clam tissue (*C. ponderosa*)	3		−36.9 to −39.1
Clam tissue (*Pseudomiltha* sp.)	17 (1)	−753	−30.9 to −37.7
Mussel	38 (2)	−829, −840	−40.1 to −57.6
Snail (neogastropod)	1		−31.5
Neogastropods	10 (2)	−210, −544	−14.6 to −32.8
Tube worm (*Lamellibrachia*)			
Tissue	1		−27.0
Tube	1		−28.1
Tube worm (*Lamellibrachia*)*	37 (1)	−586	−29.8 to −57.2
Tube worm (pogonophorans)*	22 (2)	−205, −749	−30.5 to −59.3
Tube worm (Escarpia-like)*	24		−21.4 to −48.6
Hydrothermal vent sites (Galápagos and 21°N)			
Clam tissue (*C. magnifica*)	2		−32.1, −32.7
Clam tissue (*C. magnifica*)†	4		−32.1 to −39.9
Mussel tissue (*Bathymodiolus thermophilus*)	3 (3)	−270 to −228	−32.8 to −33.9
Mussel tissue (*B. thermophilus*)	1		−32.7 to −33.6
Mussel tissue (*B. thermophilus*)	24		−32.1 to −37.2
Tube worm (vestimentiferan) tissue	1 (1)	−270	−10.9
Tube worm (vestimentiferan) tissue	1		−10.8 to −11.0
Tube worm tissue‡	4		−11.9 to −13.7
Florida escarpment site			
Mussel tissue (mytilid)	10 (3)	−567 to −247§	−74.3 ± 2.0 (SD)
Gastropod tissue (trochid)	2		−59.9 ± 0.7 (SD)
Tube worm (vestimentiferan) tissue	3 (2)	−419, −424§	−42.7 ± 0.7 (SD)
Oregon subduction zone site			
Clam tissue (*Calyptogena* sp.)	1		−35.7
Clam gills (*Calyptogena* sp.)			−51.6
Clam tissue (*Solemya* sp.)	1		−31.0
Tube worm (*Lamellibrachia*)			
Tissue	1		−31.9
Segment			−26.7

*Includes both tubes and tissues of different individuals. †Values include isolated gills and remains. ‡Values include isolated trophosomes and vestimentum. §Values reported originally as percentage of modern. The conversion to $\Delta^{14}C$ assumed modern as 0 per mil.

living in a bubbling gas stream at 630 m in Green Canyon (GC) Block 185. The mussels delta ^{13}C (-40.6 ppt) closely reflect the composition of the methane (-41.2 ppt) used by the bacterial symbionts. Biogenic methane is characterized by delta ^{13}C values <-60 ppt with few longer chain hydrocarbons, while thermogenic gas contains higher hydrocarbon gases and delta ^{13}C values heavier than -45 ppt (Bernard et al., 1977). The mussels from GC-185 have thermogenic isotopic values. Most of the mussels collected from the trawls suggest an admixture of biogenic and thermogenic methane. The gill and mantle tissue from three mussels in our study have similar isotopic compositions indicating there is transfer of bacterial carbon from the symbionts in the gill to the mussel's other tissues.

Tube worm tissues and tubes from these sites show a range of delta ^{13}C values from -20 to -58 ppt (Fig. 6-15). These values are atypical of the few previous reports from the hydrothermal vent and other cold seep sites. The vestimentiferans (Riftia pachyptila) from the hydrothermal vents all have delta ^{13}C values near -10 ppt (Table 6-4) (Williams et al., 1981; Rau, 1981). One suggested explanation of the heavy values is that CO_2 limitation during growth precludes discrimination at the site of carbon fixation. The other delta ^{13}C values for tube worms from the Florida Escarpment and the Oregon Subduction Zone show lighter delta ^{13}C values. Thus, it is suggested that the >-42 ppt tube worm values are characteristic of sulfur-based endosymbionts. Values lighter than -42 ppt in the pogonophorans may indicate contribution from methane endosymbionts. The heavy values (-20 to -22 ppt) in the vestimentiferans may reflect processes similar to those occurring at the hydrothermal vent sites. the wide range of values reported no doubt also reflect the multiple sampling sites, the patchiness of thermogenic hydrocarbon seepage, and perhaps a difference in the delta ^{13}C of the DIOC around the animals. All of the tissue and tube pairs (more than 12 pairs) analyzed show similar carbon isotopic compositions (Fig. 6-15).

The sulfur isotopic content (Table 6-3) of the seep fauna also differentiates sulfur and methane energy sources. Most animals from food webs based on phytoplankton have sulfur isotopic compositions between +13 to +20 ppt, similar to the seawater sulfate pool (+20 ppt). Fry et al. (1983) found the fauna at hydrothermal vent sites had values between -5 to +5 ppt similar to the sulfur-bearing minerals of the vents. Although the

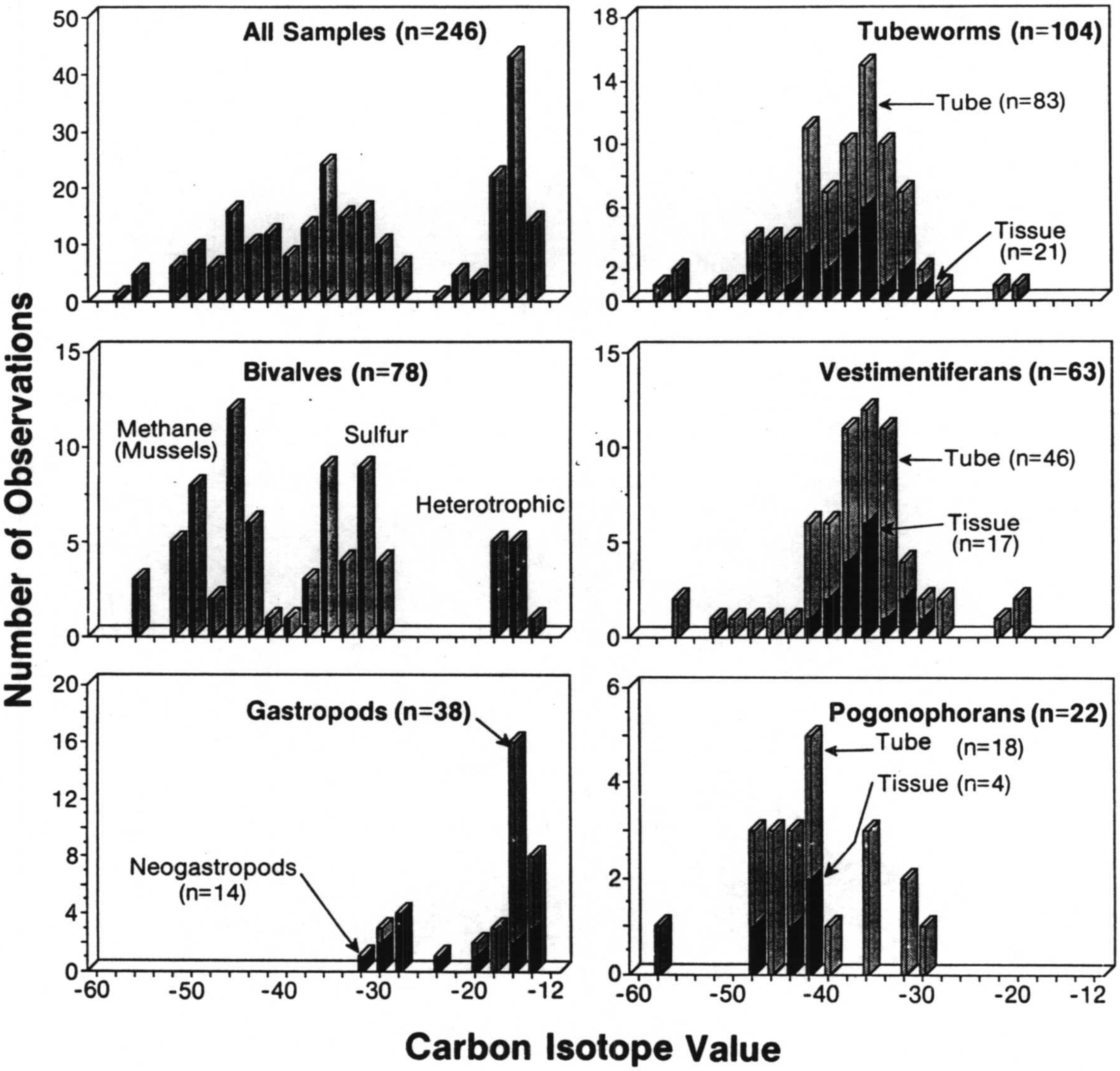


Figure 6-15. Carbon isotopic values (ppt relative to PDB) of 246 animals collected at seep sites on the Louisiana continental slope.

H_2S isotopic content of the Louisiana sites is unknown, the sulfur-based tube worms and clams have values between -12 to +2 ppt. Some neogastropods have values in this range reflecting chemosynthetic dietary carbon and sulfur, while others are characteristic of deep-sea heterotrophic values. This is consistent with Figure 6-15 which shows that most of the gastropods contain heterotrophic carbon. However, some of the neogastropods show transfer of chemosynthetic carbon into the background slope fauna which most likely results from the food source of these snails which often prey on bivalves. The methane based mussels have a sulfur value more characteristic of the heavier seawater sulfate.

In similar fashion to carbon and sulfur isotopes, nitrogen isotopes may be utilized to indicate sources of nitrogen and foodweb relationships. Hydrothermal vent communities and seep communities of the Florida Escarpment have unusually depleted nitrogen isotopic compositions relative to typical marine values (+5 to -15 ppt). (Rau, 1981; Paull et al., 1984; Minagawa and Wada, 1984). Such ^{15}N-depleted values have been attributed to fractionations of source nitrogen either through assimilation of depleted nitrate or ammonium (Paull et al., 1984; Minagawa and Wada, 1984). At the Louisiana sites, ^{15}N values range from similar to those previous studies to even more depleted (-12 ppt). Such depleted ^{15}N values have been reported for laboratory algal cultures using high (micromolar) concentrations of ammonium or nitrate, ammonium-rich hotsprings and nitrate-rich lakes in Antarctica. In all of these cases, elevated inorganic nitrogen concentrations allow for marked discrimination in the uptake of ^{14}N over ^{15}N with resulting cells being much depleted in ^{15}N. However, such unique environments are not expected at the seep sites. Normal (micromolar) levels of nitrate have not been associated with large ^{15}N depletions or anomalous values.

An alternative source of nitrogen is fixation of nitrogen gas (N_2) associated with methane from the seeps. The N_2 of the vent gas, once fixed, may in fact be the sole source of nitrogen for some of the organisms as indicated by their ^{15}N-depletion. The N_2 gas isolated from a nearby Green Canyon production oil well has a ^{15}N value of -2.9 ppt. Microorganisms fixing this gas would then have isotopic values near -6 ppt. Natural gases from other oil reservoirs have been reported to be as depleted as -14.6 ppt, so that it is conceivable that the N_2 gas associated with the seep area could be even more depleted.

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., 1988c).

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.

IMPACT ASSESSMENT IMPLICATIONS

The chemosynthetic marine communities of the Louisiana/Upper Texas continental slope possibly represent a situation analogous to the hard bottom "reef" systems on the continental shelf in that they are (1) fragile ecosystems, and (2) have significantly higher biomass than their surroundings. The importance of these communities includes the unique genetic pool associated with new and possibly rare deep-sea species, and an extremely high biomass that could possibly be an important nutritional source to the deep-sea.

The short-term environmental impact concern from deep water offshore exploration and production could come from mechanical damage to these ecosystems. Since the sites are associated with oil and gas seepage, it is reasonable to assume that many of the sites will be in close proximity to exploration and production platforms. The discharge of drilling muds and platform effluents should not have an impact on the deep-sea communities at these water depths. However, large anchors, chains, and bottom templates could cause significant mechanical damage to these ecosystems.

The long-term environmental impact of depletion of the oil and gas reservoirs underlying these seep communities could be deleterious. For example at "Bush Hill", one might expect that production of oil and gas from the Conoco field in GC-184 could result in a cessation of oil and gas seepage. There have been a number of on land reports (e.g., Horvitz, 1972) that show seepage slows or stops fairly rapidly following reservoir production. One might expect the first response to slower seepage rates would be the elimination of the mussels from the community since these are dependent on active gas seepage. The tube worms and clams that depend on the oil seepage may be more resistent to the cessation of active oil seepage. The natural life-times of these deep-sea epifaunal communities is unknown, so the impact assessment of man-induced changes in seepage patterns is difficult to ascertain.

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CHAPTER 7. THE SPATIAL DISTRIBUTION OF VESTIMENTIFERANS, MUSSELS, HYDROCARBONS AND GEOLOGIC FEATURES AT A HYDROCARBON-SEEP COMMUNITY ON THE GULF OF MEXICO CONTINENTAL SLOPE

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INTRODUCTION

In this chapter, we describe a chemosynthetic community known as Bush Hill, which occurs at a site of natural hydrocarbon seepage at a depth of 550 m on the Louisiana continental slope (Brooks et al., 1984; 1986; 1987b). The analyses of sediments and water associated with the distribution of the dominant megafauna within the community are quantified and variations in faunal abundance are compared to ambient concentrations in hydrocarbons and to geologic features. Before proceeding, some background information is in order.

Deep-sea communities of tube worms (Riftiidae) and bivalves (Vesicomyidae and Mytilidae) were first discovered at hydrothermal vents at the Galapagos Rift (Corliss et al., 1979) and the East Pacific Rise (Rise Project Group 1980). These animal assemblages were shown to be dependent upon chemosynthetic processes mediated by internal symbionts (Cavanaugh et al., 1981; Felbeck et al., 1981). Subsequent exploration has greatly increased the known geographic range of similar communities and has documented their occurrence at cold seeps as well as hydrothermal vents (Paull et al., 1984; Kennicutt et al., 1985; Suess et al., 1985; Laubier et al., 1986). Primary food sources for the bacterial symbionts of both vent tube worms and seep tube worms (Lamellibrachidae and Escarpiidae) are reduced sulfur compounds (Felbeck, 1981; Brooks et al., 1987a). An undescribed seep mussel has been shown to harbor methanotrophic bacteria in its gills and to metabolize dissolved methane (Childress et al., 1986). The physiology of these symbioses is diverse and is the subject of active research (Cavanaugh et al., 1987; Fisher et al., 1987; Distel and Felbeck, 1987).

Ecological descriptions of seep and vent communities have been based primarily upon interpretations of still and video photographs, which have provided information concerning spatial distribution and temporal variation of abundance (Hessler et al., 1985; Hecker, 1985; Tunnicliffe et al., 1985; Fustec et al., 1987; Juniper and Sibuet, 1987; Rosman et al., 1987). Despite the geographic and taxonomic diversity of the communities described to date, they share several significant characteristics. Although the depth range was large (500 to 6,000 m), all were found below the photic zone. All apparently occur at a gradient between reducing and oxidizing environments, either where reduced compounds, particularly sulfides and methane, were issuing into oxygenated waters or where anoxia occurs in the benthic substrate. The density and diversity of the communities greatly exceeded the surrounding benthic fauna. Distribution of organisms within the communities was spatially heterogeneous. Frequently the transition between the chemosynthetic community and the surrounding environment was abrupt. Patterns observed in the distribution of seep and vent faunas have been attributed to supposed spatial and temporal variations the supply of sulfides and methane. However, investigations of the distribution of these compounds within the communities have been limited (Johnson et al., 1986).

Thermogenic hydrocarbons are widespread in surface sediments on the upper continental slope of the Gulf of Mexico (Anderson et al., 1983; Brooks et al., 1984; 1985; 1986; 1987b; Kennicutt et al., 1987a; b; 1988). Preliminary studies of the biota associated with several of these hydrocarbon seeps indicate that the seeps can support communities with substantially greater biomass and diversity than is typical of the slope benthos (Kennicutt et al., 1985; Brooks et al., 1987b; Rosman et al., 1987). Transport of production from hydrocarbon seeps to the surrounding benthos may contribute significantly to the energy budget of the continental slope. However, documentation and quantification of such a contribution will be difficult. The extent of hydrocarbon seepage, mechanisms for transfer of carbon and organisms, and distributional characteristics of seep biota as they relate to hydrocarbon levels are presently obscure.

As noted above, The latter issue is the subject of this study. Distribution and abundance of an assemblage of organisms dependent on seeping hydrocarbons should reflect the pattern of seepage and the quantity of hydrocarbons present. A useful spatial description should give the areal extent of the community, the distributions and relative abundances of the dominant organisms, and the environmental variables that correlate with these distributions.

MATERIALS AND METHODS

Site Description and Field Methods

Bush Hill occurs over a salt diapir that rises about 40 m above the surrounding sea floor to a minimum water depth of 540 m. The feature is located 210 km south-southwest of Grand Isle, Louisiana, at 27°47.0'N, 92°30.4'W. It lies in the Green Canyon (GC) offshore leasing area in lease blocks 184 and 185 (see Fig. 6-7) approximately 3,500 m from the drill template of what is currently the world's deepest oil-production platform (Anonomous, 1987). The bottom in this area is a silty-clay sediment of considerable thickness; however, much of the sedimentary facies of Bush Hill itself (Fig. 7-1) have been disrupted by rising gas and liquid and by in situ formation of authigenic carbonate and sulfides (Brooks et al., 1986; Behrens, 1988).

Bush Hill and its immediate surroundings were explored during four dives of the research submersible Johnson Sea-Link-I (JSL), deployed from the support ship R/V Edwin Link. A series of sub-bottom profiles of the study area were obtained with a 3.5 kHz precision depth recorder. The JSL carried a series of sediment coring devices, each constructed of 25 mm (i.d.) PVC pipe and fitted with a handle for operation by the JSL's mechanical arm. A length of flexible tubing for collection of water samples was run from the end of the arm to an intake port in the aft dive-compartment.

Color images were recorded by a high-resolution video camera (MOS model 3,000) mounted on a pan-and-tilt unit and a 35 mm still camera (Benthos model 372) mounted vertically. Both cameras were equipped with ranging devices. The video camera carried a pair of lasers, mounted in parallel with 10 cm separation. Their beams appeared as red dots in the video record; the relative separation of the dots provided a measure of photographed subjects and of the field of view. On the 35-mm camera, a short-range altimeter recorded the distance to the bottom in each exposure. This distance, together with the acceptance angle of the lens, was used to calculate the area of the bottom and the size of the subjects in each photograph (Rosman et al., 1987).

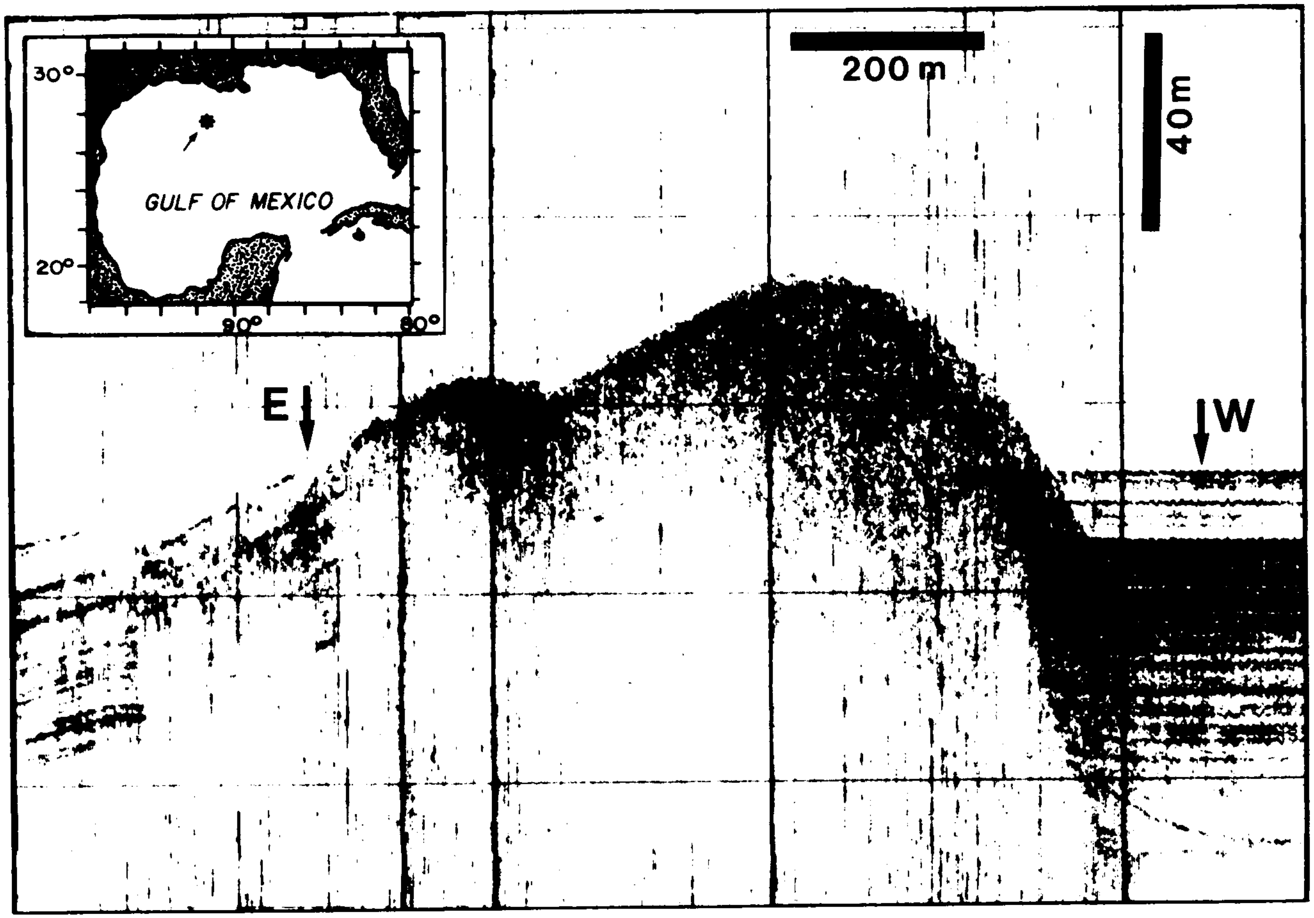

Figure 7-1. Precision depth recorder (3.5 kHz) trace of the Bush Hill diapir. Inset shows location of study site in the Gulf of Mexico. Arrows E and W mark the eastern and western extent, respectively, of the study site. See Figure 7-2B for location of PDR trace in study site (vertical exaggeration, 5x).

Dives consisted of a series of short (100 to 200 m) transects during which the pilot attempted to maintain constant speed, altitude and bearing. Start and end times were recorded for each transect. The submersible's range and bearing from the support ship were monitored with a Northstar Doppler sonar. The submersible's absolute position at the start and end points of each transect was fixed by maneuvering the ship to a position direclty over the submersibe (zenith ± 5 m) and recording the ship's position with LORAN C.

The forward sphere of the JSL provided the pilot and scientist with an unobstructed 180° view of the bottom in the submersible's path. During each transect, the video camera was allowed to run continuously while the scientist recorded a narrative describing the objects in view, the time of observations and the JSL's bearing. The zoom on the video camera was kept at maximum wide angle while on transect. Contemporaneous notes and subsequent measurement of the video images indicated that the video camera was consistently able to record all sessile objects in a 6-m swath along the bottom.

Collections of organisms, sediment cores and water samples were made while the JSL was at rest between transects. Organisms were collected with the scoop and claw devices of the mechanical arm and were placed in numbered buckets on the front basket. Cores of the upper 30-40 m of surface sediments were collected with the coring devices and placed in numbered, water-tight quivers. Water samples were collected at distances that ranged from 10 cm to 3 m above the bottom. The intake tube was flushed with ambient water prior to the collection of each sample to prevent cross-contamination of samples. Each water sample consisted of a capped 300 ml bottle and a 50 ml syringe. Syringe samples were fixed when collected with zinc acetate for measurement of total sulfides (Cline, 1969; Goldhaber et al., 1977). The location of each sample site was accurately recorded.

Observations of the Bush Hill community were concentrated at the top of the diapir, with dives originating at points on its periphery and proceeding inward (Fig. 7-2A). Usable video records were collected on 20 transects, which together surveyed 2,716.2 linear meters and collected 112.7 minutes of data. The convex perimeter surrounding the outermost limits of the video records covered about 20 hectares of the bottom (Fig.

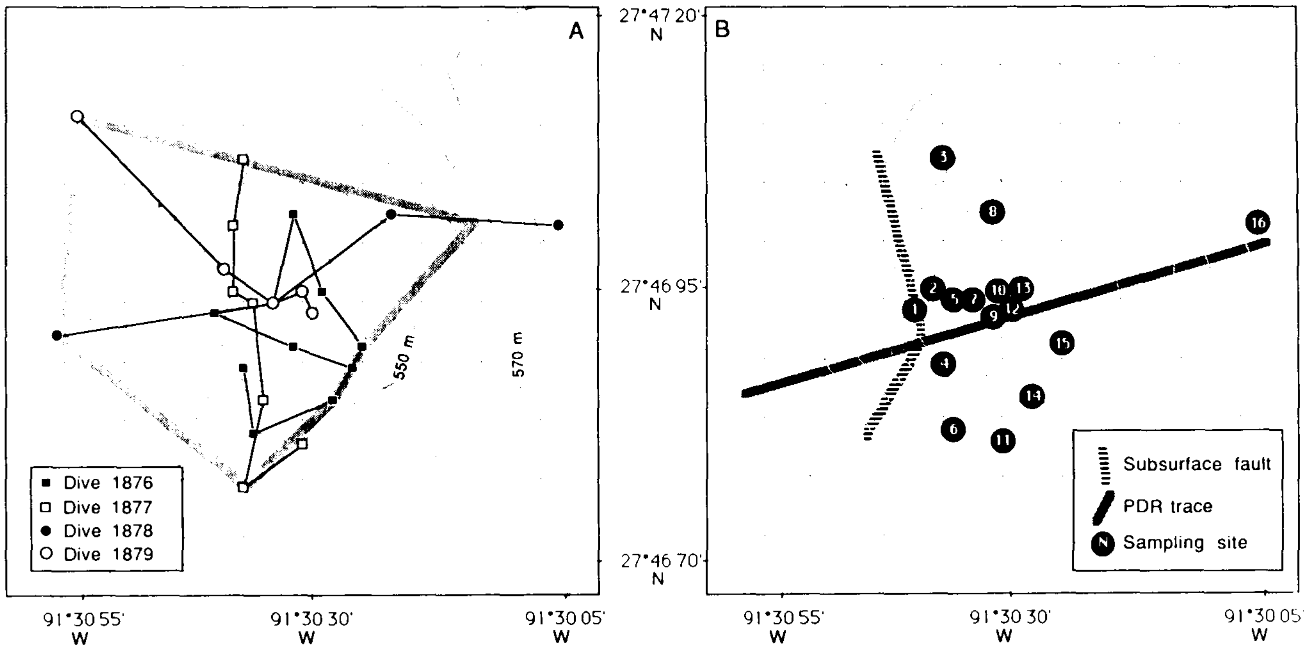

Figure 7-2. Area surveyed by Johnson Sea-Link-I. A: Solid lines show submersible transects during each dive; stippled outline shows outer extent of video coverage. B: Locations of sediment and water sampling sites; stippled line shows PDR trace (see Fig. 7-1).

7-2A), and the swath of the transects covered 7% of this area. Sediment cores and/or water samples were collected at 16 sites along the transects (Fig. 7-2B). Cores were taken at 13 of these sites, water samples at 12. Video data were not recorded on the transect extending beyond the convex perimeter to the east on dive 1,877 (Fig. 7-2A); however the observers reported no sightings of tube worms or mussels on this transect. Video records made while transiting to sample site 11 (Fig. 7-2B) were unusable. A single, isolated cluster of tube worms was observed at this site. A sediment core was taken adjacent to the cluster and a collection of the organisms was made.

Chemical Analysis

Hydrocarbons were recovered from sediments by extraction with CH_2Cl_2. Sediment samples were lyophilized and Soxhlet extracted for 12 hours. All glassware was pre-cleaned with solvents and combusted at 450°C for four hours. The collected extracts were concentrated by roto-evaporation. Extracts were analyzed by capillary gas-chromatography with flame ionization detection (GC-FID). Extract components were separated on a silicon-fused silica capillary-column with splitless injection (film thickness 0.2 μm; i.d. = 0.31 mm; length = 25 m). The GC-FID conditions for analyses were an initial temperature of 60°C with no hold time and a programmed increase of 12°C min^{-1} to 300°C (nine minute hold time). The injection port and detector were again held at 300°C. The gas chromatographs were either Hewlett Packard Model 5880 or 5790. The chemical analyses have been described in greater detail elsewhere (Brooks et al., 1986; Kennicutt et al., 1988).

Samples to be analyzed for stable carbon isotopes (delta ^{13}C) were processed by standard methods with both Craig-type and closed-vessel combustion techniques (Sackett et al., 1970; Schoell et al., 1983). Carbon dioxide was analyzed on a Finnigan MAT-251 isotope ratio mass spectrometer.

Video Analysis

The video records of the transects were replayed on a recorder equipped with freeze-frame and single-frame-advance controls. Subjects sighted in the video record included the larger mobile epifauna (fish and crabs), clusters of sessile epifauna (seep mussels, Vestimentifera and Gorgonacea) and prominent benthic features (carbonate boulders and gas seeps). Each organism observed in the video record was identified to lowest practical taxon; and the time of observation, relative to the start or end of the transect, was recorded. Video records obscured by suspended sediments were deleted from the data. The diameters of clusters of seep fauna were measured with the scale provided by the laser ranging device. The distance between any two points within the square was determined with elementary trigonometry. With the assumption that the JSL maintained constant speed and bearing during transects, the observation times could be used to determine the relative position of a video subject between navigation fixes. All samples and observations, including the location of a subsurface fault evident in the sub-bottom profiles, were mapped onto a 1 km square (Fig. 7-2) with southeast corner coordinates $27^{o}46.67$'N: $91^{o}30.6$'W, and northwest corner coordinates $27^{o}47.21$'N: $91^{o}30.01$'W. The points of the navigation fixes at the ends of transects were converted to Cartesian coordinates within this square. All organism, water and sediment samples and all video observations were then indexed by their respective coordinates.

Statistical Methods

The areal cover of tube worm bushes and mussel beds in the vicinity of each sample site was compared to the values of the chemical parameters measured in the corresponding sediment and water samples. Faunal clusters were assumed to be circular; the areal cover of each cluster was calculated from its measured diameter. Observation of clusters on the portions of transects that led to, and away from, the sampling sites provided a way to examine the tendency of the seep fauna to occur at various distances from the sites. These distances were grouped in a sequence of equal radial intervals (e.g., 0.0-1.5 m, 1.5-3.0 m, etc.), and the diameters of faunal clusters occurring in each interval were pooled to provide estimates of the areal cover of each taxon within the interval. Thus the area around each sampling site was divided into a series of concentric rings, each having a width equal to the radial interval, which were sampled on the video transects that led up to, away from, or tangentially past the sites.

Chemical parameters at each site could then be compared to the amount of faunal cover that was observed in surrounding rings. The tendency for high areal cover to occur at sites where the values of the chemical parameters were also high was examined. A two-tailed Spearman's Rho test was chosen as a robust and non-parametric measure of the correlation between high and low values of faunal abundance and chemical parameters (Conover, 1980). The confidence level of the tests of hypotheses was set at $\alpha = 0.05$. The spatial partitioning of the data made it possible to examine the effect of distance on correlation. Various radial intervals were compared.

The locations and sizes of all faunal clusters observed on the video transects were used to estimate the areal cover of the tube worm bushes and mussel beds throughout the surveyed area. The surveyed area was divided into a grid of 10-m squares. Areal cover of faunal clusters in each square was taken as the distance-weighted, moving average of all observations (Ripley 1981). The averaging function had the following form:

$$\Sigma\, w\,(d_i/h)\; z_i \;/\; \Sigma\, w\,(d_i/h);$$

where, for each grid square, the intensity z_i is the weighted average of the $i = 1, 2, \ldots, n$ estimates of areal coverage; and d_i is the distance from the location of the observation to the center of the grid square. A uniform band-width, h, of 60 m was applied to estimates of areal cover of tube worm clusters; a band width of 10 m was applied to estimates of the more sparsely distributed mussel beds. The weighting function treated the distance, x, of the observation from the grid square. It had the form:

$$w(x) = 0.9375(1-x^2)^2$$

for $-1<x<1$.

RESULTS

Community Description

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. 7-3A). 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 Escarpia-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. 7-3B), 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 the number of tube worms in a cluster increased. Low tangles, 30 to 40 cm

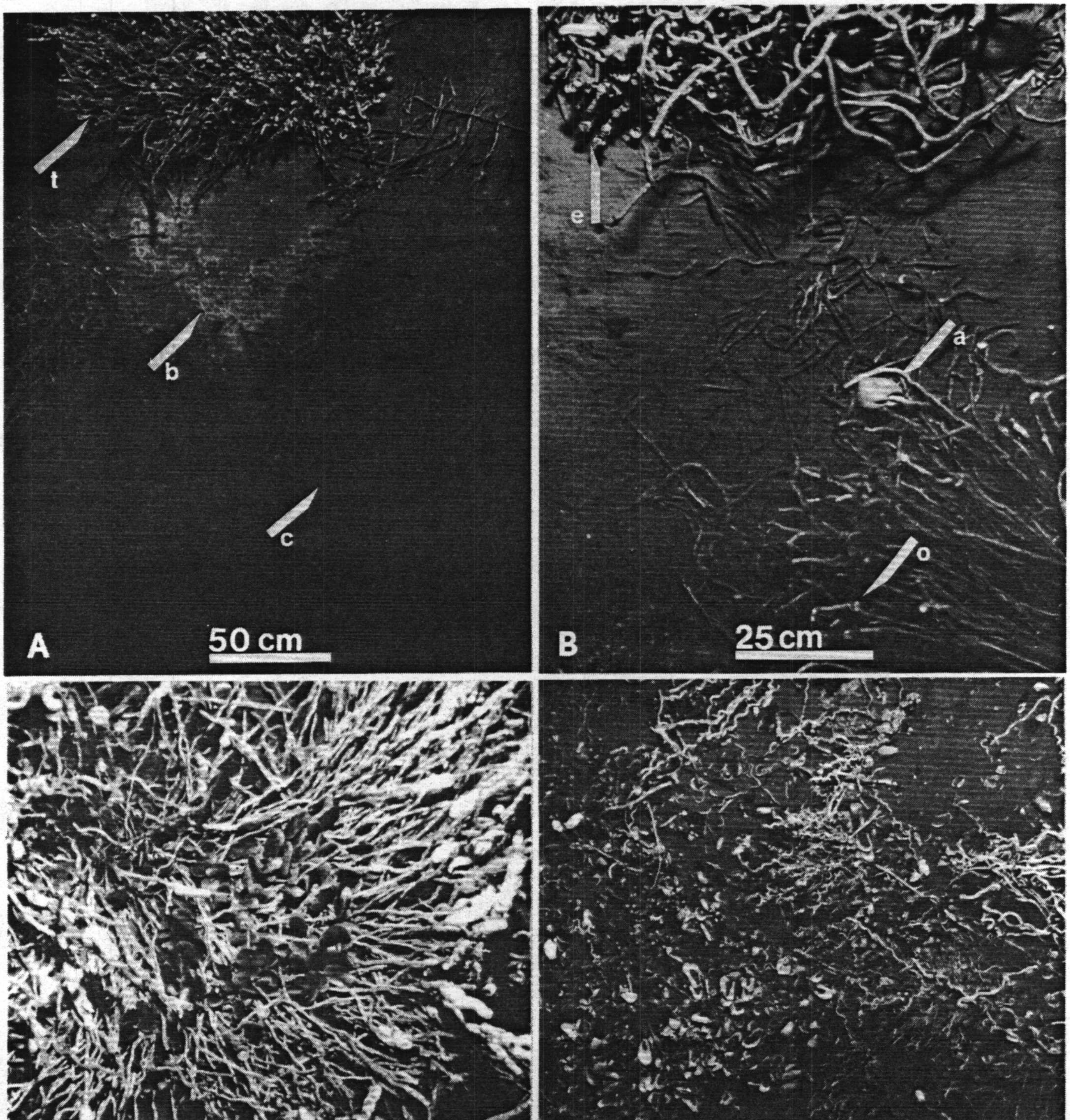

Figure 7-3. Bush Hill biota. A: Lamellibrachia sp. (t), carbonate boulder (c) and bacterial mat (b). B: Lamellibrachia sp. with attached Acesta bullisi (a) obturacular plume (o) and an escarpiid vestimentiferan (e), C: Lamellibrachia sp. with seep mussels in center, epifaunal sponge (s). D: Seep mussels and Lamellibrachia sp.

in diameter, consisted of individuals with twisted and curled tubes (Fig. 7-3D). Larger clusters, up to 1 m in diameter, had a collapsed, basket-like center and consisted of longer, less convoluted individuals (Fig. 7-3C). 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. 7-3A). 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. 7-3C); however, the larger mussel beds contained only small tube worms, if any (Fig. 7-3D). The beds were irregular in shape, often in close proximity to each other, and ranged in area from less than 1 m^2 to approximately 20 m^2. 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. 7-3D).

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., Bathyplax 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. 7-3B). 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.

Water Samples

The results of the water sample analyses are summarized in Table 7-1. Salinity values for the water samples ranged from 34.0 to 39.5 ppt. Anomalously high values were obtained at sampling sites 7 (0.5 m) and 16 (Table 7-1). Detectable hydrogen sulfide concentrations ranged from 3 to 11 micromolar but most samples (16 of 20) were below the limit of

Table 7-1. Values of chemical parameters measured in water samples: site no. refers to the sample locations shown in Figure 2B; height above bottom is given in parentheses; (bubbles) = sample collected in bubble stream; (bottom) sample collected <20 cm from bottom; nd, not detected at sensitivity of test (<3 μM); ns, not sampled. Multiple samples were collected at different distances from the bottom at Stations 7, 9, 12, and 16.

Site No.	Dive No.	Salinity ppt	Sulfide μM	Methane μM	Ethane μM	Propane μM	i-Butane μM	n-Butane μM
1 (bottom)	1876	36.0	ns	54	3	0	0	0
2 (bottom)	1877	34.4	nd	392	16	1	0	0
4 (bottom)	1876	35.2	nd	52	2	0	0	0
5 (bubbles)	1877	35.0	nd	36429	390	488	93	184
6 (bubbles)	1876	35.6	7	17474	463	111	20	21
7 (bottom)	1878	35.1	nd	238	18	3	0	0
7 (.5 m)	1878	39.5	nd	159	11	0	0	0
7 (1 m)	1878	36.4	nd	110	8	2	0	0
7 (3 m)	1878	35.6	nd	20	0	0	0	0
8 (bottom)	1876	35.3	nd	202	6	2	0	0
9 (bottom)	1879	34.6	11	2856	223	46	10	6
9 (2 m)	1879	36.1	nd	836	59	13	2	2
11 (bottom)	1877	34.0	nd	67	4	1	0	0
12 (bottom)	1879	34.9	nd	762	15	3	0	0
12 (2 m)	1879	34.9	nd	168	6	2	0	0
15 (bottom)	1876	35.2	nd	94	6	1	0	0
16 (bottom)	1878	37.7	3	47	2	4	2	0
16 (.5 m)	1878	37.7	nd	38	0	0	0	0
16 (1 m)	1878	37.5	nd	38	0	0	0	0
16 (3 m)	1878	37.8	nd	38	0	0	0	0

quantification (3 micromolar). Gaseous hydrocarbons were predominantly methane, which ranged in concentration from 20 to 36,429 micromolar. Highest concentrations of methane were obtained near the bottom over the bubbling mussel beds. At sampling sites 7, 9 and 12, near bottom levels of methane were markedly higher than levels observed higher in the water column (Table 7-1).

Sediment Samples

The results of sediment analyses are summarized in Table 7-2. The extractable organic matter (EOM) content, mainly oil, of the sediments ranged from 240 to 119,256 ppm. Gas chromatograms for sediment extracts indicated that the oil had been subjected to intense bio-degradation, and that the degree of degradation was highly variable. The organic carbon and carbonate carbon content of the sediment samples ranged from 1 to 9% and from 4 to 70%, respectively. The stable carbon isotopic composition of the organic matter ranged from -22.7 to -27.6 ppt. Values for carbonate carbon, mainly authogenic carbonate, were considerably more variable and ranged from +0.9 to -15.4 ppt. Grain size analysis showed that the sediment composition varied between sample sites. In general, the decreasing order of abundance of grain size in the sediment samples was clay, silt and sand, respectively.

Fine-scale Distribution of Seep Organisms

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 (Fig. 7-4A). 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 (Fig. 7-4B). Significant correlations with methane and EOM were only observed at small distances (≤ 7.5 m) from the sampling sites. The opposite was observed with total organic carbon. Large mussel beds were seen at distances 7.5 to 15 m from the three sites where the highest values for total organic carbon were measured. Correlation between methane and tube worms and between EOM and mussels was not

Table 7-2. Values of chemical parameters measured in sediment samples. When multiple cores were collected at the same site, the values shown are the median values observed. Carbon isotope ratios are given in standard delta ^{13}C notation versus Pee Dee Belemite standard. See Figure 7-2b for sample locations within the study area.

		Organic carbon			Inorganic carbon	
Site No.	Dive No.	Total organic carbon (percent)	$\delta^{13}C$	Extractable organic material (ppm)	CO_3 (percent)	$\delta^{13}C$
1	1876	3.3	-25.0	119256	19.7	-9.6
2	1877	7.7	-24.9	44609	12.4	-6.9
3	1877	2.2	-23.5	240	12.0	-2.7
4	1876	1.9	-24.3	51743	9.9	-12.9
5	1877	8.4	-27.0	33281	58.3	-8.1
6	1876	2.8	-22.7	63754	10.5	-12.8
7	1876	7.1	-26.0	64218	16.0	-6.8
8	1876	4.2	-25.0	1363	7.2	-0.6
10	1879	6.8	-24.6	55747	7.1	-11.2
11	1877	6.3	-25.4	11096	15.5	-8.4
13	1876	1.8	-25.1	5521	6.3	-0.9
14	1876	2.1	-24.3	40106	13.9	-12.9
15	1876	2.8	-25.0	4424	8.9	+0.6

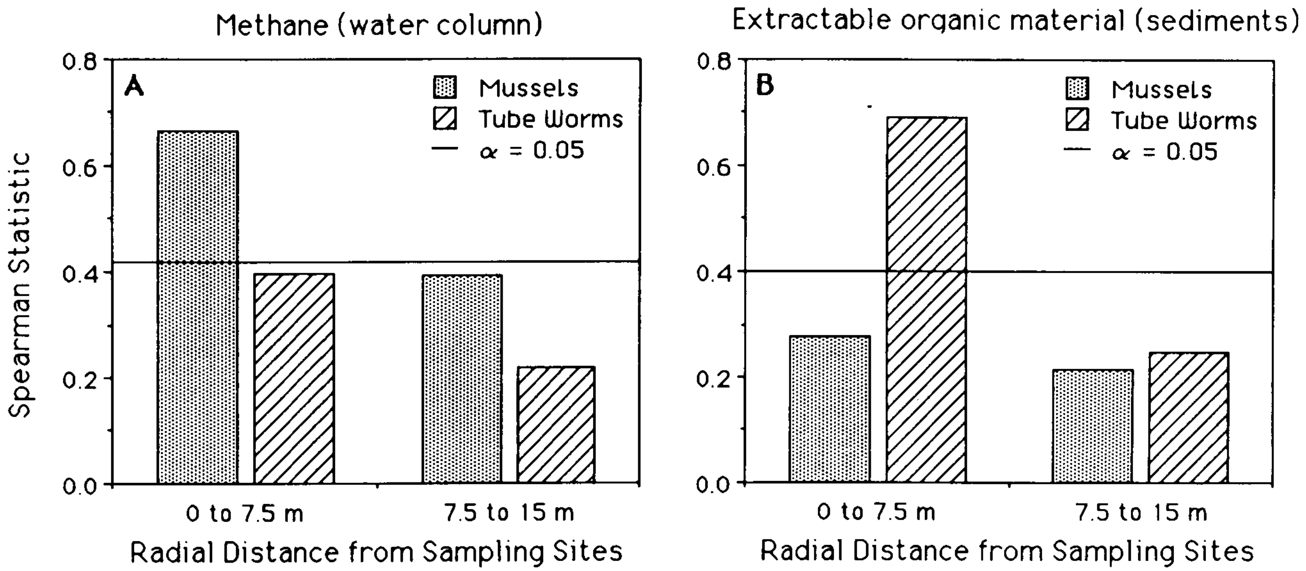

Figure 7-4. Spearman's Rho ranked correlation between values of chemical parameters and the areal cover of tube worms (Lamellibrachia sp. and escarpiids) or seep mussels. The test statistics were computed for two radial intervals from the sampling sites: 0 to 7.5 m and 7.5 to 15 m. Values greater than the α-level indicate significant positive correlation ($p < 0.05$). A: Concentration of methane in water samples; 12 paired samples for each radial interval. B: Concentration of extractable organic material (EOM) in sediment samples; 13 paired samples for each radial interval.

significant (p>0.05). No significant correlation was observed between percentage of carbonate carbon in sediment cores and the abundance of either mussels or tube worms.

Concentrations of methane at the 12 water sampling sites were paired with the area of the bottom covered by mussel beds or tube worm bushes in each of a series of concentric rings surrounding the sampling sites (Fig. 7-4A). Correlation was significant only with mussel beds and only when the values from water samples taken at the lowest distance above the bottom were used; the test statistic became non-significant when values for samples obtained at higher distances above the bottom were substituted (Table 7-1). Results of iterative applications of the test statistic converged when a ring width of 7.5 m was used. That is, correlation between methane and mussels was significant at radial distances of 0 to 7.5 m from the sampling sites and was non-significant at greater distances regardless of how these intervals were subdivided. Correlation between methane and tube worms was never significant.

Similar pairing of the concentrations of EOM in cores from the 13 sediment sampling sites with the abundance of tube worms or mussels was undertaken (Fig. 7-4B). At sites where multiple cores were taken or where cores were subdivided, the minimum, maximum, mean and median values were used in turn to examine correlation. Although the test statistics varied slightly, depending on which values were used, the overall significance was unaffected; test statistics for median values were plotted in Figure 7-4B. Iterative comparison of the correlation between EOM and tube worms at different radial intervals produced the following results: the interval 0 to 4.5 m was non-significant; the interval 4.5 to 7.5 m was significant; the pooled observations in the interval 0 to 7.5 m were significant, and all intervals greater than 7.5 m were non-significant. Correlation between EOM and mussels was never significant.

Coarse-scale Distribution of Seep Organisms

The locations of individual mussel beds (Fig. 7-5A) and tube worm bushes (Fig. 7-5B) 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. Mussel beds were sighted only in the center of

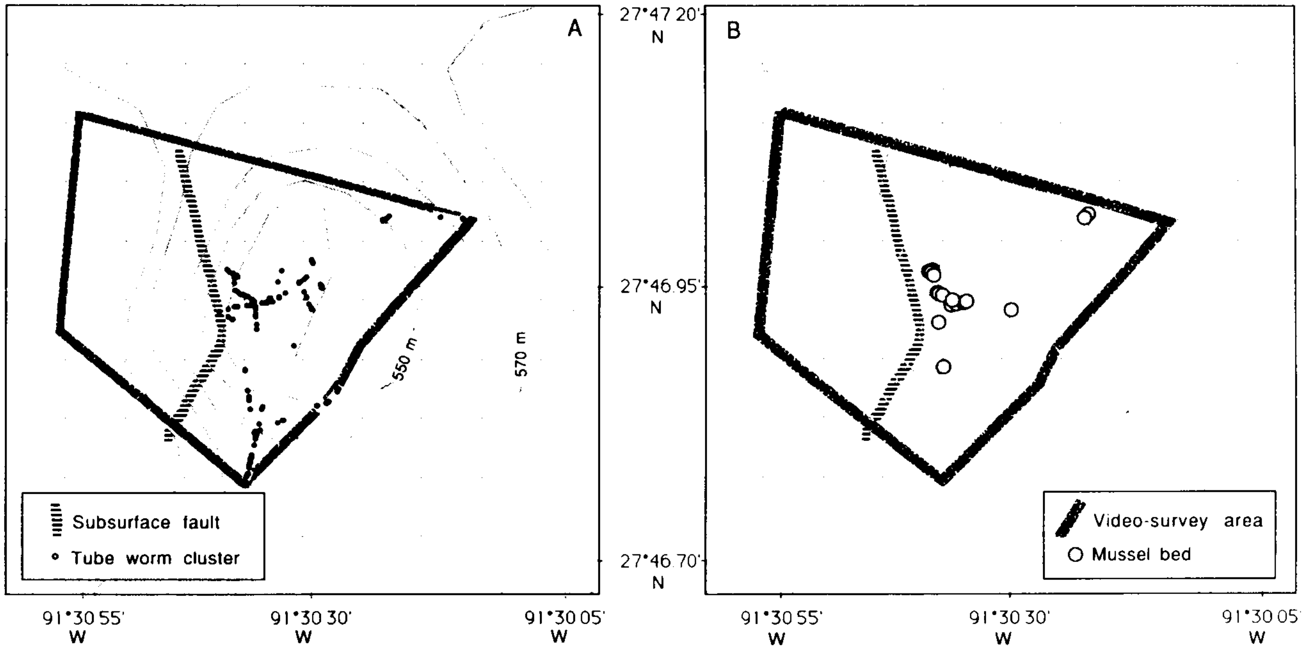

Figure 7-5. Distribution of clusters of chemosynthetic organisms at Bush Hill. A: Tube worm clusters (Lamellibrachia sp. and escarpiids). B: Seep-mussel beds. Striped line shows location of major fault; stippled line shows outer extent of video coverage.

the surveyed area and in its northeastern corner. 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. The distribution of fishes and other mobile epifauna was more nearly uniform than that of the mussels and tube worms.

Smooth surfaces describing the area occupied by tube worm bushes (Fig. 7-6A) and mussel beds (Fig. 7-6B) within the surveyed area were fitted to the estimates of areal coverage calculated from the video observations by use of the G3D procedure of SAS/Graph (SAS Institute Inc., 1985). The greatest relative abundance of tube worms was seen in the central portion of the surveyed area, which was also at the greatest elevation of the diapir. The second node of abundance, which contained a comparable number of individual bushes, was characterized by a lesser abundance of tube worms. Tube worm abundance decreased abruptly from the central node toward the western portion of the surveyed region, and decreased more gradually eastward and southward from the top of the diapir. Abundance also declined toward the north; however, an outlying aggregation of tube worm bushes occurred in the northeast corner of the surveyed area. Areal coverage of mussel beds was concentrated in the central region of the surveyed area to a greater degree than that of the tube worm bushes. Comparison of the surfaces of relative abundance (Fig. 7-6) showed that the peak abundance of mussels was offset to the northeast by a distance of 85 m from the peak abundance of tube worms.

DISCUSSION

Density of chemosynthetic organisms, often based on qualitative estimates of the numbers of organisms per unit area, has been widely used as a descriptive characteristic of vent and seep communities. We restrict our estimates to measurement of the widths of discrete clumps or clusters of seep organisms, which are recorded as scalar quantities along the video transects. Attempts to count individual animals within clusters are

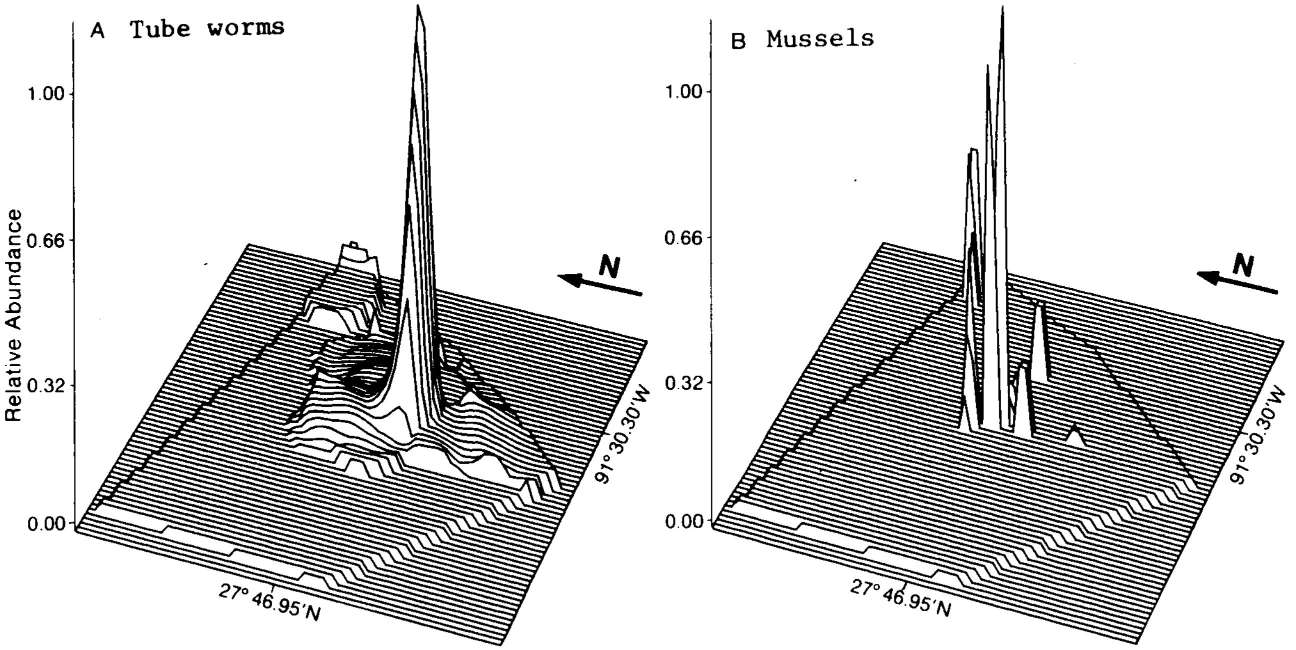

Figure 7-6. Estimated relative abundance of chemosynthetic organisms within the area of video sampling at Bush Hill. The projection was rotated counter clockwise and tilted toward the viewer. Raised edges show outer extent of video coverage (see Figs. 7-2A and 7-5). A; Relative abundance of tube worms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

rejected as inaccurate because of the pervasive layering and clustering of animals in our photographs and video records. Estimates of relative abundance are then obtained by assuming that the clusters are circular in shape and comparing the estimated area occupied by clusters at different locations within the community.

These methods are subject to certain sampling errors. For example, the limit of precision for the navigation fixes is the length of the submersible (7.5 m). Water samples could be collected directly over the faunal clusters, while sediment cores had to be taken next to the clusters. This suggests that examining spatial distributions at a scale of less than the submersible's length is unrealistic with these data. A second source of possible error is the occurrence of non-circular clusters. Examination of 35-mm photographs shows that tube worm bushes consistently have a circular outline. However, mussel beds are often irregular in shape; so a circular area is an approximation of their true areas. Despite these drawbacks, the methods were consistently applied and should provide a reliable means for comparing the relative abundance of seep organisms at locations within the surveyed area. If reliable information becomes available on the size distribution of seep mussels and tube worms and on their average densities within clusters, these methods could provide estimates of their biomass within a surveyed area.

The methane-dependent physiology of the seep mussels (Childress et al., 1986; Fisher et al., 1987) suggests that their fine-scale distribution within a seep community is determined by the availability of methane. Positive correlation between the abundance of mussels and the concentration of methane in the near-bottom water (Fig. 7-4A) is consistent with this expectation. The strength of the correlation decreased with distance from the sampling sites, which could indicate that discharges of the methane that nourished individual mussel beds are discrete rather than perfusive. This would be consistent with the variability of methane concentrations in bottom-water samples (Table 7-1). The occurrence of mussel beds is distinctly clustered within the surveyed area (Fig. 7-5B).

Similarly, the fine-scale distribution of Lamellibrachia sp. and the escarpiid should be controlled by the sources of reduced sulfur compounds (Brooks et al., 1987a). Positive correlation between the concentration of

EOM (and hence sulfide) in the sediments and the abundance of tube worms (Fig. 7-4B) is therefore reasonable because the seepage may either contain sulfides or enhance anoxia through microbial depletion of oxygen during degradation. The correlation is non-significant at distances greater than 7.5 m from the sampling sites. This suggests that the sources of EOM that provide sulfides for individual tube worm clusters are discontinuous. Unlike mussel beds, tube worm bushes are widely scattered across the top and upper flanks of the diapir (Fig. 7-5A). Note that the mussels/CH_4 relationship was also non-significant at >7.5 m.

If oily sediments provide a sulfide source, our observations do not show how Lamellibrachia sp. and the escarpiid at Bush Hill are able to make use of this source. In the hydrothermal vent vestimentiferan, Riftia pachyptila, sulfide uptake is via the branchial tentacles of the obturaculum (Felbeck et al., 1981; Arp and Childress, 1981), and sulfide concentrations in the water around clusters of R. pachyptila are in the order of 100 to 350 micromolar (Corliss et al., 1979; Arp et al., 1985; Hessler et al., 1985). These sulfide concentrations, however, are substantially higher than the levels measured at Bush Hill. The sulfide concentrations in our water samples taken away from the bottom are all below 3 micromolar The highest sulfide concentration (11 micromolar) was observed in a near-bottom sample, a stratum at least 100 cm beneath the level of the plumes in the larger bush-formations (Fig. 7-3D).

For these tube worms to utilize sulfides associated with oil-stained sediments, it is necessary to evoke either episodic releases of sulfides that were undetected by our sampling, utilization of trace levels of sulfides by these species, or direct absorbtion of sulfides through those portions of the tubes that are buried in a sulfide-rich substrate. This latter assumption would be consistent with the Brooks et al. (1987a) observation of substantially "dead" radio-carbon in Lamellibrachia sp. tissue, suggesting that the source of dissolved inorganic carbon is the sediments (old), not the ambient bottom water (recent).

The relative abundances of tube worms (Fig. 7-6A) and mussels (Fig. 7-6B) provide a description of their coarse-scale distribution within the surveyed area. The abundance of mussels shows a node centered at the top of the diapir and just to the east of a major fault (Fig. 7-5B). The occurrence of mussels away from this peak is limited. Tube-worm abundance peaks at a slightly greater distance from the fault (Fig. 7-5A) and is dispersed down the flanks of the diapir. Within the surveyed area, mussels are more aggregated and comparatively less abundant than tube worms. Neither organism is evident to the west of the fault. Secondary nodes of abundance for both organisms are located on the secondary peak of the diapir, which is at the eastern edge of the wiped-out area (Fig. 7-1). Abundance of neither organism is significantly correlated to carbonate carbon in the sediments, which is an indicator of historic seepage. Behrens (1988) attributes the seepage of gas and oil to activity within faults. Sibuet et al. (1988) observed correlation between aggregations of Calyptogena sp. and the locations of faults in a deep-sea subduction zone off Japan.

The coarse-scale distribution of tube worms and seep mussels might therefore be explained by the present-day pattern of seepage through the fault. It is reasonable that liquid-phase oil would be more widely dispersed by diffusion through porous sediments than gaseous-phase methane would be because methane will escape into the water column. However, we know of no geological study that compares the horizontal distribution of seepage at the level of resolution that is evident in the faunal distributions.

Constraints on the distribution of mussels and tube worms, other than the availability of nutrients, are not known in detail. The diapir is a heterogeneous environment, with a variety of substrates, current patterns and topographic slopes. The potential for predation by fish and crabs is significant. Differential settling rates for seep organisms could also affect their distribution on the diapir. These organisms are, however, dependent on nutrients that are only available in very restricted areas on the slope. The distribution patterns of seep mussels and tube worms reflect those of methane and EOM, respectively. The contrast between the distribution of mussels and tube worms suggests that these patterns can be appraised at two scales of variation. In the vicinity of chemical sampling points (15 to 30 m scale) sources of both methane and EOM are discrete and discontinuous. Within the surveyed area (100 to 500 m scale), both compounds are most abundant on the top of the diapir near a major subsurface fault. From the evidence of the distribution patterns of mussels and tube worms, respectively, methane sources are relatively more restricted; EOM sources are relatively more dispersed.

Methane and oil are both seeping to the surface from a deep (2,000-3,000 m) reservoir (Kennicutt et al., 1988). The oil production platform being established in the Green Canyon 184 lease block will exploit this same reservoir. Observations in terrestrial oil fields have shown that surface hydrocarbon seepage decreases or disappears after prolonged oil production (Horvitz, 1972). Oil production from the Green Canyon 184 reservoir may have a similar result. The future impact of nearby oil production on the Bush Hill chemosynthetic community is therefore an open question.

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CHAPTER 8. CONCEPTUAL MODEL OF THE CONTINENTAL SLOPE ECOSYSTEM OF THE NORTHERN GULF OF MEXICO

B.J. Gallaway and W.E. Pequegnat

INTRODUCTION

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.

GENERAL CONCEPTUAL MODEL

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 ecosytem 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), the solar energy that primarily drives this system is fixed into chemical energy by the phytoplankton in the euphotic zone (Fig. 8-1). 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. 8-1) 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. 8-1).

Rates of average productivity for the open Gulf of Mexico (55 g C/m^2/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. 8-1) 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, 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. 8-1), as well as communicate directly with higher mid-water animals above the boundary layer (Fig. 8-1). 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. 8-1; 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

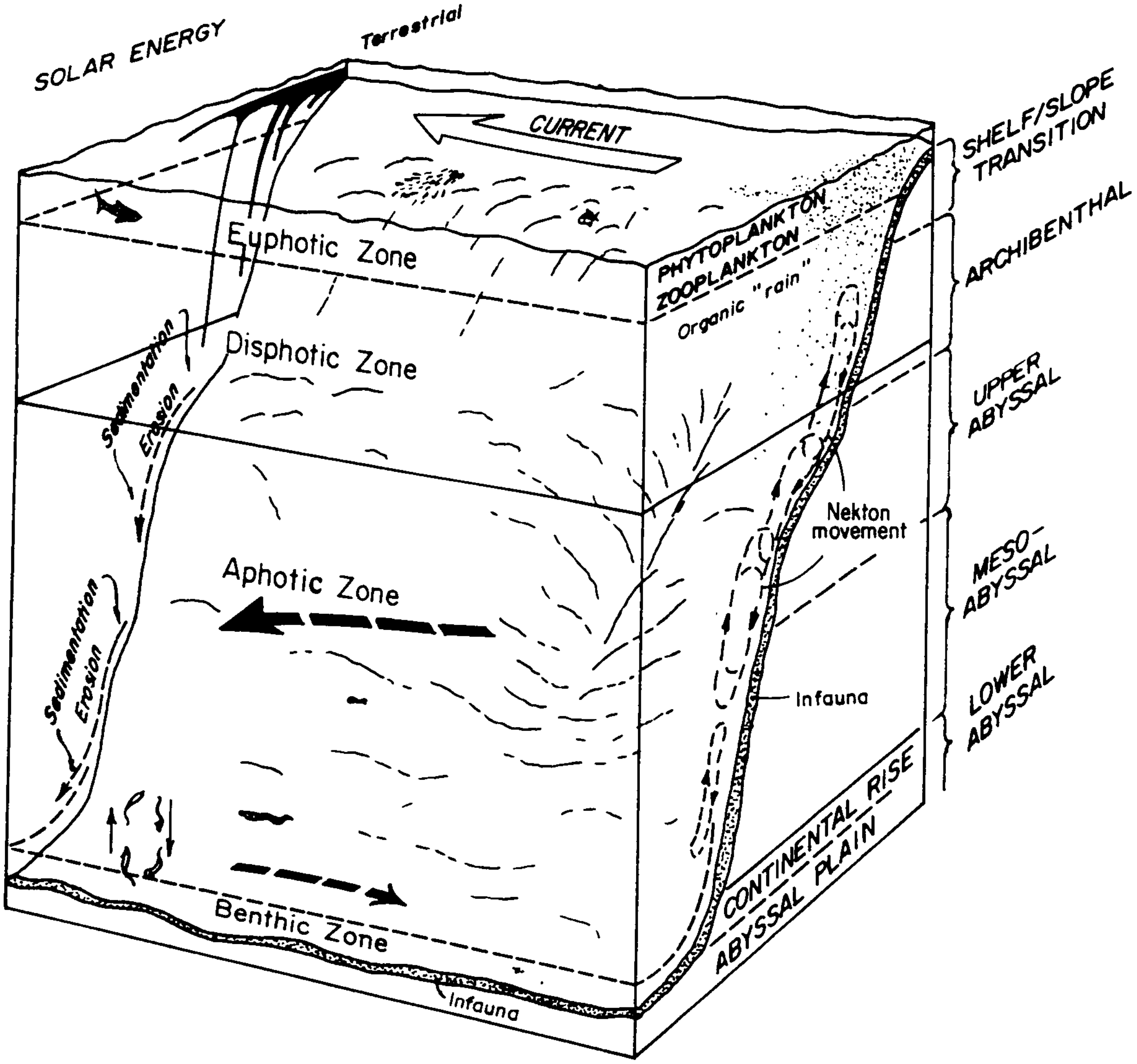

Figure 8-1. Conceptual model of the continental slope ecosystem, petroleum seep communities excepted.

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 STOCK

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. 8-2).

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. 8-2). 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 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.

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. 8-2). The meiofaunal and macrofaunal data suggest enhanced standing stocks for samples known to have been taken in the vicinity of petroleum seeps. Standing stocks of megafauna were

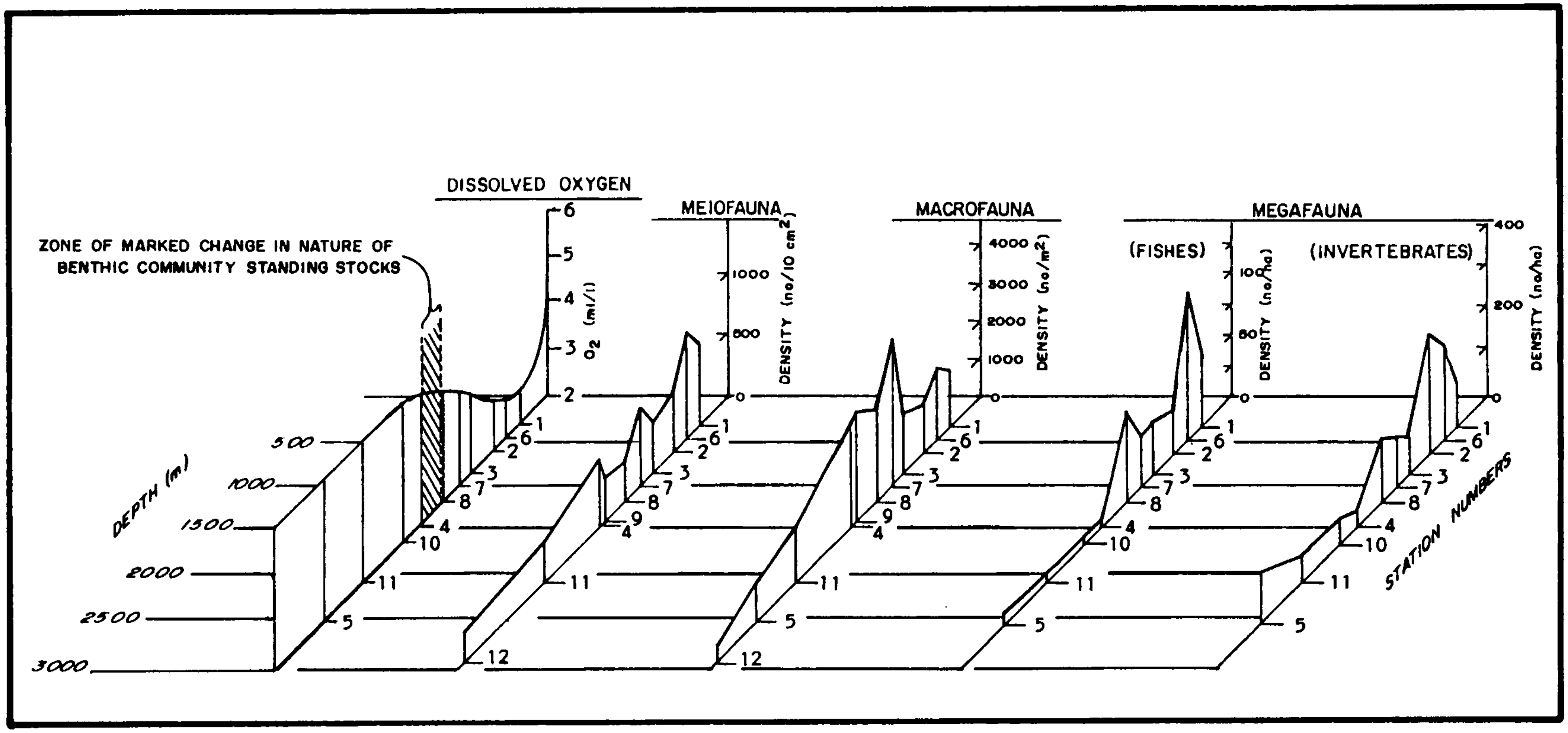

Figure 8-2. Dissolved oxygen levels as compared to the standing stocks of meiofauna, macrofauna and megafauna (fishes and invertebrates) on the central transect, fall 1984.

highest at depths between 500 and 800 m, a zone where petroleum seep communities are most prevalent. 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. 8-1) 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) 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 (Fig. 8-3). Various chemoautotrophic bacteria are the primary producers in the seep food web, which is otherwise characterized by the presence of rich

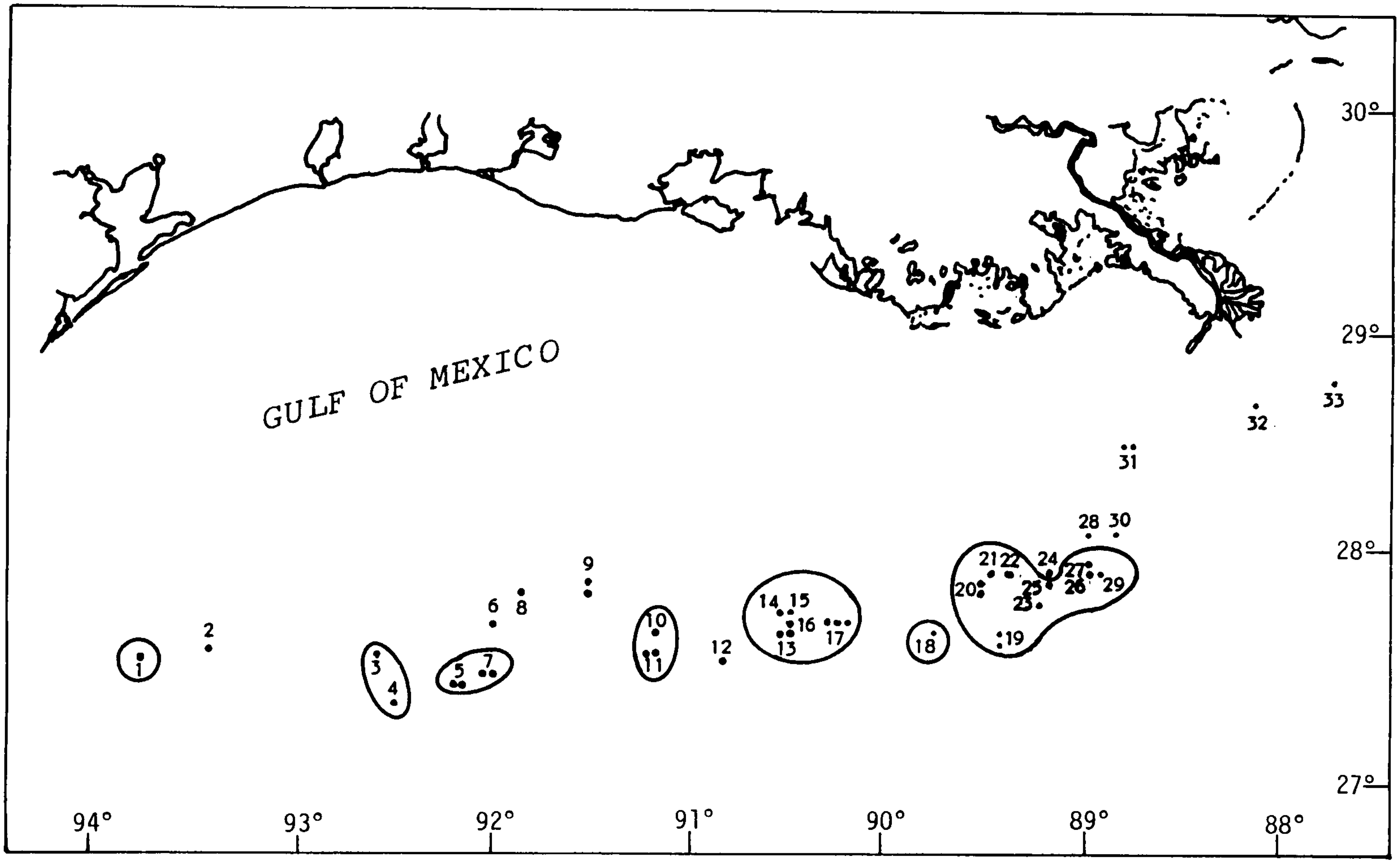

Figure 8-3. Locations of the 33 study sites on the Louisiana/upper Texas continental slope. Thirty-nine trawls were performed during R/V Gyre Cruise 86-G-1/2 in water depths between 180 and 900 m. Sites where chemosynthetic communities were observed are circled.

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, enviromental 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 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 beteween 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. In the eastern region, however, brine-seep communities have been discovered at the base of the Florida escarpment, south of our study area.

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 (western Gulf) and brine (eastern Gulf) seep communities. 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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