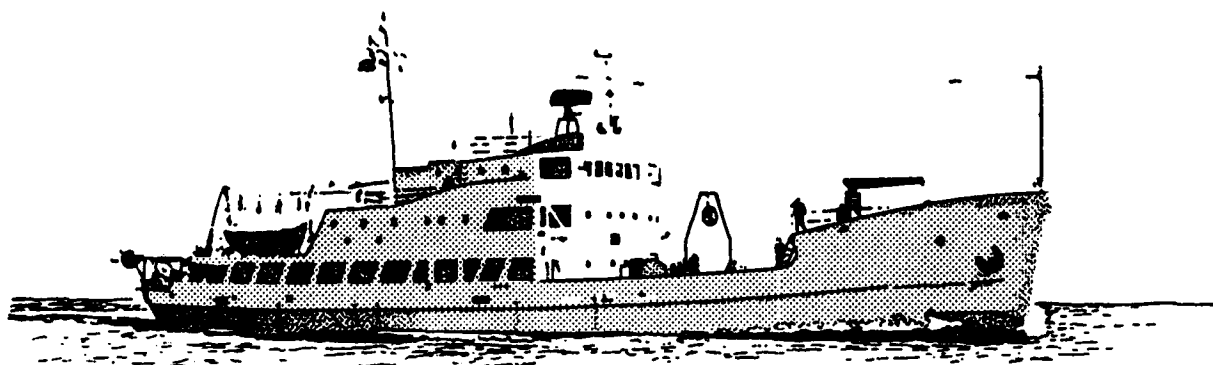EXECUTIVE SUMMARY

THE ECOLOGICAL COMMUNITIES
OF THE CONTINENTAL SLOPE AND ADJACENT REGIMES
OF THE NORTHERN GULF OF MEXICO

BY

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R/V ALAMINOS 1963-1974

UNITED STATES
DEPARTMENT OF THE INTERIOR
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PART I. INTRODUCTION

NATURE OF THE STUDY

GENERAL

This report on the deep-water system of the Gulf of Mexico is based largely upon collections of the macroinfauna and the megaepifauna made under the supervision of the senior author in the period 1964-1973. All of the field studies including investigations of chemical, geological, and physical oceanographic phenomena, were pursued aboard Texas A&M University's ship the R/V ALAMINOS, which was dedicated on 3 December 1963.

In the present study the deep Gulf of Mexico encompasses the area having the following boundaries:

    a) north: east-west extension of the 150-m isobath
    b) south: 25th parallel of N latitude
    c) east: north-south line running southward from the 150-m isobath along the east wall of DeSoto Canyon to an intersection with the 25th parallel over the Mississippi Fan
    d) west: intersection of the 150-m isobath with the 25th parallel off Brownsville, Texas.

This area includes three major canyons, viz., DeSoto, Mississippi Trough, and Alaminos; much of the Mississippi Fan, which is the largest feature of its kind in the world ocean; and the deepest part of the Sigsbee Abyssal Plain, noted for being the flatest expanse of ocean floor known. A total of 264 oceanographic stations were mounted within the above bathymetric (150-3850 m) and geographic limits.

OBJECTIVES AND RELATED TASKS

A comprehensive project of this type can have many objectives but the number can be reduced to a manageable number if a reasonable distinction is made between objectives and tasks undertaken to accomplish the objectives. The principal objectives are:

1. To describe and discuss the ecological nature and distribution of the macroepibenthic assemblages that occur in the northern Gulf of Mexico.

2. To provide a photographic documentation of the nature of the benthic environment within which these assemblages exist, including portrayal of some constituent species that exist within biobathymetric zones.

3. After analyzing available data generated by the present study and found in extant literature, to describe important gaps in our knowledge of the area, its assemblages, and functioning of the deep ecosystem and then suggest study approaches to reduce these gaps.

4. Finally attempts will be made to provide a reasonable assessment of the significance of the potential impacts on the deep

macrobenthic communities of oil and gas exploration and production.

STUDY METHODS

SAMPLING GEAR AND THEIR USE

Although five types of dredges were used in one phase or another of the study, the skimmer having a collecting gape of 3 m was employed far more than any other. Another device in consistent use was a modified otter trawl having an overall gape of 20 m and 1 inch stretch mesh in the lined cod end. In order to work satisfactorily the doors were made of metal and weighed about 250 lbs each. These devices were used to collect primarily the macro- and megaepifauna. A Campbell grab covering 0.62 m^2 and a standard Phleger corer were used to collect the macroinfauna and sediment samples, respectively.

CAMERAS

Two types of cameras were used to obtain the photographic record: a 35 mm Alpine Geophysical Associates, Model 314 was used throughout the sampling period; and a 70 mm Shipek Deep-Sea Camera manufactured by Hydro Products (Model PC-700) was used from 1969 through 1973.

PROCESSING OF SAMPLES

All samples were sorted and preserved aboard ship and ultimately sent to taxonomic specialists for species identification. The bulk of the identified specimens have been deposited in the Systematic Collection of Marine Organisms established by Dr. L.H. Pequegnat at Texas A&M University. All type specimens of new species are located in the U.S. National Museum of Natural History.

PART II. SOME OCEANOGRAPHIC ASPECTS OF THE NORTHERN GULF

DEEP BENTHIC ECOSYSTEMS: SPECIES AND THEIR DISTRIBUTIONS

THE INVERTEBRATE BENTHOS

DEFINITIONS

Most benthic studies deal with one or more of three size categories: meiofauna, ranging between 63 and 500 um, macrofauna that have a lower size of about 500 um and range up to an indefinite point that they share with the megafauna. Originally the term megafauna was used to designate animals (epifaunal) that were large enough to be photographed in their natural habitat. Rowe and Haedrich (1979) state essentially the same thing, "Megafauna, defined roughly as those organisms that are big enough to be easily visible,———." The most important megafaunal groups in the deep sea are the echinoderms, crustaceans, and demersal fishes. It is, therefore, these groups that are featured in this section. Finally, we shall discuss two important infaunal groups, viz., most of the polychaete worms and bivalve mollusks.

EPIFAUNA OF SOFT BOTTOMS

Echinodermata

One hundred eighty-seven species of echinoderms were collected from the deep Gulf of Mexico extending from the shelf break to the abyss. But, as emphasized

above, sampling was carried out principally in the clastic sediments from De-Soto Canyon to the region south of Brownsville, Texas. Only on a few occasions was sampling carried out in the carbonate sediments that stretch eastward from DeSoto Canyon. Asteroids accounted for about one-third of the total, followed by ophiuroids, holothurians, echinoids, and crinoids (Table 2). Approximately half of the echinoderm species (51%) extended their bathymetric range below the 1000-m isobath, but as one might expect it is the sea cucumbers that predominate in the deep Gulf. Some 73 percent of the holothurian species occur below 1000 m and, indeed, the median depth above and below which equal numbers of species were collected is 2300 m, a depth almost twice that of the asteroids and ophiuroids and six times that of the echinoids and crinoids. These distributional patterns reflect not only the well known relationship between solubilities of carbonates and echinoderm skeletons but also significant differences in food sources and feeding strategies.

Table 2. Number of species collected in echinoderm classes and their bathymetric distribution with median depth.

	No. of Species	% of all echinoderm spp.	No. species below 1000 m	% of group below 1000 m	Median depth (m)
Asteroidea	61	33	34	56	1050
Ophiuroidea	43	23	23	53	1200
Holothuroidea	37	20	27	73	2300
Echinoidea	31	17	8	26	450
Crinoidea	14	7	3	21	400
Total	186	100	95		$\bar{x}$ 1080

Interestingly we were fortunate while aboard the R/V ALAMINOS to have collected in the Gulf of Mexico both the largest and the smallest known asteroids in the world, namely, Midgardia xandaros and Poranisca lepida, respectively.

Asteroidea (Starfish)

Sixty-one species of starfishes were collected and identified in this study. Thirty-four or 56% of these species occur below 1000 m depth. In fact the median depth for all asteroid species from the shelf break onto the abyssal plain is 1050 m in the middle section of the continental slope. The distribution of asteroid species within each bathymetric zone clearly illustrates the greater abundance of asteroids about the median depth. The two must numerically abundant asteroids in the northern Gulf, viz., Nymphaster arenatus and Plutonaster intermedius attain peak populations near the median isobath. The 11 numerically dominant asteroids have peak populations ranging in depth from 150 m for Astropecten nitidus to 3250 m for Dytaster insignis and Litonotaster intermedius. Dytaster exhibits the largest bathymetric range, some 3000 plus m, from 800 m in DeSoto Canyon to 3850 m in the Sigsbee Deep. Incidentally this is the only asteroid collected at this the greatest known depth in the Gulf.

There are some major differences in the deep asteroid fauna between the east and west Gulf. For instance, 30 of the total of 61 asteroid species are found

only west of 90°W longtitude, whereas only 10 are limited to the east. More-over, two of the numerical dominants are limited to the west (Cheiraster mira-bilis and Benthopecten simplex), whereas only one, Astropecten nitidus, is limited to the east. If we assume that the asteroids are either at or only one trophic level removed from the top of the food chain, then it follows that so far as the Gulf is concerned the western portion must be quite productive to sustain so many top predators. Stomach analyses performed on Gulf asteroids revealed them to have fed upon sponges, bivalves, gastropods, cumaceans, echi-noids, sargassum, and tar (Pequegnat, 1979). During the heavy rains of summer in Mexico huge quantities of terrestrial vegetation (riparian and aquatic) are rafted into the Gulf and are then carried northward into the region of this study by the current regime that brought IXTOC oil to the Texas coast. When the vegetation sinks to the bottom it gives rise to detritus that sustains some of the species that comprise the food of asteroids.

Echinoidea (Sea Urchins)

Thirty-one species of echinoids were collected from the offshelf seabed of the northern Gulf. Eight of these species (26%) occur below the 1000-m isobath down to 3300 m; however, the median depth of echinoids from the shelf break to the abyss is only 450 m (Table 2). This shallower distribution of echinoids is outlined, with over half of the species having maximum populations in the Shelf/Slope Transition Zone. Within this bathymetric range the shallow end of some 200 m is dominated by the Brissopsis complex of species, whereas Phormo-soma placenta and Plesiodiadema antillarum predominate in the depth range of 700 to 900 m. It is interesting that the highly calcified Brissopsis has a narrow depth range from 150-400 m, whereas both Phormosoma and Plesiodiadema have depth ranges of 1950 and 1550 m, respectively. The lower depth limit for both of the latter species is around the 2100-2300 m isobath, which happens to mark the upper limit of the Sigsbee Escarpment of the Lower Continental Slope. It is noteworthy that Phormosoma, although large is little calcified, whereas Plesiodiadema is very small and not well calcified. The only echinoids that penetrate deeper than 2300 m are both very small. In addition to the problem of calcification, the distribution of food resources probably accounts for the observed distribution patterns. Brissopsis is a scavenger that feeds to a large extent on plant detritus, which is more plentiful on the outer continen-tal shelf and upper slope than deeper. Whereas Plesiodiadema scavenges plant materials, Phormosoma engulfs sediments (Booker, 1971), as do the small deep-living echinoids. Thus, there is little if any competition between the three echinoid dominants.

Ophiuroidea (Serpent Stars)

Forty-three species of ophiuroids were collected and identified in this study. At least twice as many species occur in the Archibenthal Zone than in any other zone, but 23 or 53% of these species occur at or below the 1000-m isobath. The median depth of distribution of these species is about 1200 m (Table 2), which is somewhat deeper than that of the asteroids but only half that of the holo-thurians. It is, however, about three times the median depth distribution of both the crinoids and echinoids. We note also that the numerical dominants reach their peak populations in quite deep water, ranging from 600 to 3250 m. In fact the most abundant deep-water ophiuroid obtained in this study (Ophio-musium planum) attains peak populations on the Continental Rise at 3250 m depth.

About twice as many ophiuroid species are limited to the western Gulf (23) as to the eastern half (12). Very little is known about the food habits of these ophiuroids; however, at least two of the numerical dominants have contained detritus-feeding palaeotaxodont bivalves. These bivalves are abundant in deep water of the western Gulf.

Holothuroidea (Sea Cucumbers)

Thirty-eight species of sea cucumbers were collected and identified in this study. Twenty-seven (73%) of these species occur below the 1000-m isobath (Table 2), and as many as 10 species occur in the Lower Abyssal Zone, five of these having maximum populations there. Even more indicative of the predilection of this group for deep-water is the fact that the median depth of their distribution is 2300 m. Moreover, eight of the 11 numerical dominants reach peak populations at depths 1000 m or over. In fact, the bathymetric range for peak populations is 900 to 3700 m, which differs markedly from that of the asteroids. Although Benthodytes typica is the most abundant holothurian in the deep Gulf, reaching peak populations at 3250 m, it is certainly outranked in biomass by the much larger Mesothuria lactea. Holothurians are well suited for deep-sea life with deposit-feeding habits and minimal development of carbonate skeletal components.

Crinoidea (Sea Lilies)

Few crinoids occur in the Gulf, compared to the other classes of echinoderms, and very few are part of the deep Gulf fauna. Only four species occur below 1000 m and none occur deeper than the Upper Abyssal Zone. Perhaps the most important reason for this paucity of species is the typical suspension-feeding mode of the sedentary types.

Crustacea

One hundred ninety-two species of benthic crustaceans were collected by the ALAMINOS in the offshelf waters of the Gulf. Although brachyuran crabs yielded the most species (Table 13), they are for the most part confined to the shelf and upper slope. In fact, the median depth for the 46 species collected is only 300 m. The number of individuals of brachyurans also show highest levels in the shallower depths. Two other diverse groups are the caridean shrimps with 33 species and the galatheid anomurans with 30 species. Emphasis must be placed on the fact that some groups such as the Gammaridea and Isopoda are not uniformly represented in the present collection in part because of their generally small size. Also, the majority of our collection of isopods was sent to Dr. Robert Menzies for identification, but no one has been able to find the specimens after his untimely death.

Approximately one-third (35%) of the crustacean species extend their bathymetric range below the 1000-m isobath. Among these it is the penaeid natantians, munidopsid galatheids, and polychelids that as groups predominate in the deep Gulf. Although the diversity of carideans is markedly greater than that of the penaeids down to 1000 m, below that point the latter supersedes the carideans.

Cirripedia (Barnacles)

The cirripedes were not a particularly abundant group among the Crustacea. Nineteen species are listed for the Gulf; roughly half of these occur in waters

deeper than 1000 m. More species occur in the Archibenthal Zone than in any other zone. Both of the two most abundant species, Arcoscalpellum regina and Verruca sp. 1, had peak populations in Horizon B of the Archibenthal Zone. A. regina, a large, leathery gooseneck barnacle (Family Scalpellidae) exhibits a broad geographic distribution in the Gulf, although it seems confined to the upper continental slope.

Table 13. Number of species collected in crustacean taxa with their bathymetric distribution including median depth.

	No. of species	% of all crustacean spp.	No. species below 1000 m	% of group below 1000 m	Median depth (m)
Penaeidea	22	17	14	64	1250
Caridea	33	17	16	48	1000
Anomura					
Paguridae, etc.	24	13	4	17	
Galatheidae					
Munida	8	4	1	13	450
Munidopsis	22	11	13	59	1150
Macrura					
Polychelidae	5	3	4	80	1000
Nephropidae	4	2	2	50	650
Brachyura	46	24	4	9	300
Tanaidacea	8	4	3	38	NA
Other Macrura	4	2	0	0	NA
Total	192	100	68		

Tanaidacea

Eight macrofaunal species of tanaids were collected in the offshelf seabed. As can be seen, all of these occurred in deep water from the middle slope onto the continental rise. All of the species are new and, except for one, belong to the genus Apseudes or Neotanais.

Amphipoda

Eleven species of gammarid amphipods were collected in grab samples. Among them were two new genera and several new species. Most were represented by only one or two individuals.

Isopoda

As noted elsewhere most of our isopod collection was lost by a taxonomic specialist. However, the most unique and important megafaunal species of the group is the giant cirolanid Bathynomus giganteus, which occurs widely in the Gulf from 400 to 2250 m depth with a peak population around the 1200-m isobath. The largest of our specimens has an overall length of about 32 cm. It is confined to the continental slope throughout its life cycle. Being a peracaridean, it broods its young. The smallest specimens in our collection measure 5.5 and 5.6 cm in length. Both were collected in July at depths ranging between 585 and 675 m.

Stomatopoda

Only two species of stomatopods were collected in this study. Both probably occur on the shelf since we took them from depths ranging from 150 to 250 m.

Pycnogonida

Only one megafaunal species of pycnogonid was obtained in this study at a depth of 1000 m.

Natantia: Penaeidea

Twenty-two species of benthonic penaeid shrimps occur in the offshelf waters of the Gulf of Mexico. Fourteen (64%) of these species occur below the 1000-m isobath (Table 13). The distribution of penaeid species within each bathymetric zone illustrates the greater abundance of penaeid species in the abyssal zones. Although the numerical dominant in the group, Penaeopsis serrata, has its peak populations along the 300-m isobath, three other dominants peak below 3000 m and well over half the species peak below 1000 m. For instance, the second most abundant penaeid, Benthesicymus bartletti, is most abundant along the 1050-m isobath from which it extends down to 2250 m. The most abundant abyssal penaeid is Benthesicymus cereus/iridescens, which peaks at 3250 m on the continental rise but extends down to and across the abyssal plain to 3850 m where it is confined to the western Gulf.

There are major differences in the geographic distribution of the penaeids. For instance, eight of the 22 species are found only in the western Gulf, and although some species such as Hymenopenaeus debilis are much more abundant in the east around DeSoto Canyon than west, none is limited to the eastern Gulf. As might be expected, most of those species that are limited to the west were taken only in small numbers and usually occurred in the southern Gulf as well. The genus Hymenopenaeus exhibited the most species (4) of the deep penaeid genera. But the four attained peak populations at different depths from H. tropicalis at 150 m through H. robustus and H. debilis at 500 and 600 m, respectively, to H. aphoticus at 2100 m. Both the genera Plesiopenaeus and Benthesicymus are represented by three species which have marked bathymetric separations. It appears that the deep benthonic penaeids can be divided into three bathymetric groups. The first group of 10 species finds its center of distribution on the upper slope. The numerical dominants here are Penaeopsis serrata followed by Parapenaeus longirostris. The second group of five species occupies the middle portion of the slope where the numerical dominant is Benthesicymus bartletti. The third group has those seven species that reach maximum numbers on the lower slope and rise where the predominant species is Benthesicymus cereus/ iridescens.

Natantia: Caridea

Thirty-three species of benthonic caridean shrimps were collected in the deep Gulf. Sixteen (48%) of these occur below the 1000-m isobath (Table 13). The distribution of caridean species within each bathymetric zone points out their greater abundances of species in the Archibenthal Zone compared to the shallower or deeper zones in contrast to the penaeid shrimp, whose greatest species abundance is in the deeper zones. It is interesting that the top five of the

numerical dominants belong to only two genera, Nematocarcinus and Glypho-crangon. Moreover, the top two species, viz., Nematocarcinus rotundus and Glyphocrangon nobilis, attain peak populations along the same isobath. Since they occur in the same geographic region, it is apparent that there must be a distinct ecological separation. For one thing, Glyphocrangon is known to be a burrower, whereas it is suspected that Nematocarcinus is not.

Macrura

The macruran decapod crustaceans are represented in the offshelf waters of the Gulf by 12 species of which the polychelids and nephropids are the most impor-tant. Among the polychelids or flatback lobsterettes Stereomastis sculpta is by far the most abundant and Willemoesia forceps, represented in our collection by a single individual, is the rarest. Their habits as adults are almost entirely unknown. In fact, no one to our knowledge has photographed any one of the group. Yet Stereomastis was taken at 74 stations in the Gulf. It is known that they have a deep-sea pelagic larva known as the eryonid. In some ways the genus Willemoesia reminds one of a neotonic eryonid. In general the poly-chelids live deeper than the nephropids. Although the polychelids live deeper than the nephropids. Although the nephropids or deep-sea lobsters are not as common as the polychelids, we have bottom photographs of two of the four spe-cies in our collection. Moreover, it is quite likely that the nephropids live in burrows.

The remaining macrurans occur on the upper slope where their burrowing habits preclude capture by ordinary deep-sea collecting gear.

Anomura

The Anomura are represented in the deep Gulf by the following five families: the Galatheidae with the genera Munida and Munidopsis; the Paguridae represent-ed by numerous species, some of which are undescribed; the Lithodidae with the crablike Lithodes agassizii; the Chirostylidae with two species, Gastroptychus spinifer and Uroptychus nitidus; and finally the Porcellanidae which has the species Porcellana sigsbeiana that ranges from the shelf down to 950 m depth.

The vertical distribution of the galatheids is quite interesting. Note that all species of Munida except one occur no deeper than 750 m. Munida micro-phthalma has a narrow bathymetric range from 1100 to 1350 m depth where it is rarely collected. Munidopsis on the other hand is represented by three times as many species as Munida and it ranges down over the continental rise to a depth of 3300 m. Interestingly three of the numerically dominant species of galatheids belong to the genus Munida and only one of the deep-living Munidop-sis (below 3000 m) is even reasonably abundant (M. bermudezi at 3300 m).

The Paguridae of the Gulf are a very complex group and their systematics is only now being pursued aggressively. Not only are several new species to be described from our collection by specialists, but individuals now assigned to Parapagurus will very likely be split into at least two and possibly more spe-cies.

Lithodes agassizii at first glance resembles a majid brachyuran crab but its anomuran relationship is belied by the presence of only four pairs of walking

legs - the fifth pair being carried forward along the carapace. It is, of course, closely related to the Alaska King Crab.

Uroptychus nitidus has a very restricted habitat living as it does only on the relatively small gorgonian corals Chrysogorgia elegans down to depths of 1000 m, and Acanella arbuscula from there to 1350 m.

The family Porcellanidae is comprised primarily of species that live in shallow water, including the intertidal zone. As a result, only one species, Porcellana sigsbeiana, is found in offshelf waters, but it ranges onto the slope from the continental shelf down to 950 m depth. However, only juveniles are found at the greater depths. Since the maximum populations are found around 200 m, it is suspected that these juveniles will move up the slope as they mature.

Brachyura

It is clear that the brachyuran crabs are a relatively shallow group with only four species occurring below 1000 m. Note also that 38 of the 46 species present in offshelf waters reach maximum populations no deeper than 550 m, which is well up on the continental slope. Moreover, all of the four species except Geryon quinquedens that occur below 1000 m are very small and delicate indicating a very specialized mode of feeding. Actually the Geryon that were collected below 1500 m were only small juveniles. The distribution of brachyurans according to zones illustrates their greater abundance in the shallower zones.

Considering the trophic-level position of the Brachyura, the fact that their diversity and numbers of individuals decline drastically below 400 m (the average depth of maximum population is 390 m) seems to support the concept that this relatively shallow area is a very productive part of the Gulf. In addition, the similarity of the above with the bathymetric distribution of the bulk of asteroids and considering that both groups possess many predatory species indicate that food for carnivores must become a severe limiting factor below depths of a 900 or so meters in the Gulf.

Fish

A total of 206 demersal fish species within 47 families were collected by the R/V ALAMINOS during the deep Gulf of Mexico cruises between 1964 and 1973. Seventy-nine species ranged into waters 1000 m or more in depth while 59 species had peak populations at 1000 m or deeper.

The Macrouridae was the most speciose family represented by 30 species, followed by Ophidiidae (23), Alepocephalidae (12) and Gadidae (11) which together constitute over one-third of the total number of species (Table 31).

The family Gadidae (codfishes) is a dominant group on the upper continental slope between the shelf break and about 500 m. As expected the cods were restricted to the upper slope; no species occurred below 800 m. Urophycis cirrata and Merluccius bilinearis are the abundant codfishes in the deep Gulf. Most gadids feed on crustaceans, worms, fish, and squid, but no stomach content data are available for U. cirrata and M. bilinearis collected from deeper parts of the Gulf. All codfishes have pelagic eggs and larvae.

Table 31. Number of species collected in the fish taxa and their bathymetric distribution with median depth.

	No. of Species	% of all fish spp.	No. species below 1000 m	% of group below 1000 m	Median depth (m)
Macrouridae	30	15	19	63	850 $\pm$ 300
Ophidiidae	23	11	15	65	1750 $\pm$ 1150
Alepocephalidae	12	6	10	83	1450 $\pm$ 700
Gadidae	11	5	0	-	450 $\pm$ 150
Bothidae	9	4	0	-	200 $\pm$ 50
Rajidae	8	4	3	38	750 $\pm$ 300
Bathypteroidae	7	3	6	86	1700 $\pm$ 800
Scorpaenidae	7	3	0	-	250 $\pm$ 150
Nettastomatidae	6	3	1	17	450 $\pm$ 450
Ogcocephalidae	6	3	2	33	400 $\pm$ 450
Triglidae	6	3	0	-	250 $\pm$ 150
Congridae	6	3	0	-	550 $\pm$ 300
Other	75	37	23	31	
Total	206	100	79		$\bar{x}$ 800

Macrourids were present from the shelf to 3350 m and predominated on the slope in the Archibenthal Zone and into the Upper Abyssal Zone to about 1500 m. Five macrourids are considered dominant species among the fish catches: Bathygadus melanobranchus, Coryphaenoides mexicanus, Gadomus longifilis, Hymenocephalus italicus, and Nezumia aequalis.

Ophidiids (cusk eels and brotulas) ranged from the shelf to the deepest part of the Gulf of Mexico. The distribution of ophidiid species with depth is fairly uniform. A gradual replacement of species along the depth gradient seems to be the trend, although more species were captured from the Upper Abyssal Zone and Horizon B than in the adjacent faunal zones. Of the 23 ophidiid species collected, the two most abundant, Dicrolene intronigra and Monomitopus agassizi were dominant members of the fish catches. Their distributions and abundances are remarkably similar and they were often collected together between 700 and 1200 m.

Alepocephalids (stickheads) generally occurred deeper than the other aforementioned fish families. Only 4 species were collected from shallower than 750 m. Nearly all of the alepocephalids seem to have a center of distribution within the Upper Abyssal Zone (975-2250 m). Although alepocephalids are characteristic deep-sea fish, no species in our collections was dominant, probably because single specimens were usually captured at a station.

Another fish family which deserves mention is the Halosauridae. Only 3 species of halosaurs were collected, Aldrovandia affinis, A. gracilis, and Halosaurus guentheri, but all were abundant enough to be ranked as dominant species. H. guentheri is most abundant on the upper slope while A. affinis and A. gracilis are most abundant on the middle slope. The latter two species have very similar depth distribution but only about 20% of the stations were common to both.

The two eels Synaphobranchus oregoni and S. brevidorsalis are combined because of the difficulty of identifying the two species. Synaphobranch eels were collected from 500-2150 m at a total of 40 stations but nearly all were taken from 650-1450 m. They are commonly seen in deep-sea photographs. Synaphobranchs are evidently active predators. Stomach content analyses revealed that they feed on rather large crustaceans like polychelids. An interesting note here is that synaphobranchs in turn are fed upon by the giant isopod, Bathynomus giganteus.

Six species of Ogcocephalidae (batfishes) were collected. Four occurred in waters less than 200 m deep and two ranged onto the slope past 1000 m depth. Dibranchus atlanticus was very abundant and was most common on the upper slope to about 900 m. D. atlanticus is reported to feed on bivalves in the shallower depths of its range and more on polychaetes and small crustaceans in the deeper depths (Rayburn, 1975).

Stephanoberyx monae (Stephanoberycidae) was the only other dominant species centered in the deeper parts of the Gulf of Mexico. The remaining dominant species, Poecilopsetta beani (Pleuronectidae), Pontinus longispinus (Scorpaenidae), Pristipomoides aquilonaris (Lutjanidae), Monolene sp. (Bothidae), and the percophiids Bembrops anatirostris and B. gobioides occurred mainly within the Shelf/Slope Transition Zone (150-450 m).

THE INFAUNA

Polychaeta

One hundred thirty-seven species of polychaete worms were collected by the ALAMINOS from the shelf break to the abyss in the Northern Gulf of Mexico. These species were distributed among 11 orders and 28 families of which the Maldanidae, Ampharetidae, Sigalionidae, Onuphidae, Eunicidae, and Polyodontidae were the most speciose. It is interesting to note that the leading four families belong to different orders.

Mollusca

Bivalvia

The list of deep Gulf of Mexico bivalves collected by the R/V ALAMINOS is somewhat incomplete due to an unfortunate loss of specimens during shipment to the taxonomic specialist. A total of 73 species among 18 families are listed. Among these, the palaeotaxodont families Malletiidae, Nuculanidae, and Nuculidae, and the family Propeamussiidae are complete. The ensuing discussion will therefore be biased toward data from these four families. Such a restricted discussion is partly justified since the palaeotaxodontids, at least, are the most abundant bivalve group in the deep Gulf below 500 m.

The glass scallops, Propeamussium sp. A and Propeamussium sp. C were the two most abundant bivalves collected. The Propeamussium species apparently form aggregations. Propeamussium sp. A was collected at 13 stations and an average of 54 specimens per hectare were taken at stations where the species was found, and the other members of the genus were collected in similarly high densities. The benthic skimmer and 20-m trawl were the most efficient gear in sampling the Propeamussiidae, probably because these animals are excellent swimmers and

could avoid the slower grabs and dredges. Glass scallops are carnivorous and probably feed while swimming by sucking water and small crustaceans and other small prey into the mantle. Other Propeamussium species identified from the Gulf with their entire depth ranges and including records from outside the Gulf (Thomas Waller, pers. comm., 1982)* are:

Propeamussium sp. A	677-1766 m
Propeamussium sp. B	475-1005 m
Propeamussium sp. C	715-1256 m
Propeamussium sp. D	364- 864 m
P. dalli (Smith, 1885)	183-1097 m

Dr. Waller is presently preparing a monograph of the Propeamussiidae and the Pectinidae.

The palaeotaxodont species are small, and unlike the glass scallops, were sampled poorly by the skimmer since many specimens could easily pass through the 6.4 mm mesh. Most stations with high recorded densities of palaeotaxodonts were sampled with the canvas-lined dredges.

The palaeotaxodonts, which are the dominant bivalves below 1000 m, are all infaunal deposit feeders. Propeamussium is carnivorous and its distribution is confined to the Archibenthal and Upper Abyssal Zones. These observations reflect the importance of feeding strategies among bivalves in relation to food sources and abundance in the deep Gulf.

Scaphopoda (Tusk Shells)

Seventeen species of scaphopods are listed, although live individuals of only 10 species were actually collected. Nine of these 10 species are of the genus Dentalium. Some of these scaphopods, particularly the deeper occurring species, cover quite a bathymetric span. Among the dominant species, Dentalium perlongum (live) had the greatest depth range of of 2400 m, while D. meridionale and D. callithrix had ranges of 1600 m and 1100 m, respectively. These three species were the only scaphopods of which numerous live individuals were taken. All three are upper- and mesoabyssal species having broad geographic ranges.

Scaphopods are actually infaunal burrowers. They burrow head first into the sediment and feed on microscopic organisms, usually forams, from the surrounding water and sediment. Few specifics are known of the ecology of deep-sea scaphopods (e.g. their predators or reproductive patterns), but their shells were often collected in great numbers from much shallower and deeper ranges than living individuals. Hence it would be helpful to have better knowledge of the live scaphopod distribution, in order to discern whether the abundant scaphopod shells are relicts of past populations or displaced deposits by currents, slumping, turbidity currents, and other transport processes.

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* U.S. National Museum of Natural History, Washington, D.C.

DEEP BENTHIC ECOSYSTEMS: ZONATION AND FAUNAL ASSEMBLAGES

DEFINITIONS: COMMUNITIES VERSUS FAUNAL ASSEMBLAGES

Although it is acceptable to use the terms community and faunal assemblage interchangeably, it has been the practice in this study to use assemblage as the word of choice. The essential point to keep in mind is that in a community one is dealing with populations of organisms that together make up the faunal assemblages of coincidental species that exhibit a high enough degree of recurrence in similar habitats as to preclude the conclusion that they are simply randomly assembled collections of species. Accepting these guidelines, we agree with Menzies et al., (1973) when they say "----. Obviously we accept the existence of communities of organisms in the sea as a reality ----."

At the present level of development of deep-sea biology, the acceptability of the above definitions is heightened by the fact that neither one of them puts any limit on the size of communities nor does either one require that attempts be made to include every species that lives in the habitat. This is important to marine benthic studies where species richness can be high and the availability of species-level taxonomic expertise may be low. Moreover, the shift from pelagic to benthic environments, the large range of size from meiofauna to megafauna, extreme differences in mobility of the constituent species, and changes in the texture of the seabed demand that several sampling techniques be employed if any reasonable approximation of a "complete" representation of the constituents of a marine community is to be achieved. The descriptions of the faunal assemblages in the following pages is limited to macro- and megafaunal components that for the most part were captured by means of dredges or trawls.

In the present study we have found, as have others elsewhere, that animal taxa are congregated in such a way that the fauna can be subdivided by statistical criteria into assemblages arranged in vertical depth zones. In fact, we have established five faunal zones from the shelf to the abyss in the northern Gulf. These conform reasonably closely to those established by Menzies et al., (1973) for the Northwest Atlantic Ocean. The principal difference is seen to be in the depth of the shelf break, some 246 m in the Atlantic and 125 to 150 m in the Gulf. Thus, we have established a Shelf/Slope Transition Zone above the Archibenthal Zone. Note also in Table 61 that there are reasonably distinctive subdivisions of the Archibenthal and Mesoabyssal Zones that we refer to as horizons.

DENDROGRAM CONSTRUCTION

BASIS

The dendrogram (Figure 93) was based on a clustering technique applied to faunal similarity between isobaths. Because of the bias in sampling toward the megafauna and macrofauna, only data on these larger groups (fishes, crustaceans, and echinoderms except Crinoidea) were used in the calculations.

This dendrogram is based upon the index of similarity I, which is calculated by using the value
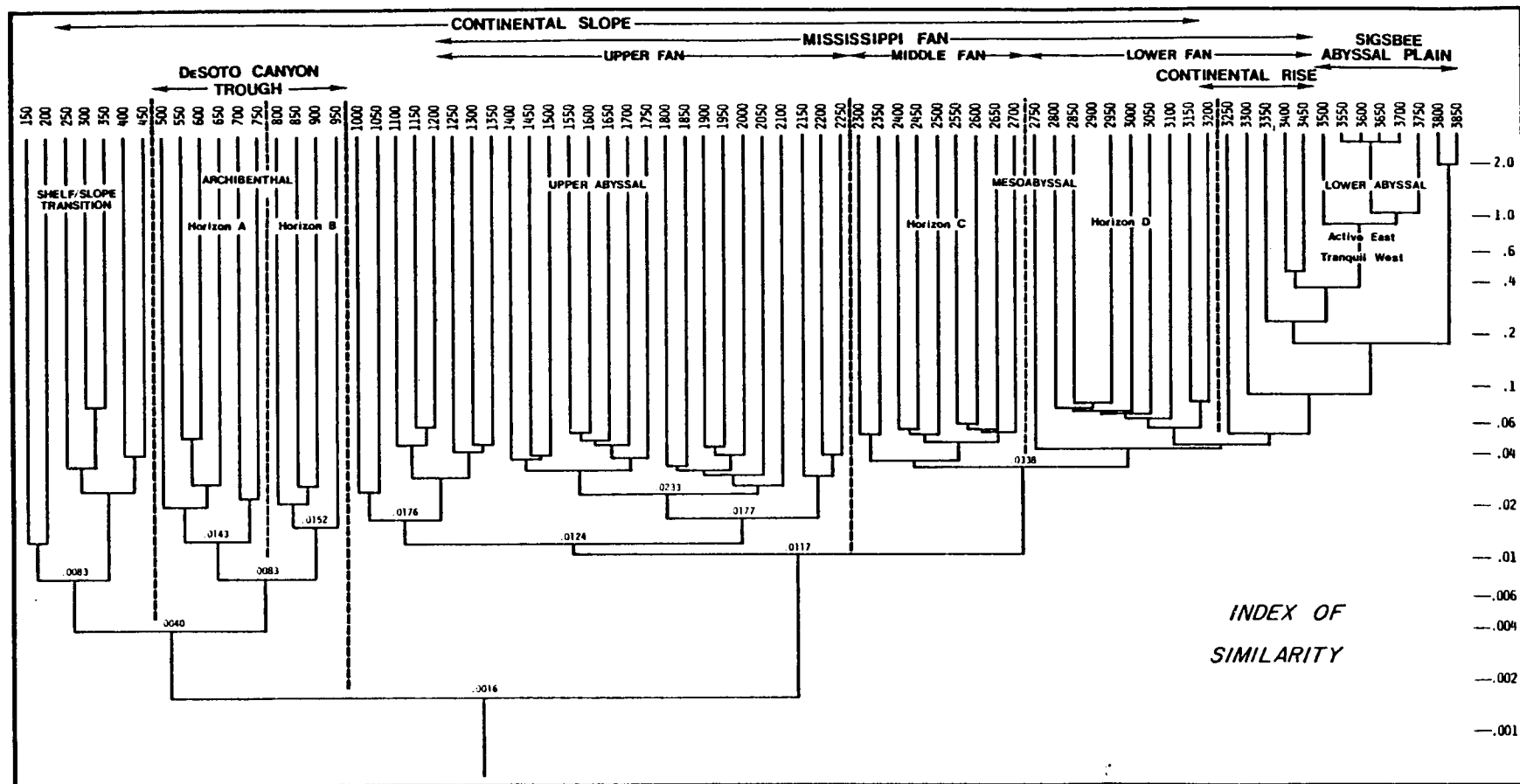
$$\frac{2j}{2ab-(a+b)j}$$

Figure 93. Dendrogram derived from calculated indices of similarity for each 50m depth interval. Faunal zones and various physiographic features of the Gulf of Mexico are indicated. The index is dimensionless and in the above example is based on all collections taken at a given isobath.

where a and b are the respective number of species in two samples and j is the number of species common to both samples.

For example, absolutely no faunal similarity exists between the 150 m and 1500 m isobaths, or between the 850 and 3800 m isobaths. Further examination of the table reveals that faunal similarity between consecutive isobaths increases with depth; that is, there is a slower rate of change in the fauna with increasing depth. This point is more dramatically reflected by construction of a dendrogram.

INTERPRETATION

The dendrogram assists one in discerning those "critical" depths along the slope, rise, and abyssal plain where apparent changes in the fauna occur. Two pronounced faunal breaks seem to occur within the upper 1000 m, one between 450 and 500 m and another at the 950-1000 m line. A less pronounced break also occurs between 750 and 800 m, the point of separation between Horizons A and B. The closely spaced separations reflect the rapid changes in fauna on the upper slope as compared to the deeper aspects of the Gulf. The dendrogram and the distribution of similarity index values appear to support the conclusion that there are four faunal assemblages on the continental slope and that two of them, viz., the Archibenthal and Mesoabyssal Zones, have less closely linked horizons. We note also that the Lower Abyssal Zone appears to incorporate most of the continental rise as well as the abyssal plain. The separation of the latter zone into Active East and Tranquil West subdivisions is based in part on the demonstrated strong bottom currents in the east and their apparent absence in the west.

The composition of the fauna on the continental slope is not wholly unique, sharing species on its upper reach with the continental shelf and on its lower part with the continental rise. Nevertheless, as a whole the slope clearly represents a distinctive biological province... Its base, however, may vary in depth from ocean to ocean. Rowe and Haedrich (1979) as well as Rex (1981) mark it at around 2000 m in the North Atlantic. In the Gulf, however, our work as well as that of Uchupi (1967) puts its upper limit at between 2900 and 3200 m (Figure 93). In either event the boundary marks a change in gradient and, proceeding seaward, by a gradual shift to greater and greater pelagic contributions to the sediments whereas Sanders and Hessler at one time (1969) believed there was a uniform and gradual replacement of species without distinct boundaries down the slope and across the rise, our work in 1976 and the present report, as well as the work of Mills (1972) and Menzies et al., (1973) show that even the mobile megafauna of the slope conform to a statistically created zonal pattern.

SPECIES COMPOSITION OF THE FAUNAL ASSEMBLAGES

As noted earlier, the present study deals with faunal assemblages, occurring in offshelf waters, but some attention must be given to their relationships with the continental shelf if for no other reason than to gain perspective on the importance of similarities and differences between shelf and offshelf assemblages. Since, however, a detailed description of the shelf assemblages was given in Pequegnat et al., (1976), only a brief mention will be made of them here.

SHELF ASSEMBLAGES

The continental shelf of the northern Gulf appears to provide ecological niches for three major groupings of organisms, some of which change habitats while completing their life-cycles or when as adults they respond by migration to very evident seasonal changes of temperature. Seaward of the estuary, we recognized three assemblages.

SLOPE, RISE, AND ABYSSAL PLAIN ASSEMBLAGES

Shelf/Slope Transition Zone (150-450 m)

Demersal fishes are certainly the hallmark of this zone. Coupling this with the rich group of asteroids and brachyurans, the majority of which are predatory, it appears that this is a very productive part of the benthic environment. Note that 90 species of demersal fishes were collected here and perhaps even of greater interest is that over two-thirds of them reach their maximum populations in the zone. Gastropod mollusks and polychaete annelids are also well represented in this zone. Noteworthy for their paucity are the sea cucumbers; contrariwise the Brissopsis group of sea-urchins are extremely abundant.

Archibenthal Zone - Horizon A (475-750 m)

Demersal fishes are abundantly represented here, but there is a reduction in total from 90 to 79 species and those with maximum population from 66 to 45. Asteroids are very well represented and the sea cucumbers have doubled in number. The Brissopsis echinoids are almost absent, but their place has been taken by the appearance of Phormosoma placenta and Plesiodiadema antillarum. Caridean shrimp species have doubled in number here, and among the galatheids the genus Munidopsis is beginning to replace Munida which predominates in the shelf areas. Gastropods and polychaetes are still very abundant.

Archibenthal Zone - Horizon B (775-950 m)

Although the total number of demersal fishes has reduced only moderately, the number of those species that reach maximum populations here is less than half that in Horizon A. This presages a major zonal change. The same is true of asteroids and echinoids. Another remarkable change is the drastic reduction in brachyuran crabs. Gastropod mollusks and polychaetes are still extremely well represented.

Upper Abyssal Zone (975-2250 m)

Even though the Upper Abyssal Zone's bathymetric range is nearly three times that of the Archibenthal Zone, its demersal ichthyofauna is only half that of the latter zone. This exponential drop in species accelerates more rapidly as one moves into the Mesoabyssal. One should note, however, that the number of demersal fishes attaining maximum populations in the Upper Abyssal is over twice that of Horizon B. This is indicative of a group uniquely adapted to this environment above the slope's escarpment. Another noteworthy point is the major increase in the number of species of large sea cucumbers. The galatheids are here represented by 11 species of the genus Munidopsis and only one of Munida. The number of brachyuran crab species continues to drop with only four present here compared with the 35 in the Shelf/Slope Transition. It is perhaps

most significant to observe that gastropod and sponge species reach peak numbers here, and polychaete numbers are still at high levels.

Mesoabyssal Zone – Horizon C (2275-2700 m)

A very sharp faunal break occurs here between the Upper Abyssal Zone and Horizon C of the Mesoabyssal Zone. For instance, the number of demersal fish species having maximum populations in the zone drops from 49 in the Upper Abyssal to 3 in Horizon C. Even if both horizons of the Mesoabyssal are included the total is only 5. Similar reductions of species are noted in other groups (maximum population species only).

Mesoabyssal Zone – Horizon D (2725-3200 m)

This horizon coincides with the lower and steep part of the continental slope in the western Gulf. There it encompasses the Sigsbee Escarpment, the lower part of which intersects with the continental rise. In the northeastern Gulf such an escarpment does not exist. Rather, it is dominated by the Mississippi Trough and the Mississippi Fan. Thus, there is a more definitive separation of faunal assemblages between Horizons C and D in the western Gulf than in the east. This seems to indicate that the degree of slope may play a significant role in species richness, possibly not directly so much as through its contribution to instability of the seabed and the frequency of slumping and related causes of turbidity flows. There are some differences in assemblage constitution between the horizons. For instance, there are nearly twice as many species of demersal fishes in C than in D and four of the species in the former are not found in D. On the other hand, among the Asteroidea there are four species that reach maximum populations in D, whereas none do in C. Other differences are readily apparent in the following analyses of the assemblages.

Lower Abyssal Zone (3225-3850 m)

If we assume that the Lower Abyssal Zone begins near the bottom of the slope's escarpments, i.e., at the intersection with the continental rise, its megafauna is depauperate but not to the degree expected by the drop in diversity observed between the Upper Abyssal and Mesoabyssal Zones. Furthermore, this zone has an interesting assemblage of benthic species that do not occur elsewhere.

We have separated the Lower Abyssal Zone into the Active East and Tranquil West subdivisions. This is intended to reflect the fact that bottom currents have been detected in the east but not in the west. Also, there is a marked difference in the sediments between the two subdivisions. Menzies et al., (1973) recognized a Lower Abyssal Tranquil Zone in the southeast Pacific Ocean (Peru). It was established at depths ranging between 5000 and 6280 m. Interestingly enough, however, the megafaunal species that they list as characteristic of this zone have counterparts in the Gulf of Mexico, to wit:

Southeast Pacific	Gulf of Mexico
Ophiomusium lymani	Ophiomusium planum
Pseudostichopus sp.	Pseudostichopus sp.
Psychropotes longicauda	Psychropotes cf. longicauda
Peniagone sp.	(Peniagone sp. present but not so deep)

It should also be pointed out that the Psychropotes longicauda and related sea cucumbers are not found in the Active East subdivisions where they could not maintain their position in moving water. In such active areas the very flat and streamlined Benthodytes typica is found.

SPECIES DIVERSITY

The present study uses the Shannon-Wiener function (H') to calculate species diversity indices for each collecting station as well as for data pooled by 50-meter depth ranges (i.e., 1200 m values would contain data from stations from 1175 m to 1225 m depths). This function is somewhat dependent upon sample size, but is affected primarily by the number of species and equitability. Thus, in comparing two stations the one with the larger number of species will have the larger index but the magnitude of the difference will depend on the evenness of distribution of individuals. Maximal diversity for a given number of species occurs when each species is represented by an equal number of individuals. This situation usually only occurs in very small samples which typically have a single individual for each of two or three species.

When corrected for patchy distribution and those stations with samples insufficient for analysis are eliminated, the species diversity indices show a general tendency to decrease with depth. Closer inspection, however indicates an initial increase of H' with depth to about 950 meters, where the highest calculated diversity (H'=5.25) occurs, followed by a gradual decrease with depth.

Analysis of variance indicates a significant difference at the 95% confidence level between diversity indices of the Shelf/Slope Transition, the Archibenthal Horizon A and Horizon B, and the Upper Abyssal and the Mesoabyssal Horizon C. No significant difference at the 95% level appears between the Archibenthal Horizon A and Horizon B, nor between the Mesoabyssal Horizon C, Horizon D, and the Lower Abyssal. Thus, based upon the distribution of species diversity, the zones appear to be divided into four distinct groups: 1) Shelf/Slope Transition, 2) Archibenthal Horizons A and B, 3) Upper Abyssal, and 4) Mesoabyssal Horizons C and D combined with the Lower Abyssal. Mean values of species diversity indices for each of these groups are 4.35, 4.81, 3.97, and 3.09 respectively.

KEY SPECIES OF THE FAUNAL ASSEMBLAGES

We know very little about the food habits of individual components of deep-sea faunal assemblages. And we have even more cursory knowledge of important food chains or webs beyond the shelf. Nevertheless, some information as to these matters has been gained for key species. Essentially they have been selected as key species on the basis of frequency of appearance in samples and numbers taken per trawl.

Fishes

Comparing the 20 most abundant fish species and their depth of peak populations in the 1976 study, which dealt with depths to 1000 m, with those in the present report dealing with the entire vertical range, we find only four are different in each list. Calculating the average depth at which the 20 species reached peak abundance, we find that in 1976 it was 800 m and abut 760 m in the present study. This indicates that demersal fish attaining significant numerical

dominance do not do so much deeper than 1500 m, which is in the Upper Abyssal Zone. The steepest decline in species diversity, however, does not occur until the Mesoabyssal Zone around the 2300-m isobath.

Invertebrates

Starfish

Unlike the situation in the fishes, the average depth of the numerical dominants increased from 625 to 1270 m. We note also that these starfish increase in numbers within the zones where the fishes begin to occur in markedly smaller numbers.

It should be noted that demersal fishes are markedly reduced in the abyss so that asteroids and, perhaps, ophiuroids are the principal predators that the mollusks must sustain.

Sea-urchins

The numerically dominant species of sea-urchins in the Gulf occur at an average depth of only 400 m. They reach peak populations either in the Shelf/Slope Transition or Archibenthal Zones. Various species of the genus Brissopsis predominate in the former, while Phormosoma placenta leads in Horizon A and Plesiodiadema antillarum in Horizon B of the Archibenthal. Moreover, there is a remarkable reduction in either the degree of skeletal calcification or size or both. Although Plesiodiadema occurs in huge numbers, it is less than one tenth the mass of Phormosoma. Only one urchin was collected in the Lower Abyssal Zone (Aceste bellidifera) and it is even smaller and more delicate than Plesiodiadema.

Sea Cucumbers

Increasing the depth parameter in the present study produced some significant changes in the numerically dominant sea cucumbers. For one thing, the average depth of the peak populations of all dominants doubled from 950 to 1900 m. For another, three of the 11 dominants reached peak populations in the Lower Abyssal Zone. Also, a higher percentage of all species of holothurians occur in the Lower Abyssal Zone than of any other invertebrate or vertebrate group. Benthodytes typica, which is the most abundant megafaunal holothurian in the Gulf, is, as are Psychropotes semperiana and Benthodytes lingua, truly deep-sea in that it generally occurs far from any observed influence of organic material derived from the land.

Some of the largest holothurians in the Gulf occur from the Upper Abyssal into the Lower Abyssal Zone. This is coherent with the fact that they are deposit-feeders. It seems likely that they utilize whatever organic material is found in the surficial sediments, including small macroinfauna and meiofauna.

Penaeid Shrimps

The key species of penaeid shrimps are easily divisable into three groups on the basis of dominance diversity and depth, viz.,

Caridean Shrimps

The key species of caridean shrimps reach maximum populations only in the uppermost three faunal zones. Although they do occur in the Mesoabyssal and Lower Abyssal Zones, they exist there only in very small numbers.

The two genera of carideans with the most species in the Gulf are Glypho-crangon, with six species, and Nematocarcinus with four. They reach peak populations at well-spaced depth invertals. Interestingly, the average depth of occurrence of the four most abundant carideans is the same as that of the penaeids, viz., 1000 m, which is just in the shallow boundary of the Upper Abyssal Zone. If, however, we tabulate the distribution of all species among zones, it is clear that the carideans tend to prefer waters less than 1000 m deep, whereas penaeids display greater species richness below that isobath.

Galatheid Crabs

The two most important genera of galatheids, namely, Munida and Munidopsis, are spaced so that competition among them is reduced. For instance, the most populous species of Munida do not occur below Horizon A of the Archibenthal Zone (750 m), whereas the most abundantly represented species of Munidopsis do not occur shallower than 750 m.

In addition to the above, we note that four species of Munidopsis are found only at depths over 3000 m.

Brachyuran Crabs

In sharp contrast with the galatheid crabs, the brachyurans are clearly shallow water forms. Only three species reach their maximum populations below 950 m (lower limit of the Archibenthal Zone) and all of these occur in exceedingly small numbers. With the exception of the Giant Red Crab (Geryon quinquedens), the brachyurans tend to decrease in size with increasing depth.

FOOD HABITS OF SELECTED KEY SPECIES

Fishes

There is currently a very limited amount of available information on the food habits of any deep-sea fish fauna. But it is typical of demersal fishes in shallower depths that their feeding habits are quite flexible. That is to say that they will devour a wide range of organisms, provided the prey are of appropriate size and consistency (Raymont, 1963). It is interesting that evidence is mounting that this applies to several deep-sea species in the Gulf as well (Bright, 1968, 1970; Rayburn, 1975). Also, Pearcy and Ambler (1974) describe some abyssal macrourid fishes off the Oregon coast as generalized feeders, utilizing mainly epifauna or pelagic animals for food. Those species that make forays from the bottom to feed upon truly pelagic prey are better called benthopelagic than demersal. Whether a fish feeds on the bottom, just above the bottom, or well up in the water column may depend upon age. For instance, young of the the macrourid Coryphaenoides armatus depend mostly on benthonic species, whereas upon attaining mature size pelagic sources predominate (Smith, 1978). Rayburn (1975) found that the principal components of the diet of some deep-sea fishes change with depth, which is another

expression of opportunistic feeding. Marshall (1966) concluded that the species of fish living near the deep-sea floor feed largely on invertebrates.

The placement and size of unpaired fins in benthopelagic fish seem also to have an influence on their feeding habits. An example of this is found in the family Macrouridae in which the subfamily Bathygadinae has the second dorsal fin rays longer than the anal fin rays. This fin positioning imposes a slight head-upward inclination while the fish is swimming. In this study Bathygadus melanobranchus exemplifies this type of fin structure and swimming attitude. It is interesting to note that this species had (1) a high percentage of calanoid copepods and some fish in its diet and (2) low percentages of polychaetes and bottom-dwelling crustaceans. Macrourids of the subfamily Macrourinae, on the contrary, are characterized by long anal fin rays with short second dorsal fin rays. This placement imposes a head-down mode of swimming. Nezumia aequalis is a representative of this subfamily. Halosaurs, although in a different family, also have a long anal fin equipped with long rays and as a consequence swim tail high. It is interesting to note that both Nezumia and Halosaurus have very high percentages of polychaetes and gammarideans in their diets.

To summarize, it appears that there are three basic modes of feeding utilized by deep-sea bottom fish ordinarily captured in trawls and dredges. They are (1) predation upon small, benthonic organisms involving ingestion of considerable amounts of sediment, (2) predation upon small benthopelagic, pelagic, or planktonic organisms, and (3) active predation upon large macrobenthonic, planktonic, or nektonic organisms. A fourth option that may be utilized by any of the above is a fall-back mode of scavenging upon plant material or deadfalls of animal carcasses. Apparently selective sediment ingestion, which is resorted to by numerous shallow water fishes, is not performed by abyssal fishes.

The first group above ingests small macrobenthonic and meiobenthonic organisms found by rooting in the sediments, and possibly by feeling for them with long tactile fin rays. These fishes, mostly non-bathygadine macrourids, morids of the family Gadidae, and halosaurids may have well-developed gustatory receptors on the lips and surrounding skin, as well as on barbels and possibly fins, with which to sense the presence of prey (Marshall, 1965). They also tend to ingest a moderate amount of sediment which may be a limited source of nutriment for them (Bright, 1968). Members of the second group, particularly the bathygadine macrourids and some ophidiids, appear to feed extensively upon benthopelagic organisms and tend not to ingest a significant amount of sediment with their diet. The third group, very active predators and anglerfishes, feeds upon the larger macrobenthos and is largely confined to the upper continental slope. Many species of this group belong to assemblages that have affinities with the continental shelf ichthyofauna. Bembrops gobioides is an excellent example of this group. This is not to say that there are not large and relatively active predators in the abyss. A number of reports of sharks of formidable size occurring on the bottom, in depths greater than 2000 m, have been made in recent years (Isaacs, 1969).

The partitioning of food resources between pairs of closely related species without competitive exclusion is illustrated by the macrourids Nezumia aequalis and Coryphaenoides mexicanus and the ophidiids Dicrolene intronigra and Monomitopus agassizii.

Nezumia and Coryphaenoides have similar structures, i.e., an inferior mouth, elongated anal fin and stiff snout, and they have similar overall geographical and vertical distributions in the Gulf, although Nezumia attains maximum populations at 900 m, whereas Coryphaenoides does at 1200 m. Moreover, Nezumia is generally more populous than Coryphaenoides. The primary food for both species is polychaetes, but it is also evident that Nezumia is a much more generalized feeder. Whereas after polychaetes Coryphaenoides depends primarily upon crustaceans (especially gammarids, cumaceans, and isopods), Nezumia not only feeds on those types but also upon calanoids, squids, bivalves, gastropods, harpacticoids, and caridean crustaceans - none of which were found in the Coryphaenoides. Interestingly, where Nezumia reaches peak populations, its diet is most varied and Coryphaenoides is most restricted, while where the latter is most abundant it depends heavily upon benthopelagic fishes to supplement a reduced intake of polychaetes and gammarids.

The relationship between Dicrolene and Monomitopus also involves similar morphological characteristics, the same geographical distribution, and overlapping vertical ranges although Dicrolene attains maximum populations around 1200 m and Monomitopus at 1050 m depth. Generally Dicrolene is more populous than the latter. In this case where an average of 78% of Dicrolene examined had ingested polychaetes, only 14% of the Monomitopus taken at the same station had polychaetes in their stomachs. Again where Dicrolene reached peak populations individuals had as many as 18 different food items in their stomachs, Monomitopus never had more than 10. These observations on the two related pairs seem to support the conclusion that the most populous species are the more generalized feeders.

Invertebrates

Most of the original data in our possession relating to the food of benthic invertebrates in the Gulf is derived from crustaceans and echinoderms. The list of these with food in their stomachs is not long, to wit:

Invertebrate	Stomach Contents
Bathynomus giganteus (Isopoda)	Synaphobranchus (eel)
Glyphocrangon nobilis (Caridea)	Yoldiella quadrangularis (bivalve)
Benthochascon schmitti (Brachyura)	Fish
Dytaster insignis (Asteroidea)	Neilonella guineensis (bivalve)
	Sponge and forams
	Sargassum
Astropecten nitidus (Asteroidea)	Gastropods and bivalves
Astropecten americanus (Asteroidea)	Gastropods
Nymphaster arenatus (Asteroidea)	Sponge and forams
Athenoides piercei (Asteroidea)	Small sponge
Tethyaster grandis (Asteroidea)	Brissopsis alta (echinoid)
Goniopecten demonstrans (Asteroidea)	Gastropods, forams, radiolarians
Persephonaster echinulatus (Asteroidea)	Bivalves, gastropods, cumaceans
Phormosoma placenta (Echinoidea)	Sediment and plants
Mesothuria lactea (Holothuroidea)	Sediment

Pequegnat (1979) reported collecting five asteroids (Persephonaster echinulatus) that were in the process of solubilizing tar within gastric fimbriae. That this choice was not the result of the absence of natural foods is demonstrated by the fact that these same individuals had mollusks in their stomachs as well.

Food Chains Involving Some Key Species

In the previous sections on fishes and invertebrates we have presented some data on food habits that comprise links in a food chain. We shall attempt to summarize and extend that information in this section.

Crustacea – crustacea – fish – crustacea – ? fish

1. Meiofauna into small crustacea
2. Crustacean eaten by larger crustacean <u>Polycheles</u>
3. <u>Polycheles</u> <u>validus</u> eaten by <u>Synaphobranchus</u> (eel)
4. <u>Synaphobranchus</u> eaten by large isopod <u>Bathynomus</u>
5. <u>Bathynomus</u> <u>giganteus</u> – top carnivore ? or eaten by fish ?

Detritus – bivalve – crustacean – fish – ? fish

1. Detritus eaten by <u>Yoldiella</u> (bivalve)
2. <u>Yoldiella</u> <u>quadrangularis</u> eaten by <u>Glyphocrangon</u> (caridean)
3. <u>Glyphocrangon</u> <u>nobilis</u> eaten by <u>Bembrops</u> (fish)
4. <u>Bembrops</u> <u>gobioides</u> – top carnivore ?

Detritus – echinoid – asteroid

1. Detritus eaten by <u>Brissopsis</u> (sea-urchin)
2. <u>Brissopsis</u> <u>atlantica</u> eaten by <u>Tethyaster</u> (starfish)
3. <u>Tethyaster</u> <u>grandis</u> – top carnivore ? very likely

Plankton – squid – fish

1. Planktonic crustacea eaten by squid
2. Squid eaten by <u>Etmopterus</u> (shark)
3. <u>Etmopterus</u> <u>schultzi</u> – top carnivore ? very likely

Detritus – bivalve – caridean – fish

1. Detritus eaten by <u>Tindaria</u> (bivalve)
2. <u>Tindaria</u> <u>amabilis</u> eaten by <u>Glyphocrangon</u> (caridean)
3. <u>Glyphocrangon</u> <u>longleyi</u> eaten by <u>Bembrops</u> (fish)
4. <u>Bembrops</u> <u>anatirostris</u> – top carnivore ?

Fish – crab – fish

1. Copepods eaten by fish
2. Fish eaten by <u>Benthochascon</u> (brachyura)
3. <u>Benthochascon</u> <u>schmitti</u> eaten by <u>Dibranchus</u> (fish)
4. <u>Dibranchus</u> <u>atlanticus</u> – top carnivore

DEEP BENTHIC ECOSYSTEMS: CONTROLLING FACTORS OF ZONATION

INTRODUCTION

As noted previously, Rowe and Haedrich (1979) declare that a universal feature in the distribution patterns of the slope fauna is its tight zonation. This is the case in the Gulf, as can be inferred from the numerous subsets in the slope cluster of our dendrogram. Why animals are narrowly zoned on the continental slope or indeed zoned at all is at best poorly understood. Moreover, most deep-sea faunal studies deal with only one major faunal component, e.g., mega-fauna, macroinfauna, or meiofauna, so that we do not know how the findings for

one category may fit with those of another. Clearly there is no reason a priori to assume that the zonation in one category will have the same set of causes as another. In this general study we are concerned primarily with the macrofauna and the megafauna; in this particular section we propose to review possible roles that physiographic, geologic, physico-chemical, and biological factors may play as controlling factors of species diversity, assemblage formation, and zonation.

PHYSIOGRAPHIC AND GEOLOGIC FACTORS

The Gulf of Mexico has been described as a mediterranean-type sea (Garrison and Martin, 1973; Watkins et al., 1978) or as a small ocean basin (Antoine et al., 1974; Uchupi, 1975) surrounded by continental masses. It covers an area of more than 1.5 million square kilometers and has many of the geomorphic features of large oceans; its continental margins are structurally complex and in some cases rather unique. Maximum water depth over the Sigsbee Abyssal Plain (about 3840 meters) greatly exceeds the sill depths of those two passageways that connect the Gulf of Mexico with the adjacent Caribbean Sea and Atlantic Ocean.

Sedimentologically, the Gulf can be divided into two major provinces, a terrigenous one to the west and a carbonate one to the east, with a variety of physiographic provinces, subprovinces, and individual features contained within each of these realms. Because of its mineral richness (Martin and Bouma, 1978) and topographic complexity (Uchupi, 1975), the Gulf of Mexico has attracted the attention of numerous investigators with seismic research efforts having contributed to the bulk of recent literature related to its geologic aspects (Martin and Case, 1975). Our literature survey abetted with personal communications (e.g., R. Rezak, Department of Oceanography, TAMU, College Station, Texas and L. E. Garrison, USGS, Corpus Christi, Texas - November 1982) revealed that very little information had been published concerning deep-Gulf surficial sediments since the work of Bouma (1972). A general discussion concerning the physiography of the Gulf of Mexico, with major emphasis and/or attention being given to details of topography and sedimentology on the northern Gulf's outer continental shelf and upper slope, can be found in Pequegnat et al. (1976).

SUBMARINE TOPOGRAPHY

Major physiographic provinces in the Gulf of Mexico include the continental shelf, the continental slope, the continental rise, and the abyssal plain (Martin and Bouma, 1978). Their division of these provinces into subprovinces was deemed to be warranted by either variations in morphologic characteristics or on the basis of geographic location.

Continental Slope - Northern Gulf of Mexico

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 contains a variety of submarine landforms and generally possesses steep, irregular topography but can sometimes have rather large, smooth areas. The steeper portion of a slope, an escarpment in particular, can be considered as the margin or edge of the continental platform even though it is generally treated as part of the slope.

Texas-Louisiana Slope

West of the Mississippi Fan, the continental slope is characterized by a hummocky topography that consists of various shaped and sized hillocks and depressions (Bouma et al., 1980). The hill-and-basin seafloor (Martin and Bouma, 1978) of the slope covers an area of about 120,000 square kilometers; its entire frontal edge abuts the continental rise by a pronounced steepening of gradient known as the Sigsbee Escarpment.

The upper limits of this declivity is at a depth of about 2100 meters and its overall elevation ranges from between 730 and 1100 meters. Its base (between 3000 and 3200 meters) abuts the continental rise, which slopes gently seaward to the abyssal plain that commences at a depth of about 3650 meters.

Mississippi Fan

This fan-shaped seafloor covers bathyl and abyssal depth zones while dominating the topography of the east-central Gulf. The fan's apex is on the uppermost part of the slope (at a depth of 1200 meters) near the mouth of the Mississippi Trough, a scour feature (Stewart and Caughey, 1976) in the continental slope that marks an earlier watercourse of the ancestral Mississippi River.

DeSoto Slope

The DeSoto Canyon (Bergantino, 1971) lies off the Mississippi-Alabama coast between the eastern limits of the upper Mississippi Fan and the west Florida continental terrace.

DeSoto Canyon, a trough which heads near the 440-m contour and terminates near the 950-m isobath, is the most significant surface feature of the upper slope in this area (Jordan, 1951). Harbison (1968) attributes its formation to a combination of erosion, deposition, and structural control by diapirs clustered in that vicinity.

Continental Rise

The Western Gulf Rise is a broad expanse of gently sloping seafloor that onlaps the Sigsbee Escarpment and merges with the Sigsbee Plain generally along the 3500-m isobath (Emery and Uchupi, 1972).

Sigsbee Abyssal Plain

The Sigsbee Plain occupies the deepest part of the Gulf basin and is essentially flat (slope of less than 1:8000) or featureless except for the prominence of the Sigsbee Knolls. These knolls are clustered near the center of the plain and stand 100-200 meters above its level (Garrison and Martin, 1973). They are the surface expressions of but a few of the large diapirs that pierce and uplift many thousands of meters of abyssal strata (Watkins et al., 1978). In the vicinity of the knolls, a maximum thickness (nearly 400 meter) of the well-stratified section of horizontally layered turbidites and interbedded pelagic oozes is revealed (Martin and Bouma, 1978). These range in age from Pliocene to Holocene (Burk et al., 1969).

SEDIMENTOLOGY

The major source of sediment for the northwestern Gulf is Mississippi River discharge with lesser amounts of weathered products being supplied by the Rio Grande and the many rivers and streams positioned between these two. During transport to and within the Gulf basin, sedimentary materials are mixed and sorted by a variety of agents before deposition. The fact that detrital sediments are being deposited on the inner continental shelf is substantiated by the nature of the material, the presence of pure indigenous faunas, and foraminifera population ratios. Phleger (1967) speculates that some detritus from land is also being deposited on the continental slope and in the basin. This suggests that sediment being supplied to the Gulf does not reach the outer shelf, or if it does, it is being deposited seaward of the shelf.

Bouma et al. (1980) stress that sea level fluctuations strongly determine the amount and type of sediment being transported to the continental slope. 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 aspects of the Gulf. Only during low stands of sea level were significant volumes of sand moved to the shelf break (Bouma et al., 1980). 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.

The Mississippi River sediment load accounts for about two-thirds of the total sediment delivered to the Gulf which Trefry (1977) suggests is eventually deposited over a large area comparable to that described in this section as the Mississippi Fan. Wilhelm and Ewing (1972) infer that deposition of the last major volume of clastic sediment on the Mississippi Fan took place during early Holocene time. Later deposits from the Mississippi and other rivers that reached the abyssal plain were, at least in part, turbidity-current controlled (Davies, 1972).

PHYSICO-CHEMICAL FACTORS

WATER MASSES

The principal inflow of marine water into the Gulf of Mexico is from the Caribbean Sea through the Yucatan Strait whose sill depth is estimated to be between 1650- 1900 m. Under normal circumstances this sill determines the greatest depth from which Caribbean water is allowed to enter the Gulf. Most of the outflowing water passes through the Florida Straits into the North Atlantic. This latter passage has a sill depth of some 800 m.

The waters entering the Gulf through the Yucatan Strait are a mixture of South Atlantic water (transported northwestward by the Guiana and Equatorial current systems) with North Atlantic water (from the west Sargasso Sea). The ratio of South Atlantic to North Atlantic water has been estimated to be between 1:4 and 1:2 (Harding and Nowlin, 1966).

The Gulf may be classified as tropical in the south and warm temperate in the north; the Tropic of Cancer, 23°27'N, passes through the western Gulf about 150 miles south of Brownsville, Texas, and through the eastern Gulf between Florida

and Cuba. Characteristic open Gulf surface temperatures are 28-30°C in the summer and 20-25°C in the winter. Over the central Gulf basin, surface salinities are generally in the range of 36.0-36.3 ppt.

Five water masses are recognized in the Gulf. These water masses are vertically layered as follows: (1) Surface Mixed Layer, (2) Subtropical Underwater, (3) Oxygen Minimum Layer, (4) Subantarctic Intermediate Water, and (5) Gulf Basin Water. Each of these water masses can be distinguished in the Gulf by distinct values, gradients, or relative maxima or minima in specific parameters.

NEAR BOTTOM TEMPERATURE, SALINITY, AND DISSOLVED OXYGEN

There is a paucity of Gulf of Mexico temperature, salinity, and dissolved oxygen data that have been collected near the bottom in depths below 200 m. The bottom hydrocast collection bottle of ALAMINOS data presented herein was lowered to within 10 m of the bottom with most being within 3 m and some being within 1 m regardless of depth.

CIRCULATION AND CURRENTS

Surface and Upper Layer

The surface circulation in the Gulf of Mexico has been studied by oceanographers throughout the twentieth century using observations from ships, hydrographic stations, driftbottles and drogues, current meters, experimental laboratory modeling, and one of our latest technologies -- satellite imagery. These efforts have established a rather well defined circulation pattern for at least the eastern Gulf.

The Gulf of Mexico may be divided into two major circulatory provinces, East and West, each distinguished by different flow regimes. Water enters the Gulf via the Yucatan Channel and leaves via the Florida Straits. The salient flow pattern in the Eastern Gulf is the Loop Current which flows in a clockwise (anticyclonic) direction. This is in essence an extension of the Yucatan Current which penetrates into the Gulf and then turns to the right to flow out the Florida Straits. Prior to about 1975 it was believed that on a seasonal basis the Loop Current extended far to the north in the spring and summer and receded during the fall and winter. Molinari and Festa (1978) found the average position of the northern edge of the Loop to be 26°N and that penetrations north and south of this mean can occur during any season. According to Molinari et al. (1979) when the Loop is far to the south in the Gulf, the circulation to the north is characterized by a series of gyres of alternating rotational flow. The number and size of the gyres are reduced as the Loop intrudes to the north. When the Loop fills the entire eastern Gulf basin, the flow in the northeastern Gulf is predominately to the east. In other cases, the flow is a function of the type of gyre, cyclonic or anticyclonic, located in the northern Gulf at the time.

Although data are insufficient to obtain a clear picture of the surface circulation over the northeastern Gulf Slope, two features are relevant. First, only rarely does the Loop seem to penetrate this far north. Secondly, the flow along the western flank of the DeSoto Canyon is frequently to the north (Molinari et al., 1979).

Currents in the western Gulf of Mexico are relatively unexplored compared to the eastern Gulf where numerous observations of the Loop Current have been made (Merrell and Morrison, 1981). Interest in the study of circulation processes of the western Gulf, however has increased noticeably in the past few years (Sturges and Blaha, 1976; Molinari et al., 1978; Clemente-Colon, 1980; Blaha and Sturges, 1981; Merrell and Morrison, 1981; Elliott, 1982).

Circulation in the northwestern part of the Gulf is dominated by a semi-permanent anticyclonic (clockwise) cell in the region between 22° and 25°N. The southward movement of this cell is prevented by the wind stress maintained cyclonic circulation of the Bay of Campeche. Two hypotheses have been proposed for the driving force of the anticyclonic cell. Sturges and Blaha (1976) and Blaha and Sturges (1978) hypothesize that the circulation is driven by the curl of the wind stress; whereas, Elliott (1982) suggests the dominant factor responsible is the periodic invasion of anticyclonic rings detached from the Loop Current. Elliott carefully documents the migration of several rings to the west and estimates this migration from the eastern Gulf to the western boundary to be about 1.1 years. He also documents the presence of intense cyclonic circulation on the northern shelf-slope. Merrell and Morrison (1981) reviewed a draft of Elliott's paper and they postulate that a combination of wind stress and detached rings is the anticyclonic driving force.

The circulation north of 25°C (over the northeastern slope) is a region of high variability. From time to time this region is occupied by a cyclonic cell. Merrell and Morrison (1981) speculate that when the Loop Current is fully extended, cyclonic cells can form on the western edge and migrate westward (anticyclones can separate from the Loop at any extension but cyclones can only form when the Loop is fully extended and a low pressure trough is present). When there is a cyclonic cell to the north of the semi-permanent anticyclonic cell there is eastward transport between them. Merrell and Morrison calculate this transport relative to 1500 m to be close to $30 \times 10^6 m^3$/sec which is comparable to the flow through the Yucatan Strait. They also contend the circulation in the northwestern region depends on whether a cyclone or anticyclone has migrated into the area. If a cyclone migrates into the area, a three-gyre system develops and the cyclone is fed by water from the Texas shelf. If an anticyclone migrates into the area, it may be weakened and perhaps even split by the shelf outflow.

Near Bottom

Pequegnat (1972) was first to document the presence of deep near-bottom currents in the Gulf of Mexico. To date there have been three additional Gulf of Mexico studies that have reported on deep near-bottom currents: Moore, 1973; Molinari et al., 1979; and Brooks and Eble, 1982. The documentation Pequegnat (1972) presents consists of data from biological evidence obtained by dredging, bottom photography, and in situ current meters. His data were collected in the East Central Gulf at bottom depths of 3046-3286 m. Speed data from six current meter measurements taken 1 m above the bottom ranged from 6 to 19 cm/sec. Near-bottom current measurements from the Northwestern Gulf continental slope are reported by Moore, 1973. Short term measurements (less than nine hours) were taken at five sites in depths of 240, 370, 542, 687, and 1150 m. Current speeds of 4-8 cm/sec were recorded for the 1150 m station; whereas, the remaining four measurements were 15-29 cm/sec. Molinari et al. (1979) investigated possible OTEC sites in the Northeastern Gulf through a literature review and

on-site data collection. Current data were obtained from two locations using moored meters suspended 65 m above the bottom in 1050 m of water. The meters were utilized during July 1977 through August 1978 with one meter collecting 91 days of data and the other collecting for 308 days. The maximum speed observed during each of the 13 collection months ranged from 10 to 30 cm/sec. On the average (a) 10% of the observation were greater than 14 cm/sec, (b) 50% of the observations were greater than 7 cm/sec, and (c) 90% were greater than 2 cm/sec. Brooks and Eble (1982) present a data report on current meter output from the deployment of three arrays along the 730 m isobath in the Northwestern Gulf of Mexico. Aside from upper level current meters, conductivity probes, and temperature probes, each of the moorings had a recording current meter 30 m off the bottom. The instruments recorded current speed and direction for about 6.5 months, from 18 July 1980 to 4 February 1981. Current data are presented as stick plots for each mooring. These data have not been fully reduced so at this time the only inferences to be drawn are that currents were present and possessed an average speed of about 7-10 cm/sec.

Current direction in the above discussion was intentionally left out because it deserves separate treatment. The long-term data collected by Molinari et al. (1979) clearly show the water movement near the bottom closely parallels the isobath or as they state "the flow is very channelized by the bathymetry." The steeper the topograhic gradient the more influence it has in directing flow. In those regions where there is little topographic gradient, the direction of flow will be more erratic since boundary influences are lessened and direction becomes more of a resultant of upcurrent flow direction, downcurrent resistance, density discontinuity, and the Coriolis effect.

Current directions given by Pequegnat (1972) would be classified with those having little topographic gradient. Data of Moore (1973) and Brooks and Eble (1982) were taken in regions of moderate topographic relief and thus should be under the influences of boundary conditions. Both studies, however, were conducted in the region described by Gealy (1955) as the "hummocky" zone. The region is characterized by localized systems of diapiric structures thus apparent flow direction (that of Moore, 1973; Brooks and Eble, 1982) will be localized and any discernment of possible large scale circulation trends must await further reduction of Brooks and Eble's (1982) data.

PART III. GENERAL ECOSYSTEM ANALYSIS

INTRODUCTION

In principle the concept ecosystem is dimensionless; hence one is justified in discussing the ecosystem of an estuary or of the continental shelf or of the continental slope, or indeed, of all of the area from the outer shelf to and including the abyssal plain, which is what we propose to do here. A marine ecosystem then is the community of organisms in a given area, including both pelagic and benthic species that are interacting with the physico-chemical environment in such manner that energy flows through trophic levels of varying diversity and in which mineralization of materials occurs to produce a true cycle from primary producers to top consumer and return.

COMPONENTS OF MARINE ECOSYSTEMS

From the trophic point of view an ecosystem has two principal components, viz.,

the autotrophic component and the heterotrophic component (Odum, 1972). The autotrophs or producers, largely green plants ranging from diatoms to sea grasses and kelps, photosynthesize organic compounds. These compounds form a strong yoke between biotic and abiotic components (e.g. CO_2, H_2O, N, etc.). The heterotrophs or consumers are divisable into predators that feed on other living organisms, and saprophages (bacteria, fungi, and some protozoa) that feed on dead organic matter and return to the abiotic sphere the nutrients needed by the autotrophs.

ENERGY FLOW

The energy stored in net primary production by the green plants is available to the array of species populations in the ecosystem which are unable to derive energy from other sources. These populations include the animals, fungi, and certain bacteria. In a typical oceanic community we observe free-floating phytoplankton in the surface layer that are the primary producers and that support, directly or indirectly, a complicated food web of herbivores, carnivores, and scavengers which extends from surface to and into the bottom. The rate of primary production is of course affected by radiation and temperature but the most critical parameter is the storehouse of nutrients in deeper layers and the rate at which they are delivered to the photic zone by vertical circulation (Riley, 1972).

NATURE OF THE DEEP GULF ECOSYSTEM

So far as the geographic emphasis in this study is concerned, the deep Gulf ecosystem is a complex of water and bottom extending from the Mexican border to and including DeSoto Canyon off the Florida panhandle. With the exception of the vicinity of hard banks at the edge of the continental shelf, the sediments are of terrigenous origin. Actually DeSoto Canyon marks the northern contact of clastic sediments with carbonate sediments to the east just as to the south Campeche Canyon runs along a similar contact of clastics with the great carbonaceous Campeche Bank which runs from Campeche Bay to Yucatan Channel.

Although it might appear that the deep ecosystem of the Gulf in the area of this study is quite uniform, in truth there are some remarkable biotal differences. In fact, the biotal differences justify referring to the western Gulf as the "true" Gulf and the eastern part as a divergence of the Atlantic Ocean via the Caribbean Sea.

We have seen that whereas some 187 species among demersal fishes, decapods, and some echinoderms are limited in their distribution to the western Gulf, only 31 species among these same groups occur only in the eastern Gulf. Some of this discrepancy may be due to sampling artifacts but the separation might well be even greater had more of the less mobile species been included in the tally. It is not difficult to suggest possible reasons for the relatively high level of endemism among the benthos in the western Gulf as compared with the eastern part. For one thing, residence time of water is greater in the west than in the east. Some of the water entering the Gulf through Yucatan Channel turns westward and becomes incorporated in the southern cyclonic gyre. Moreover, the northern two of the three gyres of the western Gulf are formed by water spinning off from the Loop Current. This water remains sufficiently long here for the development, metamorphosis, and sinking to the bottom of any meroplankters of benthos introduced from the Caribbean. In general this is not so true of

the eastern Gulf. Here the Yucatan water often flowing at the rate of 2-4 kts sweeps in and out of the Gulf rather rapidly. Accordingly, holoplankters, meroplankters, and some nekton come into and pass out of the Gulf in a matter of days (note that a 3-knot current travels 72 n miles per day). Assuming an average transit distance of 576 n miles, water in the Loop Current would remain in the Gulf a maximum of 8 days. Actually the effective time for recruitment would be about half of this, simply because in order to reach the bottom before being carried out of the Gulf, pelagic larvae would have to begin their descent during their travel in the ascending (northward) limit of the Loop.

DEEP ECOSYSTEM MODEL

In order to simplify the model we shall ignore details of the various water masses depicted and consider that any area of the deep ecosystem is comprised of three functionally distinct but interrelated layers.

The uppermost layer, extending from the surface to a depth of about 60 m, is referred to as the euphotic zone, because it receives sufficient sunlight to generate photosynthesis among phytoplankters and fixed plants. Beneath the euphotic zone, and extending to within a meter or so of the bottom, is a huge mass of water which beyond the shelf is largely devoid of sunlight. This is the aphotic zone where photosynthesis cannot occur and where the processes of food consumption, biological decomposition and nutrient regeneration take place in the cold and dark waters. The lowermost layer is the bottom itself together with the contiguous water a meter or so in thickness. This is the benthic zone, repository of sediments from above, where nutrient storage and regeneration take place in association with the solid and semi-solid substrate. Each of these zones has much in common with the others, but each is sufficiently distinct to merit individual separation and analysis. It is a marvel of the ocean that a surface layer of water whose thickness is only about 2 percent of the average depth of the world ocean can support the huge biomass living in the largest mass of water on earth as well as in the largest expanse of soil on the globe. The basis for this is a phenomenon of the geometry of small size; the combined surface area of phytoplankters far exceeds the area of the marine environment. This facilitates the rates of internal reactions and effective use of the sunlight that penetrates the sea surface. Marine plants as large as trees could not produce food as efficiently, a fact that is reflected by the limited development and minor productivity of the giant kelps (e.g. Macrocystis or Nereocystis).

Development of a model of nutrient and energy flow within the deep Gulf ecosystem must start with primary productivity of phytoplankters and identify the reservoirs wherein nutrients and energy are temporarily stored. Then the principal pathways must be designated via which the nutrients and energy are imported, exported, or transferred. Each of the three functional zones of the ecosystem is conceived as a five-reservoir food chain. Each reservoir provides nutrients and energy to the next reservoir within a given food chain, and each exchanges with its comparable reservoir of the adjacent zones. Furthermore, each reservoir gains (imports) energy and nutrients from outside the system, and each loses (exports) energy and nutrients to the outside.

Tentative Quantification of Production and Energy Flow

Data from ^{14}C measurements (El-Sayed, 1972) of production of particulate

organic carbon by phytoplankton in the Gulf appear to average about 55 g $C/m^2/yr$. The highest values appear to be found in the upwelling area north of Yucatan Channel and in the region around DeSoto Canyon. In the oceanic region the western Gulf is apparently more productive than the region east of the 90th meridian. The above average does not include the production of soluble organic carbon by the phytoplankton. Estimates as to the magnitude of this parameter range widely, as noted above; however, it appears reasonable to assume that it is equivalent to an additional 15 g C/m^2 of particulate carbon production, giving a total for a year of about 70 g $C/m^2/yr$ or 700 kcalories/m^2 in a year.

It is generally assumed that except for brief periods during major plankton blooms the zooplankton consume all the phytoplankton produced. In turn they excrete a high percentage of their food intake as nutrient-rich feces that sink to the bottom. Most of the herbivorous zooplankters are copepods with calanoids leading all others in the oceanic waters of interest to us. Extrapolating from the copepod dry weight values and assuming three generations of major species per calendar year, it is estimated that the herbivore production is on the order of 14 g $C/m^2/yr$ or 140 kcal/m^2/yr. A high percentage of this production is consumed by euphausiids, ctenophores, and chaetognaths within the zooplankton, and most of the remainder is taken up by pelagic fishes. Thus, much of the organic material transported to the bottom from this source takes the form of feces.

Since the herbivores eat most or all of the phytoplankton and may assimilate 70 percent of what they take in, then about 210 kcal/m^2/yr (21 g $C/m^2/yr$) is the energy available to the benthos.

The energy transfers and transformations in the benthic environment are poorly understood. The roles played by the microbenthos (e.g., bacteria and fungi), meiobenthos (e.g., nematodes and harpacticoid copepods), macrobenthos (e.g., polychaetes and bivalves), epifauna (e.g., decapods and holothurians), and demersal fishes (e.g., rattails and cusk eels) must be accounted for. And although we have already pointed out that benthic biomass values drop exponentially with depth, it is almost inconceivable that this array of organisms can be sustained by an input of only 210 kcal/m^2/yr, particularly if as seems likely the feces supply metazoan needs only after being acted upon by bacteria and/or fungi. We are unaware of any reliable figures on the efficiency of this transfer but judging from bacterial roles in another depauperate environment, viz., salt marshes, little more than 35-40 percent can be expected (Teal, 1962). Hence not much more than 75 kcal/m^2/yr are likely available to the rest of the benthos. As touched on previously, other sources of energy must be involved in more than a happenstance manner.

On the basis of a few samples taken by Rowe and Menzel (1971) in the deep Gulf and a reworking of the data by Rowe et al. (1974), we can estimate that the production of the macrobenthos is on the order of 3 kcal/m^2/yr (0.3 g $C/m^2/$ yr) in the western Gulf and only 1 kcal/m^2/yr over the deep part of the eastern Gulf.

The role of the meiobenthos in sustaining any part of the macrobenthos and megabenthos has not been demonstrated satisfactorily. It is known that their biomass is small but it is also estimated that their biomass may turn over as much as 10 times per year (Gerlach, 1972). Hence their production is biomass/ m^2 x 10/yr.

Among the group there are carnivores, herbivores, and detritivores, leading some investigators to speculate that this is a self-contained compartment of the ecosystem that provides no energy to other reservoirs. This, however, seems highly unlikely in view of the fact that most of the meiobenthos live in the uppermost part of the surficial sedimentary system. Consequently many of them would be consumed, incidentally or not, by sediment ingesting decapods, echinoderms, and fishes. In any event it seems unlikely that their production is greater than 0.5 g C/m^2/yr ($=$ 5 kcal/m^2/yr), assuming that they depend exclusively on the rain of organic matter from the primary producers. This would mean energy usurpation of 25 to 50 kcal/m^2 by this group alone.

Two groups are left to be accounted for, viz., the invertebrate megaepifauna and the demersal fishes. Based on the conversion factor of 1 g wet weight $=$ 0.1 g C $=$ 1 kcal, it is assumed that demersal fish production in the deep Gulf is on the order of 2 kcal/m^2/yr. This is probably somewhat greater than that of the epifauna, which is estimated to be about 1.5 kcal/m^2/yr. Obviously the usurpation of energy by these two groups is considerably greater than the percentage of assimilation. Clearly the invertebrate epifauna alone cannot support the demersal fish fauna.

Other Sources of Matter and Energy for the Deep Sea

It appears from the above estimates that the energy budget of the deep Gulf cannot be balanced unless the assimilative efficiencies of bacteria and meio-fauna are extraordinarily high, which is an unlikely prospect. We are left, therefore, with the conclusions that other sources of organic matter for impor-tation to the deep sea must be found. We believe that there are at least five such sources:

1) dissolved organic matter

2) deadfalls of animal carcasses

3) fallout of terrestrial and shallow marine plants

4) transport of animals and organically rich sediments in slumps and turbidity flows

5) active foraging of demersal fish and large benthic crusta-ceans in the midwater region from which they return to the bottom.

It is still a matter of conjecture as to the importance of large animal carcasses as a source of food for the megafauna. Bruun (1957) suggested that deadfalls, including whales, could sustain the deep-sea fauna for substantial periods of time. Some twenty years later (1977) Haedrich and Rowe suggest "... the megafaunal biomass cannot be supported by the macrofauna. The mega-fauna must therefore depend to a considerable extent on food arriving from pelagic regions in the form of large, fast-falling packets, that is, the bodies of fishes, whales, squids, and decapods."

The importation of large packets of plant material to the deep benthic region is another source of organic matter of as yet undetermined significance. Areas in the Gulf where we have dredged or trawled substantial amounts of decaying

plants invariably contain a rich benthic fauna. In some cases this must result from the refuge for the epifauna formed by the plant mass. All of the evidence that we have collected indicates that if this material is not consumed in its original form, it must be rather quickly transformed into components that are utilized by the infauna. Thus, in spite of large inputs from surface rafts no large accumulations were ever photographed by us on the bottom.

The transport of the infauna from the shelf break and upper slope into much deeper zones continues to take place in the Gulf of Mexico. The tracers that we have used to demonstrate the occurrence of this phenomenon are the shells of paleotaxodont bivalves. Three regions where we obtained definite evidence of slumping are in and below DeSoto Canyon, west of the Mississippi Delta and off Brownsville, Texas.

Another phenomenon that undoubtedly assists in supporting parts of the benthic fauna, at least at depths in the Upper Abyssal Zone, is the active foraging upon midwater pelagic life carried out by some demersal fishes. Actually it is not known what the depth limitations of this mode of feeding are, but for the rattail Coryphaenoides armatus it appears to be no deeper than the 2000-m isobath (Pearcy and Ambler, 1974; Haedrich and Henderson, 1974). Obviously to occur much deeper than that could require such a large expenditure of energy in the vertical transit as to yield a negative energy flow for the individual.

SUMMING UP

Some of the principal processes which provide matter and energy that sustain the deep-sea ecosystem of the Gulf of Mexico are portrayed in Figure 113. The entire Gulf is shown in order to map those surface currents (open arrows) that were found to transport most of the plant debris that was observed during the field study. Noting previously that there is a positive correlation between the density of the deep benthic fauna (>1000 m) and the occurrence of plant debris from Thalassia, Sargassum, freshwater aquatic plants, and tree limbs, we have placed shaded ovals where the densest bottom faunas were found. Although the cube has been placed in the western Gulf, the processes that it depicts are gulfwide in occurrence.

POTENTIAL HAZARDS FOR THE DEEP GULF ECOSYSTEM

In the preceding sections it has become clear that although the deep Gulf ecosystem has many unique features, it is vitally dependent upon surface currents and the functions of the euphotic zone for its continuing health and future existence. It is, therefore, in double jeopardy in that it will be affected indirectly by agents that are inimical to surface life and directly by pollution emanating from man's activities in the benthic region.

Chemical pollution or other modification of the euphotic zone should have only temporary adverse effects upon the euphotic zone itself because mixing and dilution should occur and because surface water currents should sweep the contaminated water away. However, the deeper layers are nutritionally dependent upon the surface layers in very complex and subtle ways. Therefore, any interference with production in the surface layers or with vertical biological and physical transport mechanisms should have adverse effects at some point downstream of the site of contamination upon the aphotic and benthic portions of the system. For example, oil pollution of the surface or intermediate
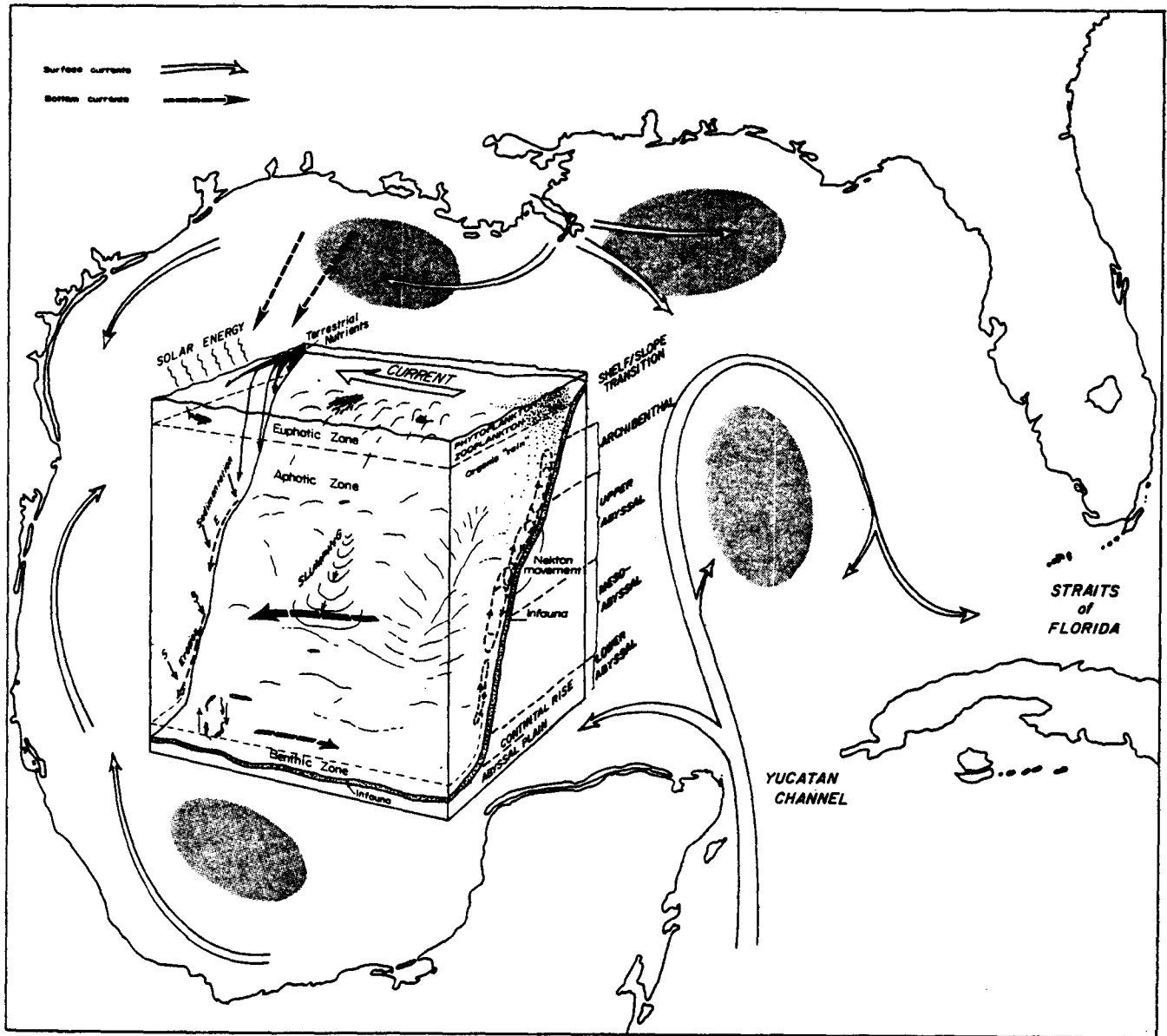
Figure 113. Processes and phenomena involved in the functioning of the deep Gulf ecosystem. Open arrows represent the general track of those surface current systems that carry plant material into the Gulf and from which it drops to the bottom. The shaded ovals indicate where most of the plant material touches down and also where the densest development of the deep benthos occurs. Both the faunal zonation system and the ecosystem zones are depicted. Note also the "rain" of particulate organic matter, sedimentation, and slumping (erosion) processes. Finally, the feeding of demersal fishes upon pelagic species is shown by the arrowed dashed ovals.

waters might be expected to interfere with feeding and vertical migrations of the zooplankton. This, in turn, would reduce the standing crops of zooplankton and decrease food availability to those animals of the aphotic and benthic zones which depend upon the zooplankton or their fecal pellets for food.

Direct chemical contamination of the aphotic and benthic zones is likely to occasion several serious consequences. The fauna of these zones tends to be more unique and more especially adapted to the prevailing local conditions than those of the surface waters. Physiologists have concluded that deep-water animals have very narrow ranges of tolerance to most environmental factors studies. In this respect they are not like estuarine and other hardy coastal animals which are adapted to survive in highly variable environments. Deep-sea animals are sensitive to even minor shifts in environmental factors. This generalization, based primarily upon studies of benthic animals, undoubtedly applies to the pelagic species of the aphotic zone, as well. Just in terms of maintaining life, the fauna of the aphotic and benthic zones must be considered very vulnerable to chemical pollution.

A great many of the species of the aphotic and benthic zones are filter-feeders and must strain their food from the water. Suspended oily materials and heavy concentrations of suspended silt would be expected to foul the delicate feeding mechanisms. The planktonic larvae of the benthic species should be especially vulnerable to such action. Many other species are deposit feeders which glean organic particles by sorting through the surface sediments. Deposition of heavy silt layers or of petroleum products upon the bottom surface should be devasting, especially to those benthic species which possess limited powers of locomotion.

Finally, there is the major suite of problems associated with underwater "blow-out" and slumping. A major underwater "gusher" would send enormous quantities of petroleum into the aphotic and benthic environments of the slope. Without question, such an event would wreak widespread havoc throughout these delicate systems because of the quantities of petroleum and because of the diversity of petroleum fractions involved. Such an event would also likely be accompanied by significant slumping, and this would result in faunal devastation in a wide path down-slope from the primary event.

Unfortunately, little solid information is available upon which definite prediction can be based. Therefore, a major vulnerability is a lack of knowledge and understanding. One likely would not be in a position to diagnose trouble when it began or to demonstrate the cause if many of the aphotic and benthic populations were suddenly eradicated. Some knowledge of the directions and velocities of the deep current patterns would at least permit prediction of the directions and rates of spread from point-source contamination. However, absolutely nothing is known about ways of ameliorating the effects of deep-water petroleum contamination or of slumping or widespread siltation of the aphotic or benthic zones. Therefore, predictability would not appear to serve any useful purpose in protecting the deep-water ecosystem. The technology of prediction and protection lag far behind the technology of exploitation. However, as suggested in an earlier section of this report, there are some biologically related techniques that might be used to discern geographic areas of the slope that have a history of slumping. These areas could be designated as hazardous drilling sites, and lease rights would not be offered for sale. In this context, predictability would serve to protect the most vulnerable parts of the slope ecosystem.

PART IV. FUTURE STUDY NEEDS

What we need to know of the deep Gulf is not restricted to one or a few disciplines or even geographic areas. Instead, we need a systematic, multidisciplinary sampling program based on existing knowledge of the deep Gulf but not necessarily designed to "fill the gaps" in the data.

The following statements attempt to summarize the major deficiences in knowledge of the deep Gulf of Mexico for later use in designing a deep benthic study in the Gulf. These data gaps are deterrents in understanding the deep Gulf ecosystem as a whole, yet understanding this ecosystem is becoming increasingly more essential as man encroaches deeper into the ocean with his exploration, mining, and dumping activities.

VOIDS IN PHYSICO-CHEMICAL DATA

CHEMICAL

One very basic void in deep-Gulf chemistry is that of organic content of the sediments and overlying water. Such data are obviously important in understanding the energy transfer of organic matter in and near sediments to the interstitial bacteria, meiofauna, and other organisms. There is undoubtedly variation in organic carbon content of deep sediments not only between isobaths but between the major geographic features (e.g., Alaminos Canyon, Mississippi Fan, DeSoto Canyon), which likely is reflected in standing stock biomass. There is still debate on the relative importance of various sources of organic material to the deep-sea and very little information is available for the Gulf.

Secondly, it is important to know much more about the levels of dissolved oxygen in the first meter of water above the bottom, and this should be correlated with Eh values in the adjacent sediments. These values alone will give us important insights into just how important the slope ecosystem is in the total bioeconomy of the Gulf system.

Another basic question often brought up in the discussion of pollution in the Gulf of Mexico concerns the actual flushing time of the Gulf. Determining the residence time of waters in the Gulf is certainly of first-order importance, yet to our knowledge this has not been done discriminately, as through isotope-dating methods.

More discriminating sediment analyses are imperative. We have reached that point in ecological investigation where it is no longer sufficient to simply analyze sediment samples for metals. Too much evidence has accumulated that argues that metals highly bound to sediment particles, especially the clay matrices, are not assimilable by organisms and thus they have essentially zero toxicity potential. Rather it is the dissolved metals and, more particularly, the valence state of dissolved metals, that we need to investigate. Hence, pore water samples should be studied appropriately to achieve these objectives. Those metals of greatest concern are zinc, manganese, copper, cadmium, lead, iron, and mercury. At the same time the presence of various organic pollutants could be determined. Both the redox potential (Eh) and pH are very important controls of the availability of toxic metals and other toxicants; hence they should be studied in situ when feasible.

PHYSICAL

Currents

Physical oceanographers were convinced that the deep Gulf was devoid of appreciable currents until 1972 when a bottom current with velocities as high as 19 cm/sec was discovered on the Mississippi Fan between 3000 and 3300 m depth (Pequegnat, 1972). Since then deep bottom currents have been discovered on the northeast and northwest Gulf upper slope (Moore, 1973; Brooks and Eble, 1982; respectively); otherwise few efforts have been concerted toward study of the currents on the Gulf slope and none on the currents of the lower slope and abyssal plain. A primary interest in piecing together the overall deep Gulf ecology is to determine the duration, speeds, and patterns of currents traversing the continental slope. If such currents do exist, they serve as a mode of transport for nutrients and perhaps larvae.

Slumping and Turbidity Flows

The stability of the sediment layer on the upper slope has become a serious concern, particularly to those involved in site selection and construction of oil production platforms in the slope petroleum province. The last 10 years has seen much progress toward understanding sediment movement on the northern Gulf continental outer shelf and slope, mainly in the form of slumps and mudslides (Garrison and Martin, 1973). The normally "static" deeper environments are probably periodically inundated with sediment on one hand or supplied with fresh organic material on the other. The effects of slumping and turbidity flows on the fauna is yet another gap in the knowledge of the deep Gulf.

DEFICIENCIES IN BIOLOGICAL DATA

Up to now the emphasis in respect to deep-Gulf biological studies has been on the megafauna and macroepifauna with only a moderate amount of study being devoted to the macroinfauna and meiofauna. Thiel (1975) emphasized how these artificial groupings have little taxonomic or ecologic justification and are merely convenient to sample collection and processing. Thus, those faunal assemblages identified to date and, indeed, the system of zonation proposed by previous workers has to a large extent been based on but a fraction of the total benthos. Obviously, ecological assemblages have other important components, including the bacteria, meiofauna, and benthopelagic components.

Morita (1979) stressed the need for further investigations on microbiology of the deep sea, particularly on bacteria metabolic rates, biochemistry, physiology, and utilization of DOC and POC in the deep environments. He outlined six important factors to be considered in deep-sea microbial studies which have not yet been employed in the deep Gulf.

Thiel (1979) pointed out how lack of suitable data prevented comparisons of deep-sea macrofauna and meiofauna abundance; that is, no synoptic data is available from both size groups from the same sampling program or region. Meiofauna densities seem to decrease more slowly with depth, and are roughly 1000 times higher than macrofauna densities (Thiel, 1979). Moreover, there is promise of correlating meiofauna densities to C/proteins and N/proteins ratios in the sediment (Dinet, 1979). It is requisite to include meiofauna in future deep-Gulf biological investigations, for several reasons: 1) meiofauna are

easily collected quantitatively, 2) smaller sample sizes of benthos adequately represent meiofauna populations, and 3) meiofauna respond quickly to changes in the environment and are basically immobile, rendering them good indicators of pollution and other disturbances. To date, very little is known of meiofaunal populations on the Gulf slope and deeper, but a deep-Gulf survey which includes this important component would certainly allow better evaluation of energy transfers and vulnerabilities in deep-Gulf ecosystems.

The benthopelagic component, a most difficult component of deep-sea ecosystems to study, is another deficiently researched aspect of the deep Gulf. Many benthopelagic organisms, e.g., fishes and cephalopods, are capable of transferring considerable amounts of organic matter from the pelagic to benthic environment and vice-versa. Hinga et al. (1979) concluded that near-bottom organisms (which they define as organisms living on or near, but not in the sediment) consume much of the organic carbon that reaches the deep-sea. It is therefore important to attain some idea of the relative importance of the somewhat semitransient benthopelagic component to the benthos as a whole.

The macro- and megafauna and demersal fish taxonomy and surveys have been adequately worked out for the deep Gulf. The remaining data gaps pertaining to these and the aforementioned biological components include quantitative biomass measurements, trophic relationships, reproductive patterns, and seasonal changes.

SUGGESTED FUTURE INVESTIGATION

AREAS AND DEPTHS TO BE SAMPLED: CANYON SYSTEMS AND MISSISSIPPI FAN

There are three significant canyon systems in the northern Gulf of Mexico. These are:

1. DeSoto Canyon in the northeastern Gulf, which lies between the easternmost extension of the clastic sediment system and the western reach of the carbonate sediments of Florida. In truth the "trough" of this canyon is rather short, stretching only from a depth of about 450 m down to between 950 and 1000 m, but there is evidence of considerable sediment movement in the lower extension of the canyon down to its intersection with the Mississippi Fan. The canyon has been studied reasonably well biologically but much more attention should be given to it between the 2250 and 2700 m isobaths.

2. The Mississippi Trough which lies in the north-central Gulf on the outer edge of the prograding delta of the Mississippi River: this canyon like feature is known to have been extremely active as a sediment transporter in the late Pleistocene and, indeed, is still an environmentally active site.

3. Alaminos Canyon, which lies in the northwestern Gulf is now known to traverse a very active area of slumping and turbidity flows. Although the area around the canyon has been studied moderately well, the canyon walls deserve very special attention down to the point where they contact the Sigsbee Escarpment.

It is suggested herewith that these regions and their environs should be studied by means of Y-shaped transects. Both walls, as well as the central valley, of each canyon would be studied. It is recommended that if at all feasible each canyon should be surveyed initially by means of a deep submersible craft.

SOME NOTES ON THE NATURE OF THE ECOLOGICAL PROJECT

As stated previously, up to now the emphasis in deep biological studies has understandably been on the megafauna with only a moderate amount of attention being devoted to the macroinfauna. Accordingly, it is recommended that at strategic depth stations the proposed study should sample the meiofauna and macrofauna by means of boxcores. Also, insufficient attention has heretofore been paid to the benthopelagic component; hence this, too, should be sampled, primarily be means of an appropriate sled.

It is emphasized that bacteria would not be neglected. Rather they would be studied in another context, viz., that of seabed metabolism.

THE ROLE OF SEABED METABOLISM IN ANAYSIS OF IMPACT ASSESSMENT

It is expected that high-density pollutants, including some components of petroleum, may be capable of deleteriously impacting those living parts of the ecosystem that exist in or are dependent upon the sediment bed. Thus, in order to understand just how pervasive such impacts may be, some attention should be given to what we are calling seabed metabolism. Initial steps in this substudy should comprise the following:

1. Deployment of sophisticated suspended material traps (often referred to as sediment traps). This permits calculation of the input of potential energy to the seabed that will be available to drive the system. The traps should be equipped to surface upon command.

2. The effective transfer of this potential energy to the cryptic system can be investigated by taking subcores from box cores. A press should be used to obtain samples of the true pore water.

Other subcores from the box core can be utilized for

> a) microbiology
> b) meiofauna
> c) sediment texture

It may be advisable to employ a method for calibrating or gaining insight into the meaning of the metabolic levels determined by the above techniques. This can be done to a large extent by determination of the adenylate energy pool of the sediment system, utilizing material from a subcore of the above mentioned box core. The adenylate energy charge pool represents the available concentrations of three adenine nucleotides: adenosine-5'-triphosphate (ATP), adenosine-5'-diphosphate (ADP), and adenosine-5'-monophosphate (AMP). This pool provides the metabolic energy for the regulation of metabolic enzymes which, in turn, control all functions of an organism.

The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

The Minerals Management Service Mission

As a bureau of the Department of the Interior, the Minerals Management Service's (MMS) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS), collect revenue from the Federal OCS and onshore Federal and Indian lands, and distribute those revenues.

Moreover, in working to meet its responsibilities, the **Offshore Minerals Management Program** administers the OCS competitive leasing program and oversees the safe and environmentally sound exploration and production of our Nation's offshore natural gas, oil and other mineral resources. The MMS **Minerals Revenue Management** meets its responsibilities by ensuring the efficient, timely and accurate collection and disbursement of revenue from mineral leasing and production due to Indian tribes and allottees, States and the U.S. Treasury.

The MMS strives to fulfill its responsibilities through the general guiding principles of: (1) being responsive to the public's concerns and interests by maintaining a dialogue with all potentially affected parties and (2) carrying out its programs with an emphasis on working to enhance the quality of life for all Americans by lending MMS assistance and expertise to economic development and environmental protection.