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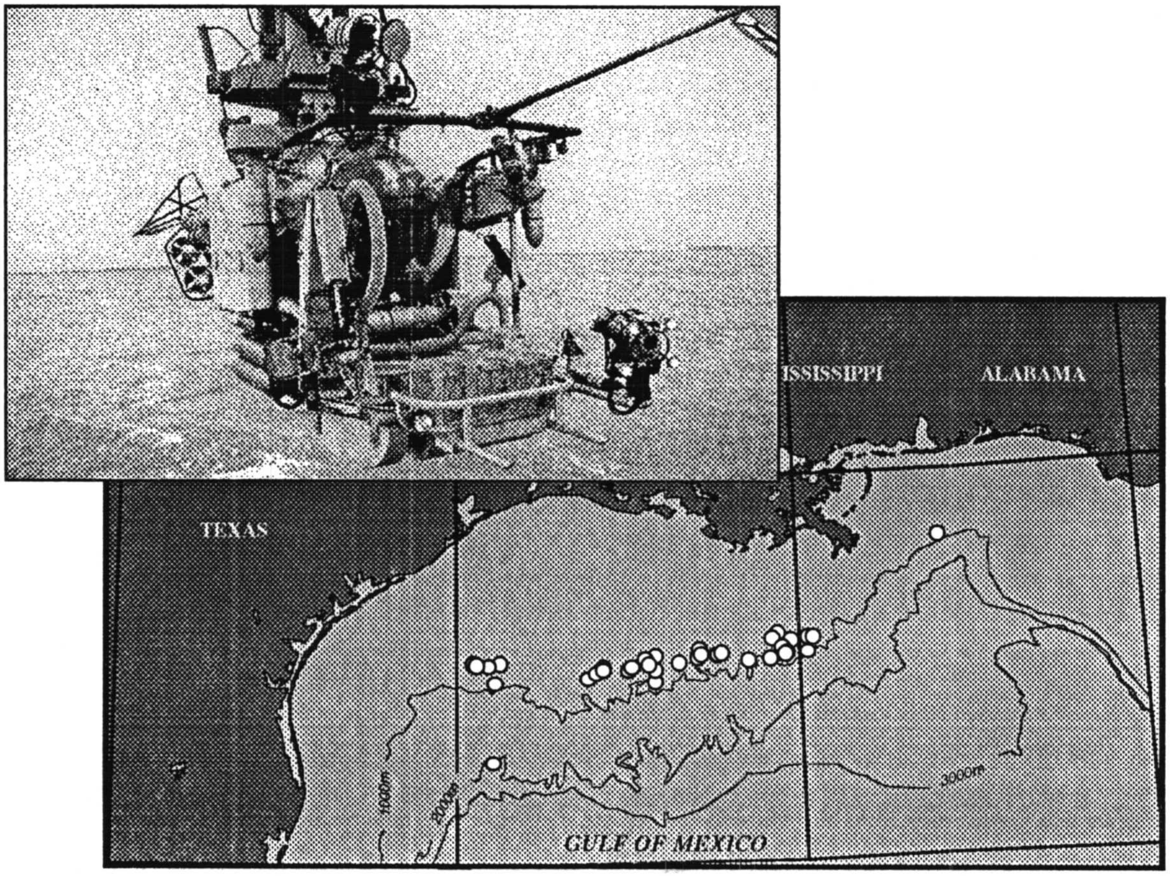
MMS 92-0033

Northern Gulf of Mexico

Chemosynthetic Ecosystems Study

Literature Review and Data Synthesis

Volume I: Executive Summary



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

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Volume I: Executive Summary

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COVER PHOTOGRAPH

The foreground photograph shows the submersible *Johnson Sea-Link I* preparing for one of its many dives to study chemosynthetic ecosystems. The map depicts the locations of known chemosynthetic ecosystems in the northern Gulf of Mexico.

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EXECUTIVE SUMMARY

1.0 Introduction

The Chemosynthetic Ecosystems Study is being conducted by ten principal investigators (PIs) under the overall management of the Geochemical and Environmental Research Group (GERG) of Texas A&M University. At this juncture, the Study has completed the first of two scheduled research cruises, is completing preliminary processing of material collected on that cruise, and has begun preparing for the second research cruise in August 1992. This document is the first of three reports that will be produced by the Study; it will focus on a review of published literature pertinent to the subject and a limited synthesis of data collected prior to commencement of the Study.

Each of the PIs has written an independent overview of the published literature in his topic area and of his unpublished results which are sufficiently advanced to release; all literature citations have been combined in a single section to avoid repetition. In addition, a collection of the core literature pertinent to the Gulf of Mexico communities has been assembled and reproduced in an appendix to this report. This collection includes the discovery papers, review articles, and a series of papers entitled: Gulf of Mexico Hydrocarbon Seep Communities I through VII, which has been dispersed among a variety of journals. Citations of these works are given in bold-face type to distinguish them from general references. The reader is encouraged to consult the original sources collected in the appendix for additional depth and detail. These sources should be cited in reference to this report, when possible, since they have passed peer-review and are available in wider circulation.

Information on the composition and geographic distribution of communities in the Gulf of Mexico is germane to the management concerns of MMS and to completion of the Study field effort. Certain sites where chemosynthetic communities are known to occur were selected as primary study sites for the Chemosynthetic Ecosystem Study; these sites were visited during the Year I field effort and will be revisited during the Year II field season. This report provides detailed information on the Study sites and the sampling stations within these sites. It also updates and expands information on distribution and composition previously presented by **Kennicutt et al.** (1988) and **MacDonald et al.** (1990b).

2.0 Definition of Chemosynthetic Communities

"Chemosynthetic communities" is a term somewhat loosely used for a variety of mostly deep-sea marine assemblages. "Chemosynthetic" derives from a trophic classification of bacteria that are the primary producers in these unusual food chains. A brief digression to define terms will help place the Gulf of Mexico chemosynthetic communities found at hydrocarbon seeps within a broad and growing array of functionally similar assemblages now known to have a wide distribution in the World Ocean.

Organisms are classified according to how they obtain their source of carbon for tissue synthesis. Carbon may be acquired directly from CO_2 (autotrophic) or from consumption of organic compounds produced by other organisms (heterotrophic). A classification criterion describes the source of energy for carbon fixation: Cells containing chlorophyll utilize sunlight as the energy source and are termed photoautotrophic or, more commonly, photosynthetic. Various prokaryotes (bacteria), which use chemical energy obtained by oxidation of reduced compounds and the carbon from CO_2 to synthesize new organic compounds are referred to as chemoautotrophic or chemoautolithotrophic. Almost all other organisms (animals, fungi and protozoans) are chemoheterotrophs because they use organic carbon compounds for energy and tissue synthesis.

The term chemosynthesis is used to describe chemoautotrophic processes at hydrothermal vents (**Jannasch 1989**). This term is helpful because chemosynthesis and photosynthesis are both autotrophic processes; however, while both employ the same pathway for carbon fixation, chemosynthesis *consumes* oxygen whereas photosynthesis *produces* oxygen. Access to oxygenated sea water is therefore just as important for chemosynthetic communities as is access to reduced compounds. **Fisher** (1990) has pointed out that the methanotrophic bacterial symbionts, which are critical in the hydrocarbon seep communities, are not strictly autotrophs because they use methane, which is an organic compound, as a source of carbon. The important point is that certain bacteria can produce organic compounds in complete darkness and do so quite decoupled from the photosynthetic food chain that supports most life on earth.

Chemosynthesis is an entirely microbial process, but production by symbiotic chemosynthetic bacteria can support dense, thriving assemblages of higher organisms. The bacteria usually occur as intracellular symbionts in specially-evolved tube worms and bivalves: the host invertebrate provides protection and metabolic assistance in obtaining the reduced chemical substrates, while the bacteria perform the actual chemosynthesis. However, there are communities, such as those at the Mid-Atlantic Ridge, where the dominant invertebrates (shrimp) subsist by grazing on free-living chemosynthetic bacteria (Van Dover et al. 1988). The defining features of a chemosynthetic community are an interface between an abundant supply of reduced compounds and oxygenated seawater, and a population of invertebrates able to exploit, usually via symbiosis, the production of chemosynthetic bacteria. For the purposes of this report, we define a chemosynthetic community as *a persistent, largely sessile assemblage of marine organisms dependent upon chemosynthetic bacteria as the primary food source.*

3.0 World-Wide Chemosynthetic Communities—Historical Perspective

The initial discovery of chemosynthetic communities occurred unexpectedly during geological investigations of sea-floor spreading centers in the eastern Pacific Ocean. At these mid-ocean ridges, formation of new oceanic crust injects molten basalt. Seawater descends through the fractured crust, contacts the hot basalt, and is exhaled as a chemically enriched hydrothermal fluid through discrete vents along the ridge axis (Edmond et al. 1982). Photographs of dense assemblages of clams (later identified as *Calyptogena* sp.), which were taken by the photo-sled ANGUS (Lonsdale 1977), gave the first indication that hydrothermal venting might have a biological effect. Subsequently, the submarine *Alvin*, guided in part by the photographs, found an area where shimmering water indicated the active flux of hydrothermal fluids and dense invertebrate communities were found (Corliss et al. 1979).

This first community, which came to be known as Rose Garden, was colonized by clusters of the tube worm, *Riftia pachyptila*, a mussel, *Bathymodiolus thermophilus*, a clam, *Calyptogena magnifica*, and other sessile and mobile invertebrate species. All of these organisms were found at densities greatly exceeding those of the typical deep-sea benthos (Hessler and Smithey 1983; Hessler et al. 1985; Hessler et al. 1988a). The chemoautotrophic capacity of these fauna was first detected in the tube worm (Felbeck 1981; Cavanaugh et al. 1981) and was later demonstrated for clams and mussels as well (**Fisher 1990** and this report). This discovery, widely lauded as the most important finding of marine biology in the twentieth century, has since yielded a very large volume of published research (Jones and Bright 1985; Tunnicliffe 1991). Investigations at other ridge crest sites have subsequently documented numerous other examples of chemosynthetic communities sustained by hydrothermal venting.

In 1983, the submarine ALVIN was again involved in the discovery of chemosynthetic communities; in this case, they were associated with cold brine seepage in the Gulf of Mexico (Paull et al. 1984). At these sites, ancient brine descending through the porous carbonates of the Florida Platform emerges at the base of the Florida Escarpment. The fluid is denser than sea water and contains microbial methanes and sulfides from both geothermal and microbial sources (Cary et al. 1989; Cavanaugh et al. 1987; Paull and Neumann 1987). The density of the brine tends to impede its mixing with seawater and maintains discrete seeps where the escarpment wall and adjacent sediment meet (Cary et al. 1989, Paull and Neumann 1987). These seeps provide the interface between reduced compounds and oxygenated sea water needed for chemosynthesis, but the geological process that produces their habitat is distinctly less dynamic and vigorous than hydrothermal venting. The chemosynthetic fauna at the Florida Escarpment are functionally similar to hydrothermal vent fauna; tube worms and mytilid mussels and, very rarely, vesicomyid clams are present (R. Turner personal communication).

The existence of chemosynthetic communities at the Florida Escarpment proved that these fauna were not restricted to volcanically active areas. Discovery of the chemosynthetic communities associated with hydrocarbon seeps in the northern Gulf of Mexico came just months after the Florida Escarpment findings **(Kennicutt et al. 1985**. Additionally, deep sea communities of chemosynthetic fauna have been found in fossil water seeps associated with sediment accretion and compaction in subduction zones (Suess et al. 1985; Ohta and Laubier 1987; Faugères et al. 1987), sediment slumping caused by undersea earthquakes (Mayer et al. 1988), rotting deadfalls such as whale carcasses (Smith et al. 1989) and, recently, on sacks of rotting food-stuffs in a sunken ship (Dando et al., in press)

4.0 Gulf of Mexico Petroleum Seep Communities - Historical Perspective

A series of surface ship and submarine operations over the last seven years has identified numerous hydrocarbon seep communities in the Gulf of Mexico. The 1984 discovery of thermogenic gas hydrates in deep ocean sediments was the finding that maintained the early exploration (**Brooks et al. 1984**). Hydrates were recovered off Louisiana from water depths of 530 to 560 m on the continental slope in areas that were known to contain substantial oil seeps (Anderson et al. 1983). The hydrates, obtained by piston coring, ranged in size from minute crystals to pieces several centimeters in diameter. Hydrates were distributed from the top of the sediment column to a sediment depth of at least several meters. The hydrates were composed of hydrocarbon gases, including methane through butane, and were often dispersed in oil-stained carbonate rubble within the cores. At the time of the initial discoveries, the effect of oil-stained sediments and solid hydrates on the benthic ecology of the area was unknown.

The seismic signature of marine sediments typically features distinct stratification. Hydrocarbon seepage obscures these strata and produces a seismic "wipe-out" zone (**Behrens 1988**). Piston cores taken in wipe-out zones were often found to contain sediments with oil, gas, or gas hydrates. Trawls taken at two "wipe-out" zones retrieved hydrothermal vent-type organisms including bivalves, gastropods, and tubeworms (**Kennicutt et al. 1985**). Two cruises (86-G-1 and 86-G-2) were then undertaken to test the hypothesis that communities based on chemosynthesis are broadly distributed on the Gulf of Mexico continental slope in oil seep areas that could be identified geophysically by either seismic "wipe-out" zones or bubble plumes. Thirty-nine trawls were taken on the upper Gulf of Mexico slope in seismic "wipe-out" zones. Hydrothermal vent-type organisms (either tubeworms, mytilids and/or clams) were preferentially associated with "wipe-out" zones in the Green Canyon (11 sites), Garden Banks (4 sites), Ewing Bank (1 site) and East Breaks (1 site) lease areas. At 19 of the 39 trawl sites organisms contained $d^{13}C$-depleted tissues, indicative of chemosynthetically fixed carbon (**Kennicutt et al. 1988**). A number of new species of tube worms (M. Jones, Smithsonian Institution) and mytilids (R. Turner, Harvard University, R. Lutz and R. Gustavson, Rutgers University) are being described from the trawl collections.

The use of sulfur-based chemoautotrophy by the symbionts of the vestimentifera tube worms, the vesicomyid clams and lucinid clams from the trawl sites has been confirmed by a variety of techniques (**Brooks et al. 1987**). These organisms have been shown by electron microscopy to have bacterial endosymbionts. They possess the enzymes necessary to produce energy for the oxidation of sulfur compounds as well as to fix inorganic carbon. Substantial levels of elemental sulfur are also stored in their tissues.

The addition of sulfide has been shown to stimulate the fixation of carbon in vestimentiferans and may also stimulate carbon fixation in the clams (Fisher and Childress, in preparation). Thus it appears that these species rely primarily on sulfide-based chemosynthesis, but a complete carbon and energy budget is needed to confirm this. In contrast, one species (Seep Mytilid I) has methanotrophic symbionts and can potentially meet all of its carbon and energy needs from the uptake of methane (**Childress et al. 1986**; Fisher et al. 1987).

5.0 Management Issues Regarding Seep Communities

Ecologists were initially concerned with the age and species structure of chemosynthetic communities (c.f. Grassle 1986; Lutz et al. 1985), their persistence in the face of evident environmental instability (Fustec et al. 1987; Hessler et al. 1985, 1988b), and the zoogeographic problems raised by the extreme isolation of most vent fields (Tunnicliffe 1991, Tunnicliffe and Jensen 1987). The possibility that these communities could be directly affected by human activities remained remote so long as their occurrence was restricted to open ocean locations at near abyssal depths.

Discovery of chemosynthetic fauna at oil seeps in the northern Gulf of Mexico indicate that communities will be found in the one deep-sea benthic zone that is certain to be subject to human activity: oil seeps that are of primary interest to the energy industry. However, their discovery simultaneously placed the communities under the jurisdiction of U.S. environmental legislation, insuring that energy industry activities will be subject to regulatory restrictions (**MMS 1988**). With management concerns closer to the forefront, ecological investigations, while not altering their scope, acquired additional relevance. Any discussion of the structure, longevity, and propagation of chemosynthetic communities in the northern Gulf of Mexico must now be sensitive to how conclusions reached might affect development of management policy.

6.0 Geological Environments for Chemosynthetic Communities

Chemosynthetic communities occur primarily where geological factors concentrate certain reduced inorganic compounds at the seafloor, where they can be utilized by an opportunistic benthos. Thermal springs on mid-ocean ridges were the first such phenomena to be discovered (Corliss et al. 1979). Near the ridge axis, the process of seafloor spreading forms hot oceanic crust that is cooled by hydrothermal circulation. Hot water brings methane or organic matter to the seafloor in a reducing environment where microbes can metabolize H_2S or CH_4. Similar communities were found in other areas that did not have hydrothermal circulation. Gas and oil seeping into surficial sediments in the northern Gulf of Mexico provide the basis for many such colonies (**MacDonald et al. 1990b**). Brine seepages elsewhere in the Gulf do the same by carrying methane to the seafloor (Paull et al. 1984; **MacDonald et al. 1990a**). Chemosynthetic organisms have even been found on the Laurentian Fan, where slumping provided suitable nutrients by merely exposing organic rich layers (Mayer et al. 1988). Additionally, chemosynthetic organisms have been discovered in sites of conate outwatering of accretionary prisms in subduction zones (Swinbanks 1985; Suess et al. 1985; Kulm et al. 1986; Ohta and Laubier 1987).

Hydrocarbon and brine seeps appear to be widespread because of the world-wide abundance of oil basins and the salt associated with them. Hydrocarbon seeps have been found in the Gulf of Mexico (**MacDonald et al. 1990b**), California Borderland (Spies and Davis 1979; Richmond and

Burdick 1981), Alaska (Nelson et al. 1978; Kvenvolden et al. 1979), the North Sea (Hovland and Judd 1988), and Antarctica (Whiticar et al. 1985). They probably occur in any basin with significant accumulations of hydrocarbon source sediments (Link 1952; Landes 1973; Wilson et al. 1974; Hovland and Judd 1988). Though hydrocarbon seeps and seep communities have been widely observed, studies of these features and their organisms are still rudimentary, and, except for the Gulf of Mexico, chemosynthetic communities have not been documented. Most efforts have gone into descriptions of the communities and their local environments, but comparatively little has been written about the processes causing these environments, which would allow us to extrapolate this data to predict other occurrences.

7.0 Non-Symbiotic Microbiota as Associated with Chemosynthetic Communities

Members of the bacterial genus *Beggiatoa* are filamentous and gliding in character and have the capability of oxidizing reduced sulfur (hydrogen sulfide and thiosulfate) to elemental sulfur, which is deposited within the cells (Kowallik and Pringsheim 1966). Winogradsky worked with these organisms in the late 1800's, and while he did not obtain pure cultures, he believed them to be autotrophic in character and to require hydrogen sulfide (Winogradsky 1887). In 1912, Keil was able to work with pure cultures of *Beggiatoa* and demonstrated chemoautotrophic growth under microaerophilic conditions. More than 70 years elapsed before these observations were confirmed. During the intervening years, most of the work dealt with fresh water isolates, most commonly *B. alba* and *B. leptomitiformis*. These studies concerned enrichment and cultivation (Faust and Wolfe 1961; Strohl and Larkin 1978), heterotrophic and mixotrophic growth (Pringsheim 1970; Nelson and Castenholz 1981), utilization of sulfur compounds under aerobic and anaerobic conditions (Nelson and Castenholz 1981; Schmidt et al. 1987), and responses to light (Nelson and Castenholz 1982). In 1982, the isolation of marine strains of *Beggiatoa* and the demonstration of nitrogen fixation by these strains (and not by comparable freshwater strains) suggested an interesting link between the sulfur and nitrogen cycles (Nelson et al. 1982). Using one of these strains in gradient cultures, the work of Winogradsky and Keil was substantiated by Nelson and Jannasch (1983) who demonstrated autotrophic CO_2 fixation and RuBP-carboxylase activity.

In addition to fresh water environments, *Beggiatoa* sp. have been observed as dense mats on both coastal (Grant and Bathmann 1897) and deep sea sediments (Nelson et al. 1989; Jannasch et al. 1989). In the latter case, the massive aggregations are located at a hydrothermal vent (HTV) site, specifically the Guaymas Basin. While *Beggiatoa* filaments had been noted at other deep sea hydrothermal vent sites (Jannasch and Wirsen 1981), they were never as massive in appearance as at the Guaymas Basin. Recently, mats of these organisms have been observed at deep sea seep sites that are not hydrothermal in character, such as the cold petroleum seeps in the Gulf of Mexico, which are the basis for the present study.

8.0 Physiology, Biochemistry, and Ecology of Vent and Seep Invertebrates with Chemoautotrophic or Methanotrophic Symbionts

The discovery of thriving biological communities associated with hydrothermal vents (HTV) in 1977 (Corliss et al. 1979) captured the immediate interest of marine scientists and the general public. Since then, similar communities have been discovered at numerous other HTVs and a variety of sites, known collectively as cold seeps, where the flux of chemically enriched fluids is diffused through an overlying sediment drape. Hydrocarbon seeps are one form of cold seep. The abundant biomass of the chemosynthetic communities at hydrothermal vents and cold seeps is mainly supported by the symbiosis of chemoautolithotrophic bacteria and sessile invertebrates. Three types of symbiont-hosting organisms predominate the HTV communities: tube worms (Phylum Vestimentifera, Jones, c.f. *Riftia pachyptila*), clams (Vesicomyidae c.f. *Calyptogena magnifica*), and mussels (Mytilidae, Bathymodilinae *Bathymodilous thermophylis*). Tunnicliffe (1991) lists some 260 species among 33 orders in her review of the biology of hydrothermal vents. Collectively, the fauna of these communities is taxonomically distinctive; sixteen new families have been described from collections of vent and seep animals (Grassle 1985). The density of individuals in the tube worm thickets and mussel beds that are typical of these communities is particularly impressive when compared to the low faunal abundances of the surrounding deep sea floor (Hessler and Smithey 1983). These animals comprise a previously unknown type of ecosystem (Reviewed by Grassle 1986; Jones 1985; Fisher 1990; Childress and Fisher 1992).

Since the original discovery of the hydrothermal vent communities, chemoautotrophic symbioses have been demonstrated in over 100 species of marine invertebrates (and inferred in many more) found in a variety of both deep-sea and near-shore habitats (See reviews by Reid and Brand 1986; Southward 1987; Fisher 1990; Somero et al. 1989). The differences in species composition among the various known communities suggest that they have arisen from distinct colonization and adaptational histories. The major sessile fauna of the shallow HS sites in the Gulf of Mexico are similar to that of many HTV sites, but differ in their comparatively shallow depths of occurrence (~500 m versus ~2000 m depths at the HTVs). This adaptation to relatively low pressures allows specimens of the fauna to be maintained alive without use of pressurized aquaria. This greatly facilitates successful completion of experiments that require living or fresh tissue.

Vestimentiferans, vesicomyid clams, and mytilids are represented at the cold hydrocarbon seep sites in the Gulf of Mexico, as are two other families of bivalves with chemoautotrophic symbionts (Solemyids and Lucinids). In addition, a small pogonophoran is abundant at some of the sites. Bivalves from the Solemyid and Lucinid families are found in numerous marine reducing environments and in general do not require a dynamic vent/seep environment.

9.0 Regional Distribution of Chemosynthetic Fauna and the Design of the Field Program

In the years since the initial discovery of chemosynthetic communities dependent on hydrocarbon seepage in the Gulf of Mexico (**Kennicutt et al. 1985**), investigations have expanded their geographic range to include the Texas, Louisiana, and Alabama continental slope, (depth range <500 to 2200 m). The variety of geologic processes that can be expected to support chemosynthetic communities has also been expanded. Surveys and collections made from submarines have been the principal methods used for this research, but geophysical and geochemical data have also made a significant contribution. In Section 2.0, we defined a chemosynthetic community as a persistent, deep-water aggregation of sessile metazoans supported by chemoautotrophic bacteria—usually symbionts. Functionally, this definition adequately describes all of the Gulf of Mexico communities. However, the spatial boundaries, temporal longevity, and species compositions that characterize chemosynthetic communities at hydrocarbon seeps have not yet been defensibly established. Nor is it clear that these characteristics can be rigorously determined by observations from a submarine when the field of view is restricted, position is known only approximately, and sampling sites are selected subjectively. These concerns must be addressed to quantify the number, extent, or biomass of seep communities, or to gain insight into the underlying geological processes that support seep communities.

Analysis of existing data and new field efforts for the Chemosynthetic Ecosystems Study are organized in relation to six study sites, designated here by the lease block in which they are located: Viosca Knoll 826, Green Canyon 184/5, 233/234, and 272, Garden Banks 386, and Alaminos Canyon 645 (see Table 1 and Figure 1). General descriptions of the communities and the geological environment of the sites have been developed by analysis of the videotaped observations from the *NR-1* and *Johnson-Sea-Link* cruises (see below). These descriptions also contribute to the general categorization of chemosynthetic communities in this region. Within each site, we have established sampling stations by deploying permanent markers (e.g. cement-filled buckets or small buoys) at representative points within each community. The stations will be subject to thorough photographic documentation as a means for assessing natural changes in the communities. They will also be the locations for recoverable experiments (e.g. growth experiments) and collection of water and sediment samples.

Table 1. Sites where chemosynthetic metazoans have been collected by trawl (Trl) or submarine (Sub), or definitively photographed by submarine, remotely-operated vehicle (ROV), or photosled (Photosl). Numbers in map code column refer to positions charted in Fig. 1; observations from sites separated by less than 1 NM have been pooled; Fauna indicates the type of chemosynthetic fauna found: V=vestimentiferan tube worms, M=Seep Mytilids, C=vesicomyid or lucinid clams, PG=pogonophoran tube worms; codes in bold face followed by asterisk (e.g. **1* VM**) are Sampling Sites for the present study. Lease block designators follow MMS standard abbreviations. Depths for trawl collections or pooled data are approximations. Data sources give precedence to observations published in the open literature.

Map code (Fig 1)	Fauna	Latitude (North)	Longitude (West)	MMS Lease Block	Depth (m)	Obs method	Data source
1*	**VM**	26°21.20'	94°29.80'	AC0645	2200	Sub	1
2	M	27°23.50'	94°29.45'	EB0602	1111	Trl	2
3	PG	27°27.55'	93°08.60'	GB0500	734	Trl	2
4	VC	27°30.05'	93°02.01'	GB0458	757	Trl	2
5	M	27°31.50'	92°10.50'	GB0476	750	Sub	3
6	MC	27°33.40'	92°32.40'	GB0424	570	Sub	3
7	V	27°35.00'	92°30.00'	GB0425	600	Sub	3
8	VC	27°34.50'	92°55.95'	GB0416	580	Sub	3
9	VC	27°36.00'	94°46.00'	EB0376	776	Sub	3
10	PG	27°36.15'	94°35.40'	EB0380	793	Trl	2
11	MC	27°36.50'	92°28.94'	GB0382	570	Sub	3
12	VC	27°36.60'	94°47.35'	EB0375	773	Trl	2
13*	**VC**	27°36.82'	92°15.25'	GB0386	585	Sub, Trl	2, 3
14	VC	27°37.15'	92°14.40'	GB0387	781	Sub, Trl	2, 3
15	V	27°37.75'	91°49.15'	GC0310	780	Trl	2
16	VC	27°38.00'	92°17.50'	GB0342	425	Trl	2
17	C	27°39.15'	94°24.30'	EB0339	780	Trl	2
18	C	27°39.60'	90°48.90'	GC0287	994	Trl	2
19	C	27°40.45'	90°29.10'	GC0293	1042	Trl	2
20	VC	27°40.50'	92°18.00'	GB0297	589	Trl	2
21*	**VMC**	27°40.88'	91°32.10'	GC0272	720	Sub, Trl	2, 3, 4
22	VC	27°42.65'	92°10.45'	GB0300	719	Trl	2
23	V	27°43.10'	91°30.15'	GC0229	825	Trl	2
24*	**VM**	27°43.30'	91°16.30'	GC0233	650	Sub	5
25	VMC	27°43.70'	91°17.55'	GC0233	813	Trl	2
26	VM	27°44.08'	91°15.27'	GC0234	600	Sub	3, 6
27	VM	27°44.30'	91°19.10'	GC0232	807	Sub	3
28*	**VM**	27°44.80'	91°13.30'	GC0234	550	Sub	3, 7
29	VC	27°45.00'	90°16.31'	GC0210	715	Sub	3
30	C	27°45.50'	89°58.30'	GC0216	963	Sub, Photosl	8, 2
31	VMC	27°46.33'	90°15.00'	GC0210	796	Sub	3
32*	**VM**	27°46.65'	91°30.35'	GC0184/5	580	Sub, Trl	2, 3, 9
33	VM	27°46.75'	90°14.70'	GC0166	767	Sub, Trl	2, 3
34	VM	27°49.16'	91°31.95'	GC0140	290	Sub	10
35	V	27°50.00'	90°19.00'	GC0121	767	Sub	3
36	VM	27°53.56'	90°07.07'	GC0081	682	Photosl	11
37	VC	27°54.40'	90°11.90'	GC0079	685	Trl	2
38	VM	27°55.50'	90°27.50'	GC0030	504	Sub	3
39	VPG	27°56.65'	89°58.05'	GC0040	685	Trl	2
40	C	27°57.10'	89°54.30'	MC0969	658	Trl	2
41	V	27°57.25'	89°57.50'	EW1010	597	Sub, Trl	2, 3
42	V	27°58.70'	90°23.40'	EW1001	430	Sub, Trl	2, 3
43*	**VC**	29°11.00'	88°00.00'	VK0826	545	Sub, ROV, Trl	3, 4, 12

Data sources: 1–**McDonald et al** (Submitted), 2–**Kennicutt et al.** (1988), 3–GERG unpubl. data, 4-**Callender et al.** (1990), 5–**MacDonald et al.** (1990b), 6–MacDonald (1990b), 7–MacDonald et al. (1990a), 8–Rosman et al. 1987, 9–**MacDonald et al.** (1989), 10–Roberts et al. (1990), 11–Boland 1986, 12–Boss (1968), Gallaway et al. (1990), Volkes (1963).

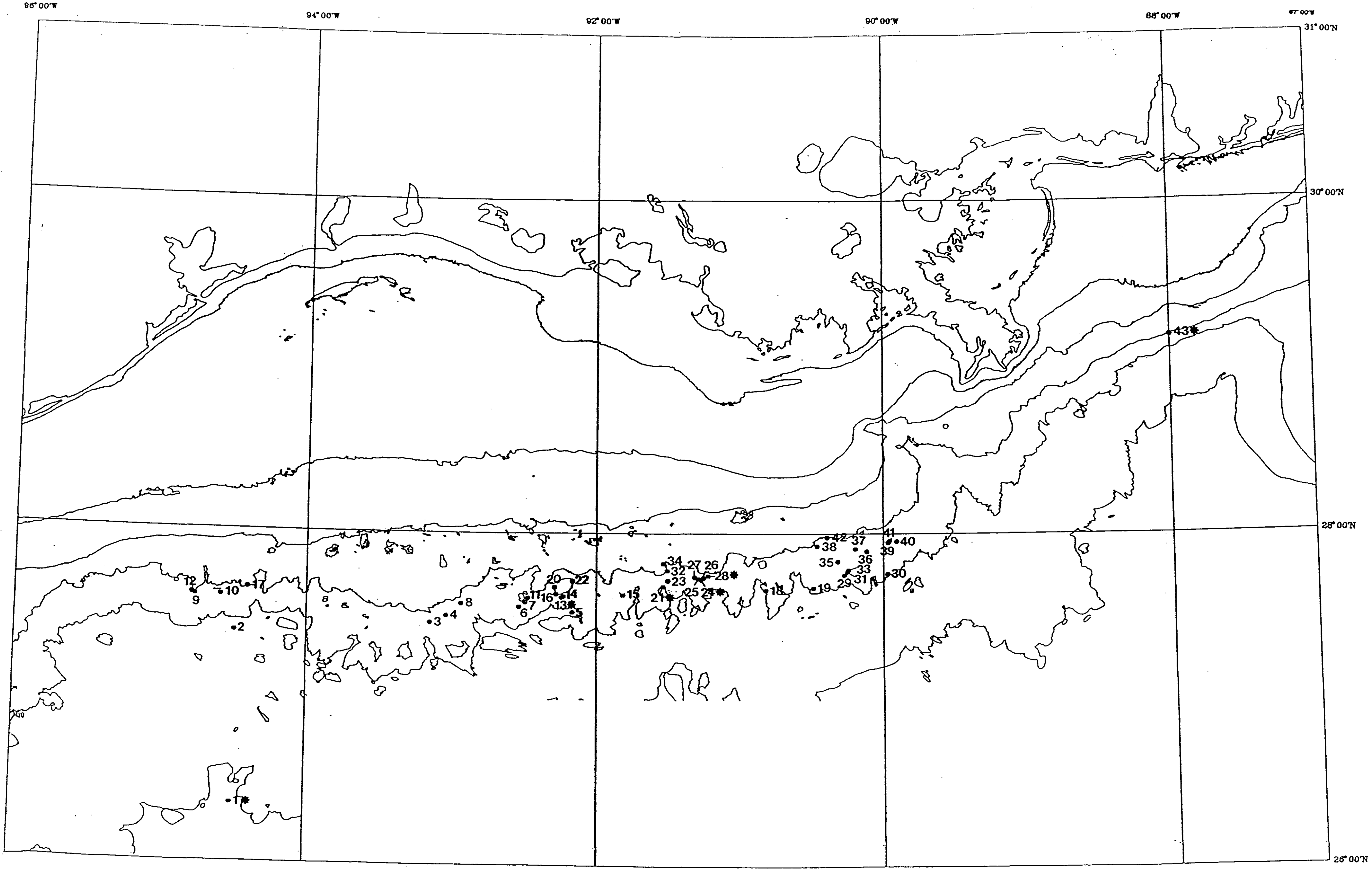
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Figure 1. Locations where vestimentiferan tube worms, seep mytilids, or vesicomyid clams have been collected or photographed in the northern Gulf of Mexico. Observations separated by less than 1 NM have been pooled. Numbers refer to Table 1; locations marked with and asterisk (*) are Study Sites for the MMS Chemosynthetic Ecosystems Study.

10.0 Literature Cited

Anderson, R.K., R.S. Scalan, P.L. Parker, and E.W. Behrens. 1983. Seep oil and gas in Gulf of Mexico slope sediment. Science, 222:619-621.

Behrens, E.W. 1988. Geology of a continental slope oil seep, northern Gulf of Mexico. AAPG Bull., 72:105-114.

Boland, G.S. 1986. Discovery of co-occurring bivalve Acesta sp. and chemosynthetic tube worms Lamellibrachia. Nature (London), 323: 759.

Boss, K.J. 1968. New species of *Vesicomyidae* from the Gulf of Darien, Caribbean Sea (Bivalvia; Mollusca). Bull. Mar. Sci., 18:731-748.

Brooks, J.M., M.C. Kennicutt II, R.R. Fay, T.J. McDonald, and R. Sassen. 1984. Thermogenic gas hydrates in the Gulf of Mexico. Science, 225:409-411.

Brooks, J.M., M.C. Kennicutt, C.R. Fisher, S.A. Macko, K. Cole, J.J. Childress, R.R. Bidigare, and R.D. Vetter. 1987. Deep-sea hydrocarbon seep communities: evidence for energy and nutritional carbon sources. Science, 20:1138-1142.

Cary, C., B. Fry, H. Felbeck, and R.D. Vetter. 1989. Multiple trophic resources for a chemoautotrophic community at a cold water brine seep at the base of the Florida escarpment. Mar. Biol., 100:411.

Cavanaugh, C.M., S.L. Gardiner, M.L. Jones, H.W. Jannasch, and J.B. Waterbury. 1981. Prokaryotic cells in the hydrothermal vent tube worm, *Rifita pachyptila*: possible chemoautotrophic symbionts. Science, 213:340.

Cavanaugh, C.M., P.R. Levering, J.S. Maki, M.E. Lidstrom, and R. Mitchell. 1987. Symbiosis of methylotrophic bacteria and deep-sea mussels. Nature, 325:346-348.

Childress, J.J. and C.R. Fisher. 1992. The biology of hydrothermal vent animals: physiology, biochemistry and autotrophic symbiosis. Oceanogr. Mar. Biol. Annu. Rev., 30:337-341.

Childress, J.J., C.R. Fisher, J.M. Brooks, M. C. Kennicutt, II, R. Bidigare, and A. Anderson. 1986. A methanotrophic marine molluscan symbiosis: mussels fueled by gas. Science, 233:1306-1308.

Corliss, J.B., J. Dymond, L. Gordon, J.M. Edmond, R.P. von Herzen, R.D. Ballard, K. Green, D. Williams, A. Bainbridge, K. Crane, and T. H. van Andel. 1979. Submarine thermal springs on the Galapagos Rift. Science, 203:1073-1083.

Dando, P.R., A.J. Southward, and E.C. Southward. In press. Cold-seep fauna in sunken ship on the Iberian slope. Nature.

Edmond, J.M., K.L. Von Damm, R.E. McDuff, and C.I. Measures. 1982. Chemistry of hot springs on the East Pacific Rise and their effluent dispersal. Nature, 297:187-191.

Faugères, J-C., D. Desbruyères, E. Gonthier, R. Griboulard, J. Poutiers, A. de Resseguier, and G. Vernette. 1987. Témoins sédimentologiques et viologiques de l'activité tectonique actuelle du prisme d'accrétion de la Barbade. Compte Rendu de l'Academie de science Paris II, 305:115-119.

Faust, L. and R.S. Wolfe. 1961. Enrichment and cultivation of *Beggiatoa alba.* J. Bacteriol., 81:99-106.

Felbeck, H. 1981. Chemoautotrophic potential of the hydrothermal vent tube worm *Rifita pachyptila* Jones (Vestimentifera). Science, 213:336-338.

Fisher, C.R. 1990. Chemoautotrophic and methanotrophic symbionts in marine invertebrates. Aquatic Sciences, 2:399-436.

Fisher, C.R. and J.J. Childress. 1992. Organic carbon transfer from methanotrophic symbionts to the host hydrocarbon-seep mussel. Symbiosis, in press.

Fisher, C.R., J.J. Childress, R.S. Oremland, and R.R. Bidigare. 1987. The importance of methane and thiosulphate in the metabolism of the symbionts of two deep-sea mussels. Mar. Biol., 96:59-71.

Fustec, A., D. Desbruyères, and S. Kim Juniper. 1987. Deep-sea hydrothermal vent communities at 13°N on the East Pacific Rise: microdistribution and temporal variations. Biol. Oceanogr., 4:121-164.

Gallaway, B.J., L.R. Martin, and G.F. Hubbard. 1990. Characterization of the chemosynthetic fauna at Viosca Knoll Block 826. Unpublished report to Oryx Energy Inc. LGL Ecological Research Assoicates Inc., Dec. 1990. 35 pp. maps and photographs.

Grant, J. and U.V. Bathmann. 1987. Swept away: resuspension of bacterial mats regulates benthic-pelagic exchange of sulfur. Science, 236:1472-2474.

Grassle, J.F. 1985. Hydrothermal vent animals: distribution and biology. Science, 229:713-717.

Grassle, J.F. 1986. The ecology of deep-sea hydrothermal vent communities. Adv. in Mar. Biol., 23:301-362.

Hessler, R.R. and W.M. Smithey, Jr. 1983. The distribution and community structure of megafauna at the Galápagos Rift hydrothermal vents. In: Rona P.A., K. Boström, L. Laubier, and K.L. Smith Jr., eds. Hydrothermal processes at seafloor spreading centers. New York: Plenum Press. pp. 735-770.

Hessler, R., P. Lonsdale, and J. Hawkins. 1988a. Patterns on the ocean floor. New Scientist, 24:47-51.

Hessler, R.R., W.M. Smithey, M.A. Boudrias, C.H. Keller, R.A. Lutz, and J.J. Childress. 1988b. Temporal change in megafauna at the Rose Garden hydrothermal vent (Galapagos Rift; eastern tropical Pacific). Deep-Sea Res., 35:1681-1709.

Hessler, R.R., W.M. Smithy, and C.H. Keller. 1985. Spatial and temporal variation of giant clams, tubeworms and mussels at deep-sea hydrothermal vents. In: Jones, M.L., ed. Hydrothermal vents of the eastern pacific: an overview. Bull. Biol. Soc. Wash., 6:411-428.

Hovland, M. and A.G. Judd. 1988. Seabed pockmarks and seepages. London: Graham and Trotman. 293 pp.

Jannasch, H.W. 1989. Chemosynthetically sustained ecosystems in the deep sea. In: Schlegel, H.G. and B. Bowien, eds. Autotrophic bacteria. Springer Verlag (Berlin), pp. 147-166.

Jannasch, H.W. and C.O. Wirsen. 1981. Morphological survey of microbial mats near deep-sea thermal vents. Appl. Environ. Microbiol., 41:528-538.

Jannasch, H.W., D.C. Nelson, and C.O. Wirsen. 1989. Massive natural occurrence of unusually large bacteria (*Beggiatoa* sp.) at a hydrothermal deep-sea vent site. Nature, 342:834-836.

Jones, M.L. 1985. On the Vestimentifera, new phylum: six new species and other taxa from hydrothermal vents and elsewhere. Bull. Biol. Soc. Wash., 6:117-158.

Jones, M.L. and C.F. Bright. 1985. Bibliography of hydrothermal vents and related areas, their bioats, ecological parameters and ancillary data. Bull. Biol. Soc. Wash., 6:495-438.

Kennicutt II, M.C., J.M. Brooks, R.R. Bidigare, and G.J. Denoux. 1988. Gulf of Mexico hydrocarbon seep communities – I. Regional distribution of hydrocarbon seepage and associated fauna. Deep-Sea Res., 35:1639-1651.

Kennicutt II, M.C., J.M. Brooks, R.R. Bidigare, R.R. Fay, T.L. Wade, and T.J. McDonald. 1985. Vent-type taxa in a hydrocarbon seep region on the Louisiana slope. Nature, 317:351-353.

Kowallik, U. and E.G. Pringsheim. 1966. The oxidation of hydrogen sulfide by *Beggiatoa*. Am. J. Bot., 53:801-806.

Kulm, L.D., E. Suess, J.C. Moore, B. Carson, B.T. Lewis, S.D. Ritger, D.C. Kadko, T.M. Thornburgh, R.W. Embley, W.D. Rugh, G.J. Massoth, M.G. Langseth, G.R. Cochrane, and R.L. Scamman. 1986. Oregon subduction zone: Venting, fauna, and carbonates. Science, 231:561-566.

Kvenvolden, K.A., C.H. Nelson, D.R. Thor, M.C. Larsen, G.D. Redden, J.B. Rapp, and D.J. DesMarais. 1979. Biogenic and thermogenic gas in gas-charged sediments of Norton Sound, Alaska. Offshore Technology Conference, Houston, Texas, Paper 3412.

Landes, K.K. 1973. Mother nature as an oil polluter. AAPG Bull., 57:637-641.

Link, W.K. 1952. Significance of oil and gas seeps in world oil exploration. AAPG Bull., 36:1505-1540.

Lonsdale, P. 1977. Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. Deep-Sea Res., 24:857-863.

Lutz, R.A., L.W. Fritz, and D.C. Rhoads. 1985. Molluscan growth at deep-sea hydrothermal vents. Bull. Biol. Soc. Wash., 6:199-210.

MacDonald, I.R., G.S. Boland, J.S. Baker, J.M. Brooks, M.C. Kennicutt II, and R.R. Bidigare. 1989. Gulf of Mexico hydrocarbon seep communities II. Spatial distribution of seep organisms and hydrocarbons at Bush Hill. Marine Biology (Berlin), 101:235-247.

MacDonald, I.R., N.L. Guinasso, Jr. , J.F. Reilly, J.M. Brooks, W.R. Callender, and S.G. Gabrielle. 1990a. Gulf of Mexico hydrocarbon seep communities: VI. Patterns in community structure and habitat. Geo-Mar. Let., 10:4 244-252.

MacDonald, I.R., J.F. Reilly II, N.L. Guinasso, Jr., J.M. Brooks, R.S. Carney, W.A. Bryant, and T.J. Bright. 1990b. Chemosynthetic mussels at a brine-filled pockmark in the northern Gulf of Mexico. Science, 248:1096-1099.

Mayer, L.A., A.N. Shor, J.H. Clarke, and D.J.W. Piper. 1988. Dense biological communities at 3850 m on the Laurentian Fan and their relationship to the deposits of the 1929 Grand Banks earthquake. Deep-Sea Res., 35:1235-1246.

Minerals Management Service. 1988. Implementation of measures to detect and protect deep water chemosynthetic communities. MMS Gulf of Mexico Regional OCS Office. Notice to lessees and operators of federal oil and gas leases in the outer continental shelf Gulf of Mexico. 88-11:1-3.

Nelson, D.C. and R.W. Castenholz. 1981. Use of reduced sulfur compounds by *Beggiatoa* sp. J. Bacteriol., 147:140-154.

Nelson, D.C. and R.W. Castenholz. 1982. Light responses of *Beggiatoa*. Arch. Microbiol., 131:146-155.

Nelson, D.C. and H.W. Jannasch. 1983. Chemoautotrophic growth of a marine Beggiatoa in sulfide-gradient cultures. Arch. Microbiol., 136:262-269.

Nelson, C.H., K.A. Kvenvolden, and E.C. Clukey. 1978. Thermogenic gas in sediment of Norton Sound, Alaska. Offshore Technology Conference, Hoston, Texas, Paper 3354.

Nelson, D.C., J.B. Waterbury, and H.W. Jannasch. 1982. Nitrogen fixation and nitrate utilization by marine and freshwater *Beggiatoa*. Arch. Microbiol., 133:172-177.

Nelson, D.C., C.O. Wirsen, and H.W. Jannasch. 1989. Characterization of large autotrophic *Beggiatoa* abundant at hydrothermal vents of the Guaymas Basin. Appl. Environ. Microbiol., 55:2909-2917.

Ohta, S. and L. Laubier. 1987. Deep biological communities in the subduction zone of Japan from bottom photographs taken during 'Nautile' dives in the Kaiko project. Earth and Planetary Science Letters, 83:329-342.

Paull, C.K. and A.C. Neumann. 1987. Continental margin brine seeps: their geological consequences. Geology (Boulder), 15:545-548.

Paull, C.K., B. Hecker, R. Commeau, R.P. Freeman-Lynde, C. Neumann, W.P. Corso, S. Golubic, J.E. Hook, E. Sikes, and J. Curray. 1984. Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. Science, 226:965-967.

Pringsheim, E.G. 1970. Contributions toward the development of general microbiology. Ann. Rev. Microbiol., 24:1-16.

Reid, R.G.B. and D.G. Brand. 1986. Sulfide-oxidizing symbiosis in Lucinaceans: implications for bivalve evolution. Veliger, 29:3-24.

Richmond, W.C. and D.J. Burdick. 1981. Geologic hazards and constraints of offshore northern and central California. Offshore Technology Conference, Houston, Texas, Paper 4117.

Roberts, H.H., P. Aharon, R. Carney, J. Larkin, and R. Sassen. 1990. Sea floor responses to hydrocarbon seeps, Louisiana continental slope. Geo-Mar. Let., 10(4):232-243.

Rosman, I., G.S. Boland, and J.S. Baker. 1987. Epifaunal aggregations of Vesicomyidae on the continental slope off Louisiana. Deep-Sea Res., 34:1811-1820.

Schmidt, T.M., B. Arieli, Y. Cohen, E. Padank, and W.R. Strohl. 1987. Sulfur metabolism in *Beggiatoa alba.* J. Bacteriol., 169:5466-5472.

Smith, C.R., H. Kukert, R.A. Wheatcroft, P.A. Jumars, and J.W. Deming. 1989. Vent fauna on whale remains. Nature (London), 34: 27-28.

Somero, G.N., A.E. Anderson, and J.J. Childress. 1989. Transport, metabolism and detoxification of hydrogen sulfide in animals from sulfide rich marine environments. Rev. Aquat. Sci., 1:591-614.

Southward, E.C. 1987. Contribution of symbiotic chemoautotrophs to the nutrition of benthic invertebrates. Microbes in the sea. Chichester: Horwood Ltd.

Spies, R.B. and P.H. Davis. 1979. The infaunal benthos of a natural oil seep in the Santa Barbara Channel. Mar. Biol., 50:227-237.

Strohl, W.R. and J.M. Larkin. 1978. Enumeration, isolation and characterization of *Beggiatoa* from freshwater sediments. Appl. Environ. Microbiol., 36: 755-770.

Suess, E., B. Carson, S.D. Ritger, J.C. Moore, M.L. Jones, L.D. Kulm, and G.R. Cochrane. 1985. Biological communities at vent sites along the subduction zone off Oregon. Bull. Biol. Soc. Wash., 6:475-484.

Swinbanks, D. 1985. Japan finds clams and trouble. Nature, 315:624.

Tunnicliffe, V. 1991. The biology of hydrothermal vents: ecology and evolution. Oceanography and Marine Biology Annual Rev., 29:1-85.

Tunnicliffe, V. and R.G. Jensen. 1987. Distribution and behavior of the spider crab *Macroregonia macrochira* Sakai (Brachyrura) around the hydrothermal vents of the northeast Pacific. Can. Journal of Zoology, 65:2443-2449.

Van Dover, C.L., B. Fry, J.F. Grassle, S. Humphris, and P.A. Rona. 1988. Feeding biology of the shrimp *Rimicaris exoculata* at hydrothermal vents on the Mid-Atlantic Ridge. Mar. Biol., 98:209-216.

Volkes, H.E. 1963. Studies on tertiary and recent giant Limidae. Tulane Studies in Geology, 1(2):75-92.

Whiticar, M.J., E. Suess, and H. Wehner. 1985. Thermogenic hydrocarbons in surface sediments of the Bransfield Strait, Antarctic Peninsula. Nature, 314:87-90.

Wilson, R.D., P.H. Monoghan, A. Osanik, L.C. Price, and M.A. Rogers. 1974. Natural marine oil seepage. Science, 184:857-865.

Winogradsky, S. 1887. Uber Schwfelbakterien. Botanical Centralblatt, 45: 489-507.

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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.