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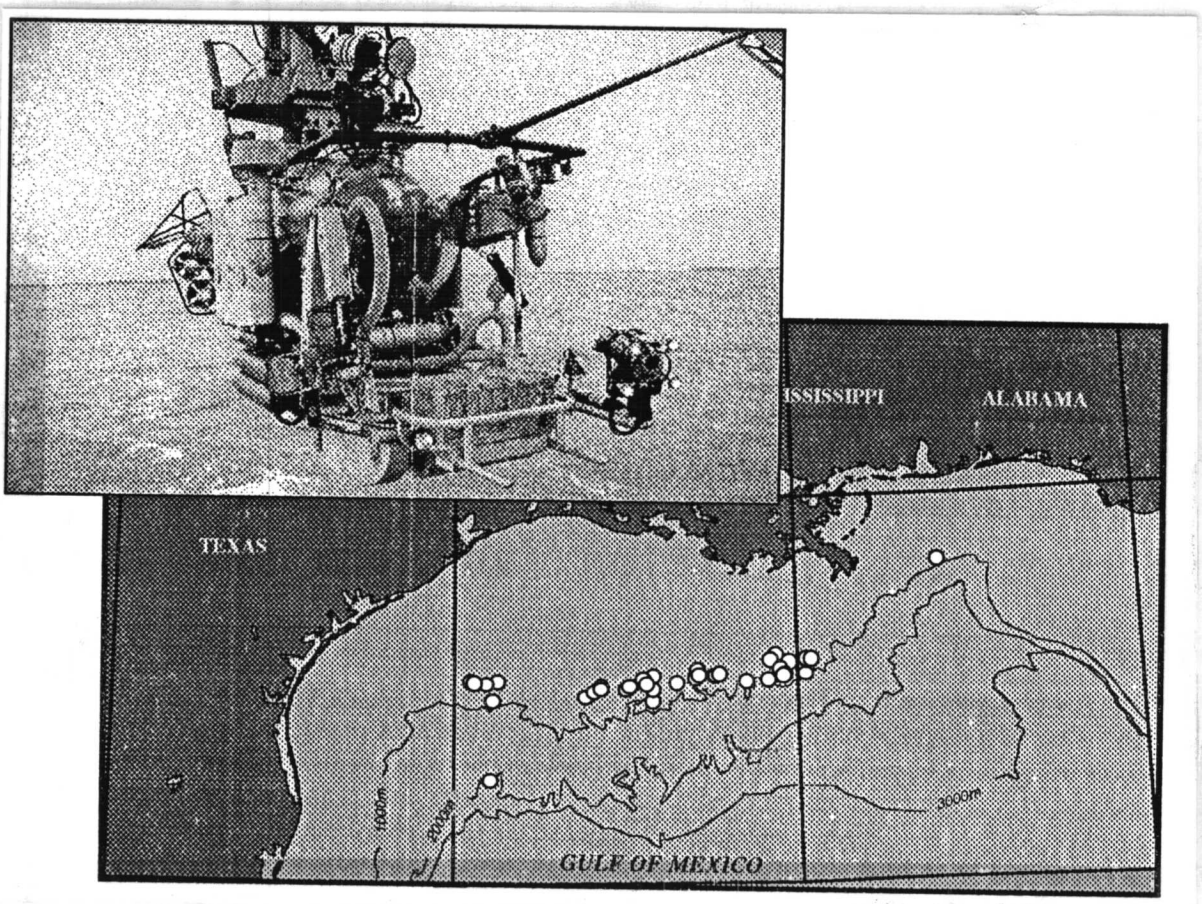
MMS 92-0034

Northern Gulf of Mexico

Chemosynthetic Ecosystems Study

Literature Review and Data Synthesis

Volume II: Technical Report



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

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Literature Review and Data Synthesis

Volume II: Technical Report

Editor

Ian R. MacDonald

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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.

ABSTRACT

The Chemosynthetic Ecosystems Study is a three-year program that has been undertaken to determine the geological, geochemical, physiological, and ecological factors that control the formation and persistence of chemosynthetic communities at hydrocarbon seeps. Dense aggregations of vestimentiferan tube worms, mytilid mussels, and vesicomyid clams are known to colonize natural hydrocarbon seeps in the northern Gulf of Mexico at wide-spread locations in water depths of 300 to 2200 m. These animals derive all of their food from chemoautotrophic bacterial symbionts, which in turn utilize sulfide and methane associated with the seeping hydrocarbons. The aggregations thus exploit a food supply entirely decoupled from sunlight and surface productivity. The aggregations generally support communities of heterotrophic animals such as fish or crustaceans, many of which are common elsewhere on the continental slope. Because the communities are comparatively lush, and because they occur in seafloor localities that are likely to be near to drilling or energy production activities, there is concern to protect them from possible harmful impact. This report reviews literature pertinent to the study and synthesizes previously collected data. The report comprises an Executive Summary, which presents a brief overview of the findings, a Technical Report, which presents the detailed findings, and an Appendix volume, which includes 19 papers considered to be core literature on the subject.

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1.0 Introduction

I.R. MacDonald and J.M. Brooks

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 (Table 1.1 lists the names, responsibilities, and affiliations of the PIs). 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 (Figure 1.1 shows a project time-line). 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.

The terms of the Study specify the first report as a synthesis volume describing chemosynthetic communities in general, comparing the communities in the northern Gulf of Mexico with those in other areas of the World Ocean, and offering a conceptual framework for the biological and non-biological processes that limit their development, distribution, growth, and structure in this region. In fulfilling these terms, there are a variety of materials to present. Although recently inaugurated, the Study has its inception in discoveries dating from 1984 (Paull et al. 1984; **Kennicutt et al. 1985**), and in results obtained from a steady progression of research during the intervening years. Consequently, many of the requirements for this report have been met in part or full in peer-reviewed literature published by the PIs. Other requirements, such as information on the regional distribution of communities, benefit from inclusion of the most recent

Table 1.1. Principal Investigators for the Chemosynthetic Ecosystems Study. Affiliation abbreviations are:

TAMU *Texas A&M University*;
GERG *Geochemical and Environmental Research Group*;
OCNG *Oceanography Department*;
LSU *Louisiana State University*;
PSU *Pennsylvania State University*;
WHOI *Woods Hole Oceanographic Institution*;
UA/DISL *University of Alabama Dauphin Island Sea Lab.*

Principal Investigator	**Affiliation**	**Major Responsibility**
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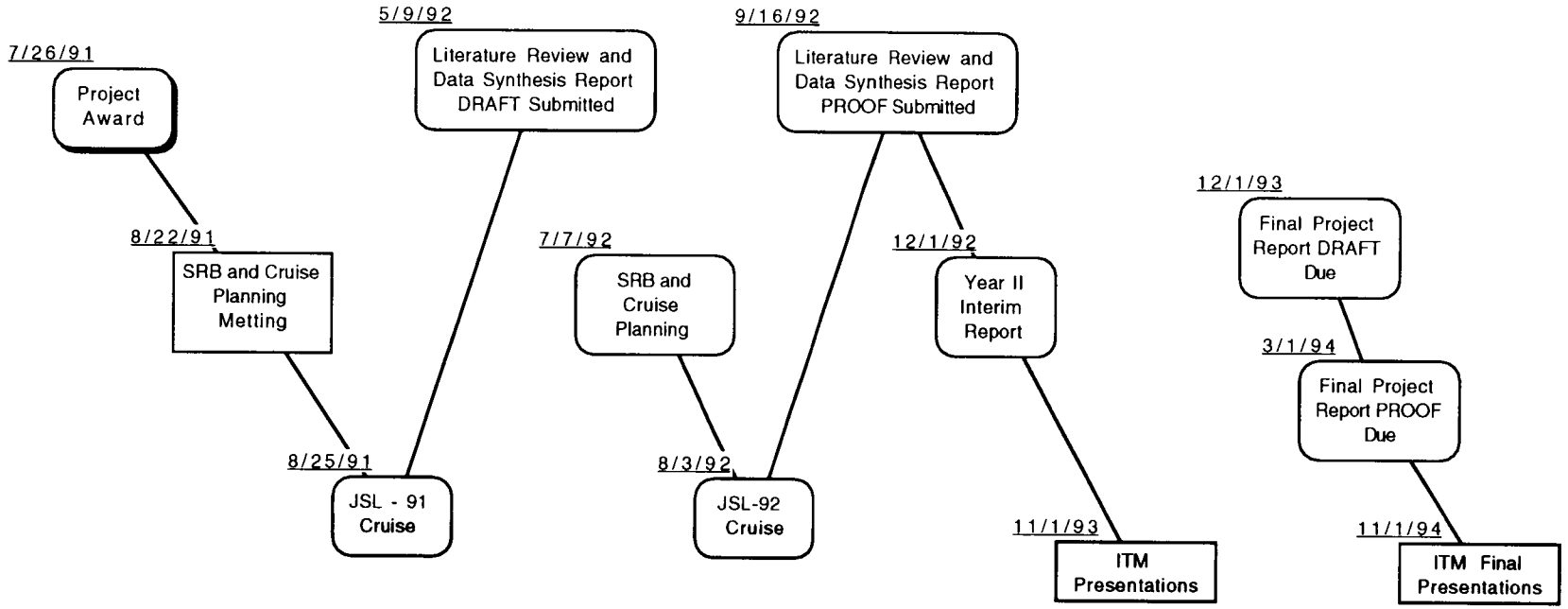


Figure 1.1 Project timeline.

findings. Additionally, the microbiology work unit has been completed and is ready for dissemination with this report.

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).

1.1 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.*

1.2 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 (Edmonds 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).

1.3 Gulf of Mexico Petroleum Seep Communities - A 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 $\delta^{13}C$-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).

Stable carbon isotopic analysis of more than 200 selected organisms from the 39 trawls confirmed the importance of chemosynthetic production

for the benthic ecosystem at the wipe-out areas. Vestimentiferans, pogonophorans, mytilids, and clams contained tissues with $\delta^{13}C$ values that indicate a chemosynthetic carbon source (Figure 1.2). The $\delta^{13}C$ notation is defined as follows:

$$\delta^{13}C = \frac{(^{13}C/^{12}C)\ \text{sample} - (^{13}C/^{12}C)\ \text{PDB}}{^{13}C/^{12}C\ \text{PDB}} \times 1000$$

where PDB is a PeeDee Belemnite standard. Non-chemosynthetic organisms were in the -14 to -22‰ range. Vestimentiferans and pogonophoran tissues had $\delta^{13}C$ values ranged from -20 to -58‰. All pogonophoran tubes and tissues had $\delta^{13}C$ values (-30 to -58‰) indicative of chemosynthetic carbon. However, $\delta^{13}C$ of the vestimentiferan tubes values ranged from -20 to -56‰, with three values greater than -28‰. The wide distribution of the $\delta^{13}C$ values of the vestimentiferan tubes probably results from different degrees of fractionation due to differing growth rates or variations in bacterial complements. The $\delta^{13}C$ values of the vestimentiferan tissues range from -30 to -45‰, which overlaps the main mode of $\delta^{13}C$ values for vestimentiferan tubes. This overlap implies that translocation of chemosynthetic carbon occurs.

Unlike the $\delta^{13}C$ values of the tube worms, the $\delta^{13}C$ values of the bivalves (Figure 1.2) clearly fell within three groupings characteristic of heterotrophic, sulfur- and methane-based carbon sources. A number of interesting observations were apparent from the carbon isotopic values:

(1) The carbon of the mytilids was extremely depleted in ^{13}C (<-40‰) compared to other organisms. This is consistent with the

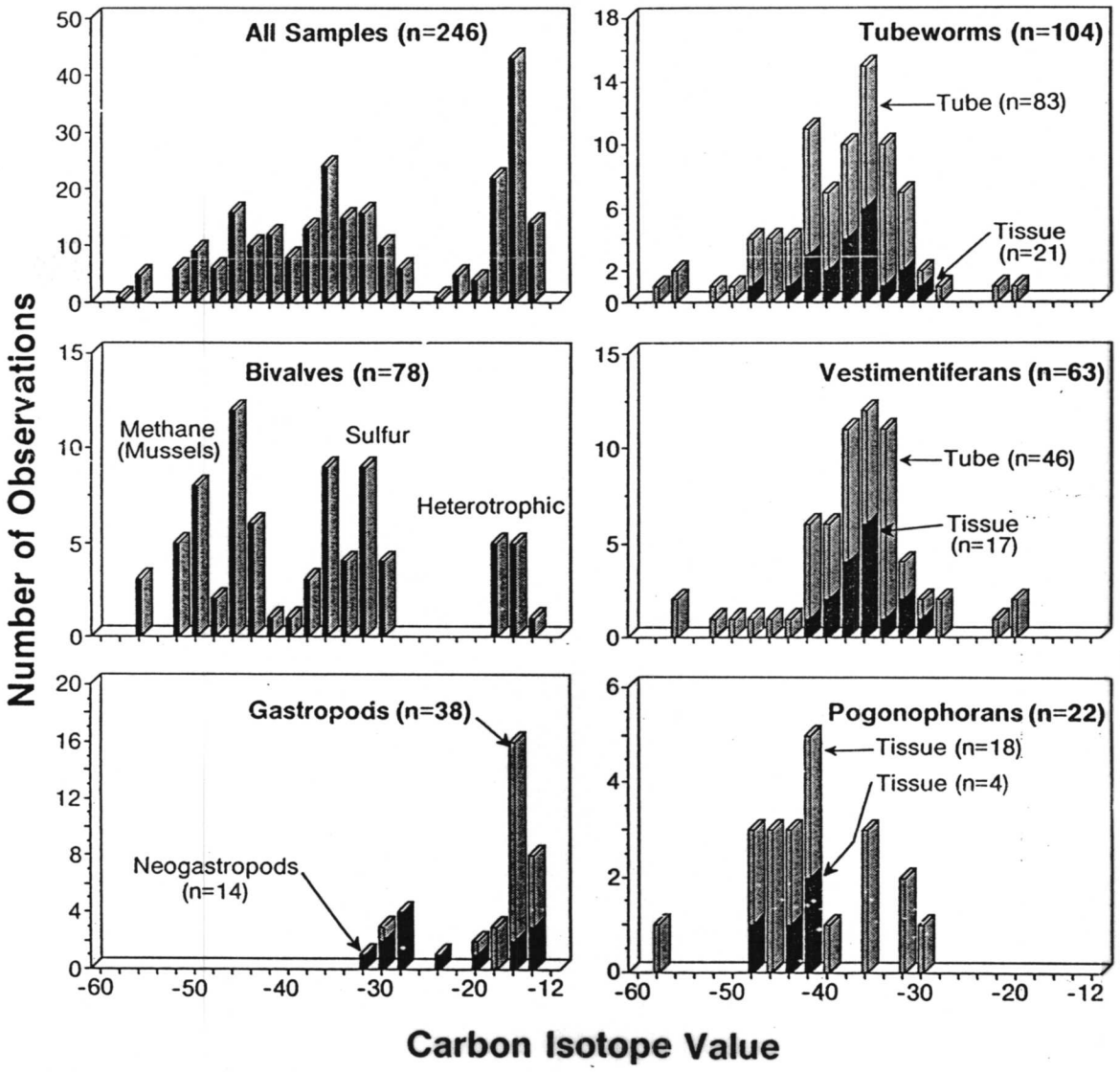


Figure 1.2 Carbon isotopic values (per mil relative to PDB) of 246 animals collected at seep sites on the Louisiana continental slope.

observations of **Childress et al.** (1986) that the mytilids assimilate and methane as their sole carbon and energy source. Mytilid gills, foot and mantle had similar isotopic compositions, which suggests translocation of chemosynthetic carbon throughout the organism.

(2) Vesicomyid and lucinid clams are hosts for chemosynthetic thiotrophic bacteria. The $\delta^{13}C$ values of these clams were between -27 to -40‰, less ^{13}C-depleted than those of the mytilids.

(3) The carbon isotopic compositions of some of the neogastropods indicate that they feed on chemosynthetic carbon sources, which identifies a pathway for chemosynthetic carbon to enter the heterotrophic deep-sea food chain.

One piston core was taken at each of the 39 sites to determine the amount of migrated hydrocarbons present in the sediments associated with these chemosynthetic communities. Seven cores were visibly oil-stained. All of the trawl samples recovered at these seven locations yielded at least one species of chemosynthetic organism and generally represented the most abundant catches of chemosynthetic organisms. Elevated levels of hydrocarbons were present in all cores from the 19 areas where chemosynthetic ecosystems were retrieved, which suggests that these ecosystems are predominantly driven by oil and gas seepage. Hydrogen sulfide may be derived either from sulfate reduction in seawater or from sulfide associated with the seeping oil. The methanotrophic symbionts of the mytilids can directly utilize methane in seeping gas.

Extensive sampling of sediments in the northern Gulf of Mexico continental slope has demonstrated the widespread occurrence of hydrocarbons. Visible oil seepage to the sea surface was observed at the

Green Canyon-184 and 190/234 areas. At one of these areas, extensive molecular and isotopic analyses have demonstrated that near-surface sediment bitumens and surface slicks are derived from reservoirs 6000-9000 ft deep in the subsurface **(Kennicutt et al. 1988)**. Nine locations on the Louisiana slope (530 to 2400 m water depth) were identified that contained either biogenic or thermogenic gas hydrates in shallow sediments (<6 m). Analyses of bitumens from several thousand cores taken on the continental slope suggest that oil and gas seepage is a widespread phenomenon on the Gulf of Mexico continental slope. This seepage supports widespread populations of chemosynthetic organisms in this area of the deep-sea. Polynuclear aromatic hydrocarbon analyses of seep organisms indicated that tube worms have as much as 5 ppm of naphthalenes in their tissues.

These discoveries significantly expanded the geographic area of the deep ocean where (l) hydrates are known; (2) oil seepage has been documented; and (3) dense assemblages of chemosynthetic fauna have been collected. These discoveries are distinct from the Pacific hydrothermal vents and the Florida Escarpment brine outflow because they are associated with natural, mature oil seepage. Oil and gas seepage is common on the Louisiana/Texas continental slope; therefore, it is probable that chemosynthetic communities are widely distributed in this region.

The shipboard studies were followed by a series of submarine dives in late 1986 1987, and 1988. MMS originally funded six Johnson *Sea-Link* submarine dives (four on Green Canyon 184-185 lease block site known as "Bush Hill"; see Figure 2.3) as part of the Benthic Slope Study in late 1986. The results from the initial six dives can be found in **MacDonald et al.** (1989). The Office of Naval Research awarded GERG time on the *NR-l*, a

nuclear-powered submarine, in 1987 (23 dive days), 1988 (18 dive days), 1989 (29 dive days), and 1990 (14 dive days). NOAA, through the NURP program, awarded GERG and collaborators 30 dives on the *Sea-Link* in 1987. In 1988, NURP awarded GERG and LSU 34 dives on the *Pisces*. In 1989, GERG received 10 days of *Sea-Link* dive time.

1.4 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. 1984), 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 and Jensen 1987; Tunnicliffe 1991). 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.

2.0 Regional Geology of the Northern Gulf of Mexico

W.W. Sager and W.W. Schroeder

2.1 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. 1990c**). 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.

2.2 Tectonics Cause Seeps in the Gulf of Mexico

Seeps have two geologic common denominators: tectonism and fluid flow. In the Gulf of Mexico, the fluids are usually hydrocarbons or brine, and the conduits are faults arising from salt tectonism. Both are widespread in the Gulf because of its geologic history.

The Gulf of Mexico contains little oceanic crust; what little there is is deeply buried and has poorly defined magnetic anomalies, which allows for numerous uncertainties about its tectonic history (Walper, 1981; Hall et al., 1982; Pindell and Dewey, 1982; Pindell, 1985; Buffler and Sawyer, 1985; Klitgord and Schouten, 1986; Salvador, 1987). Nevertheless, those aspects critical for understanding seep geology, the depositional history, and late Cenozoic tectonics are relatively clear (Worrall and Snelson, 1989).

The Gulf began to form in the Late Triassic and Early Jurassic with rifting between North and South America as Pangea began to break up. During the initial rifting, terrigenous synrift sediments, such as red beds,

collected in the nascent basin. Soon, during the mid-Jurassic, the Gulf had limited access to the sea and evaporites formed with thicknesses as great as 5-7 km (Worrall and Snelson 1989). Seafloor spreading began sometime during the mid to Late Jurassic, creating the oceanic crust underlying the Sigsbee Abyssal Plain (Buffler et al. 1980). This split the evaporites into two belts; the Louann Salt, which underlies the northern Gulf of Mexico continental margin (Martin 1978; 1980), and the Yucatan deposit, along the southeastern Mexico margin (Buffler 1983)(Figure 2.1). Widening of the Gulf allowed more continuous exchange with the sea and the deposit of marine sediments began (Pindell and Dewey 1982). Important hydrocarbon source beds were formed during the Late Jurassic and Early Cretaceous (see Section 3 of this volume). The heterogeneous carbonate sequence known as the Smackover Formation was deposited during the Jurassic Oxfordian stage. These carbonates were followed by two major reef trends, the Sligo in the Early Cretaceous and the Stuart City during the Middle Cretaceous (Wu et al. 1990a,b; Worrall and Snelson 1989).

During the Late Cretaceous and early Tertiary, the reefs mostly died off and worldwide sea level began to decrease. Sedimentation in the Gulf switched to terrigenous sands and silts, and during the Cenozoic Era the northern Gulf continental margin prograded seaward by the stacking of fluvial deltaic sediment wedges. The total thickness of these sediments is as much as 16 km (Worrall and Snelson 1989). Many of these sediment layers contain enough organic material that they, too, are hydrocarbon source beds. However, perhaps their most notable contribution is that they provide the impetus for salt movement.

The buried Jurassic salt behaved differently from most sediments: it is soluble in water, ductile, and virtually incompressible. The first

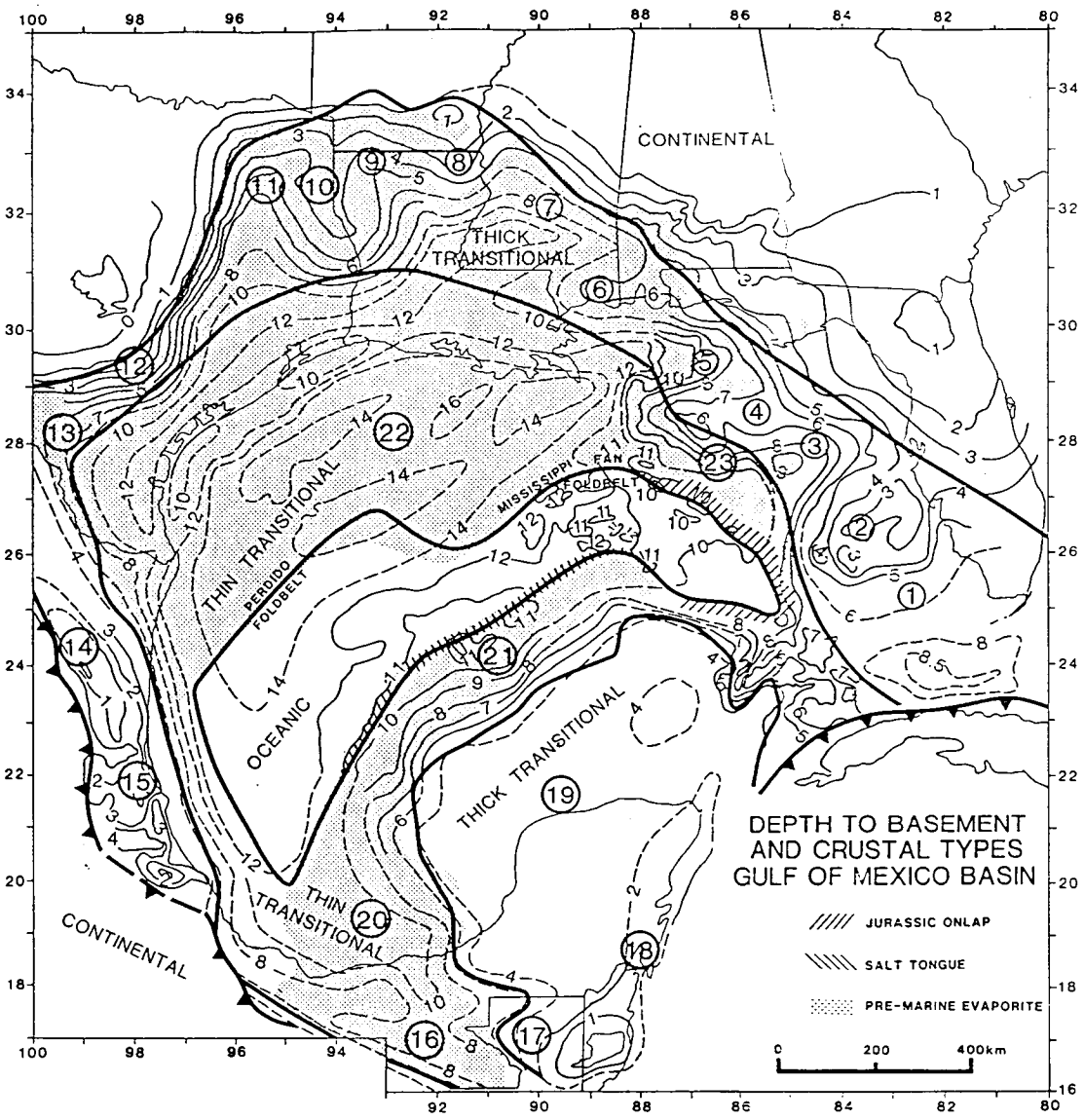


Figure 2.1 Map of the Gulf of Mexico region showing (1) generalized depth to basement in kilometers, (2) distribution of four crustal types: continental, thick transitional, thin transitional, and oceanic crust, and (3) known distribution of mid-Jurassic pre-marine evaporites (Louann salt and equivalent rocks)(stippled area). Basement includes oceanic crust plus all rocks lying below (older than) pre-marine evaporites. Solid contours indicate areas where top of basement is well constrained by seismic reflection data and well control, while dashed contours are areas where top of basement is speculative and based on other geophysical data and extrapolation of trends from adjacent areas. Circled numbers refer to major named basement highs, lows basins, arches, etc. as follows: (1) South Florida Basin, (2) Sarasota Arch, (3) Tampa Embayment, (4) Middle Ground Arch-Southern Platform, (5) Northeast Gulf Basin-Apalachicola Embayment, (6) Wiggins Uplift, (7) Mississippi Salt Basin, (8) Monroe Uplift, (9) North Louisiana Salt Basin, (10) Sabine Uplift, (11) East Texas (Salt) Basin, (12) San Marcos Arch, (13) Rio Grande Embayment-Burgos Basin, (14) Tamaulipas Arch, (15) Tuxpan Platform, (16) Macuspana Basin, (17) Maya Arch, (18) Quintana Roo Arch, (19) Yucatan Block, (20) Campeche Salt Basin, (21) Sigsbee Salt Basin, (22) North Gulf Salt Basin, and (23) West Florida (Salt) Basin (from Buffler and Sawyer 1985).

sediments to be deposited on the salt were less dense that the salt, so they "floated" on top of it. However, with increasing overburden, the sediments compacted and became denser. Because the sediments were unevenly distributed, buoyancy caused the salt to mound and rise. Where the salt could overcome the cohesiveness of the overlying sediments, it broke through to form ridges and diapirs and associated faults (Figure 2.2; Jackson and Seni 1983; Jackson and Galloway 1984; Jackson and Talbot 1986; Worrall and Snelson 1989). These tectonic activities released hydrocarbons trapped in the buried sediments and gave them conduits to the surface.

Views of salt tectonics have changed significantly over the past 10 to 15 years. The old view was that the salt primarily moved vertically and that most salt bodies are diapirs pushing upward and piercing overlying sediments (Martin 1978). More detailed recent studies have shown that lateral movement has been equally important (Simmons 1991). The new view compares sediments to a rolling pin squeezing the filling (salt) from an unbaked pastry. These sediments cause differential loading which provides a lateral force. With no buttress to seaward and with ductile salt at the base, the salt/sediment pile has extended and moved laterally (Figures 2.3 and 2.4; Humphris 1979; Jackson and Galloway 1984; Worrall and Snelson 1989; Wu et al. 1990b).

Salt movement appears responsible for most of the topography and fault pattern of the northern Gulf of Mexico continental slope. The Louann Salt underlying the region is deformed by progressive loading from a flat layer to low relief features (rollers and anticlines), then to moderate relief structures (ridges and massifs), and finally to isolated, high-relief bodies (stocks and diapirs) (Figure 2.5; Jackson and Seni 1983; Jackson and Galloway 1984; Jackson and Talbot 1986; Wu et al. 1990b). Because of

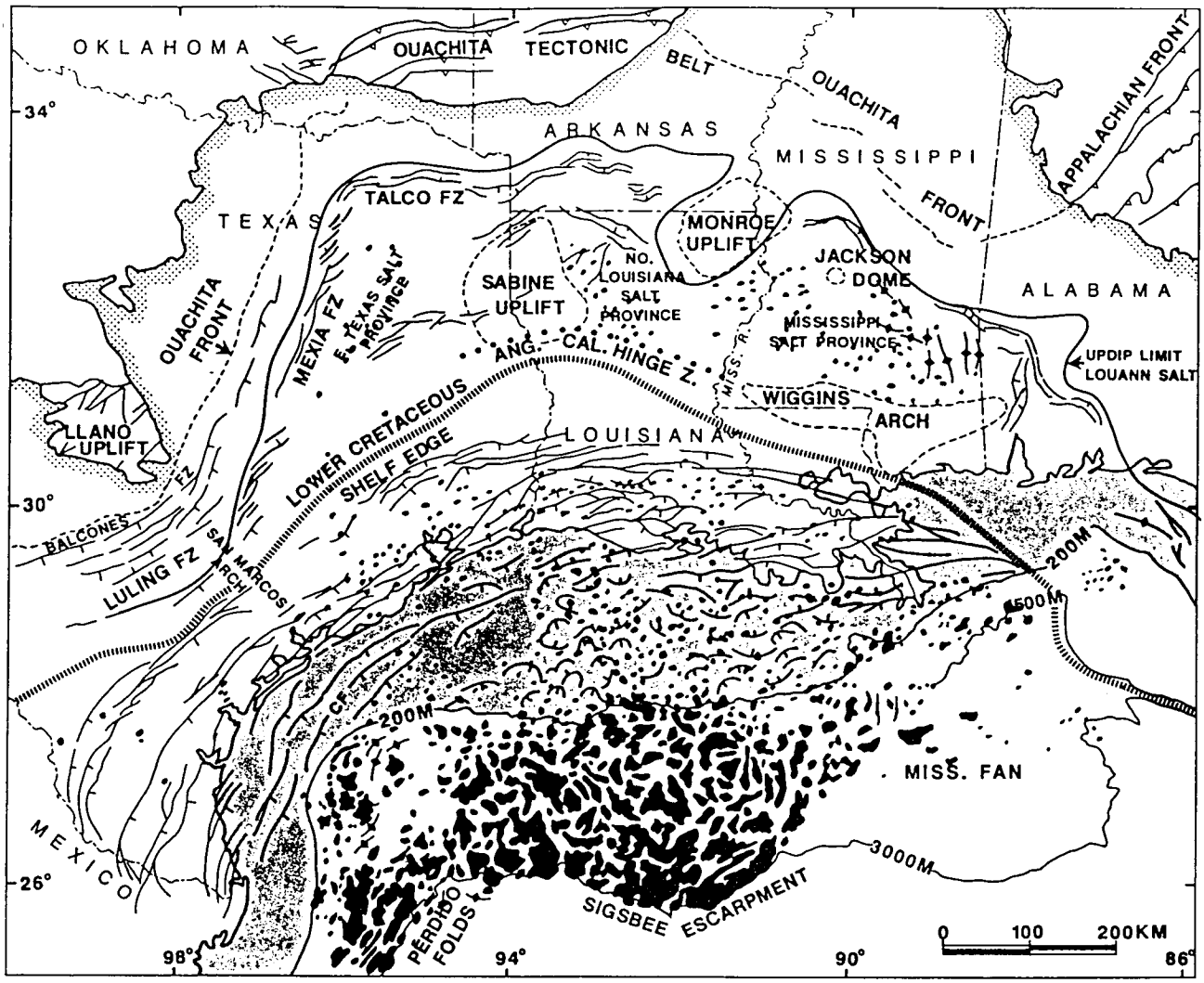


Figure 2.2 Tectonic map of the northwestern Gulf of Mexico. Salt features and most of the onshore structural trends based on compilation of Martin (1978). Shelf area (0-200 m water depths) is shown in gray. (from Worrall and Snelson, 1989).

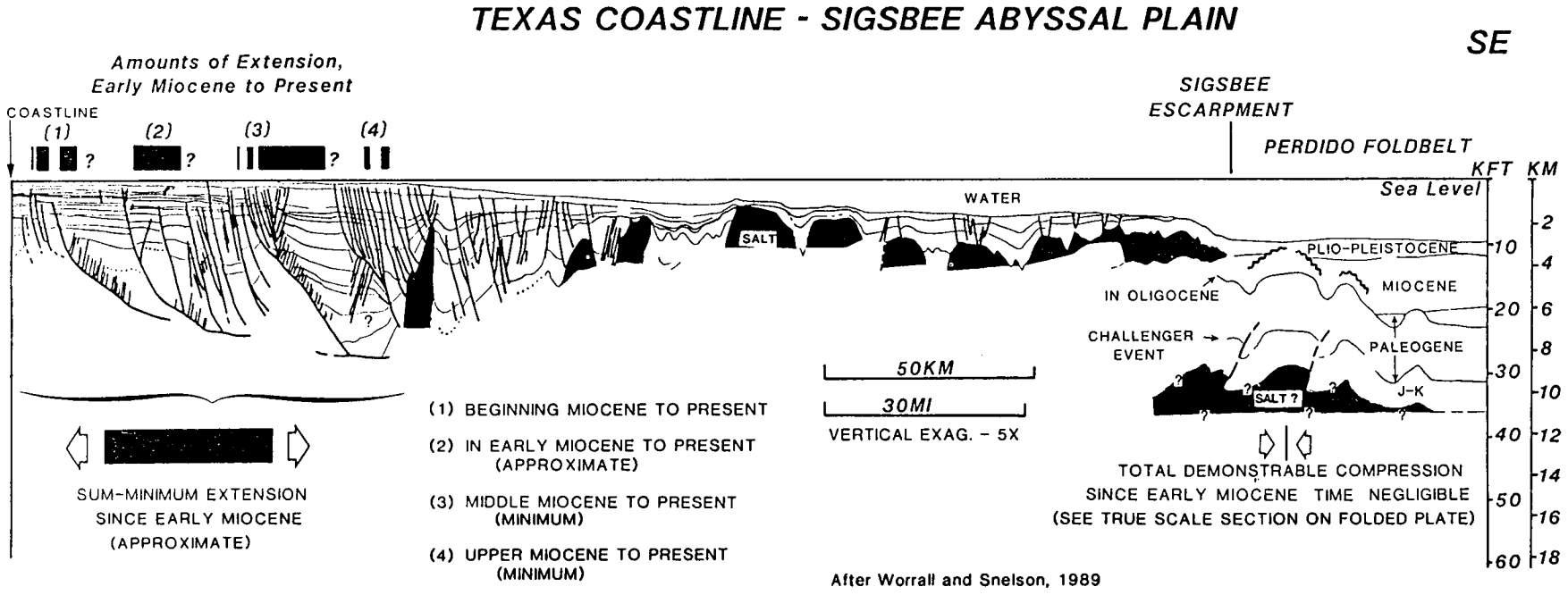
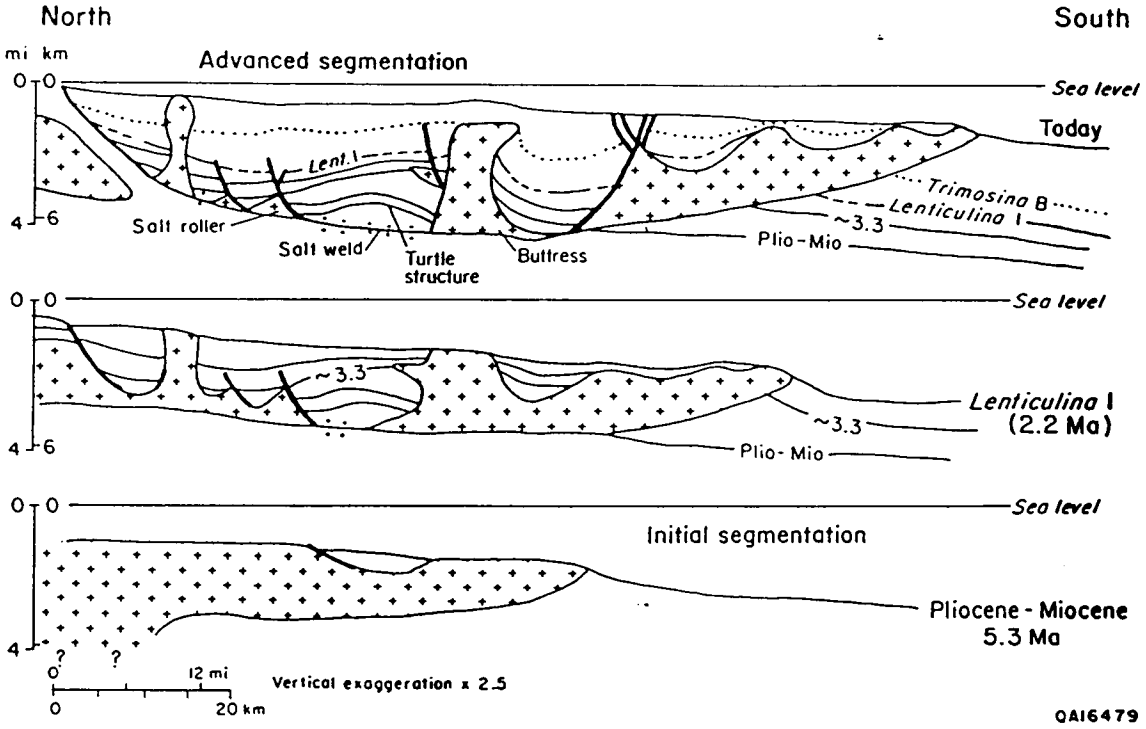


Figure 2.3 Generalized cross section of the northwestern Gulf of Mexico showing salt and deep faults (from Wu et al. 1990b).

A



B

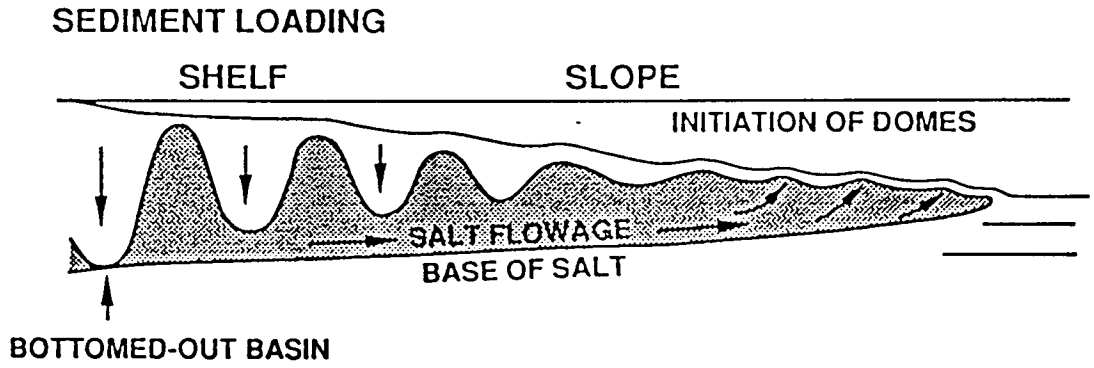


Figure 2.4 Schematic diagrams showing evolution of salt structures beneath the Gulf of Mexico slope. Differential loading squeezed salt seaward and up-section, causing salt withdrawal, segmentation, and diapirism. Intraslope basins formed where salt withdrawal occurred (A: from Seni and Jackson 1992; B: from Humphris 1979).

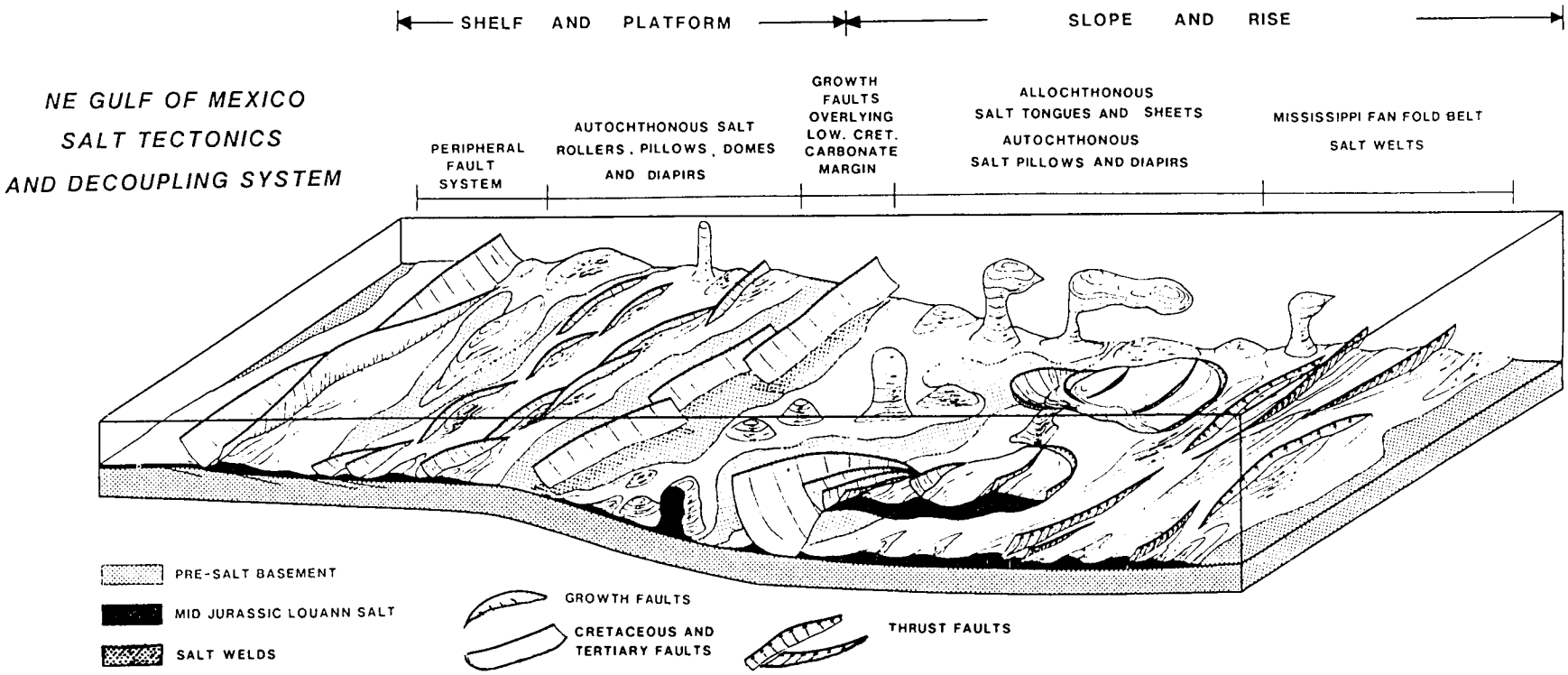


Figure 2.5 Schematic summary of salt tectonics and faulting in the northern Gulf of Mexico (from Wu et al. 1990b).

differential sediment loading, there is typically a progression from more mature, high-relief features landward to less mature, lower-relief features seaward (Figures 2.4 and 2.5; Jackson and Talbot 1986; Seni and Jackson 1992; Wu et al. 1990b). One of the most spectacular salt features of the northern Gulf is the Sigsbee Salt Nappe, a huge, wedge-shaped allocthonous mass of extruded salt that has been slowly moving seaward and upward through the sediment column since about Eocene time (Worrall and Snelson 1989). The toe of the nappe is the coalesced front of 5-6 salt tongues (Simmons 1991). It forms the Sigsbee escarpment and has travelled approximately 80-150 km seaward (Buffler et al. 1978). Behind the escarpment, sediment piling and salt withdrawal have formed typically ovoid intraslope basins (Simmons 1991).

The seaward salt transport leads to an extensional regime: so extensional, normal faults predominate in the northern Gulf of Mexico (Worrall and Snelson 1989). Although some thrust faults have been found, most are a result of local mass movements, such as slumps or gravitationally unstable blocks (e.g., Huber 1989), so they are neither large nor widespread. Many faults in the Gulf are either "growth" or "antithetic" faults. Growth faults are normal, often listric (curved, with steepness lessening with depth), faults caused by differential subsidence that is contemporaneous with sedimentation, which causes the fault to have a greater offset with time. Antithetic faults are secondary extensional faults that form in the hanging wall of a growth fault because of motion along the parent fault. They have dips that oppose the parent and typically form in a "fence-row" pattern along it (Figure 2.6). Usually only a few antithetic faults near the curved "tail" of an active growth fault are active themselves because the extension is greatest as

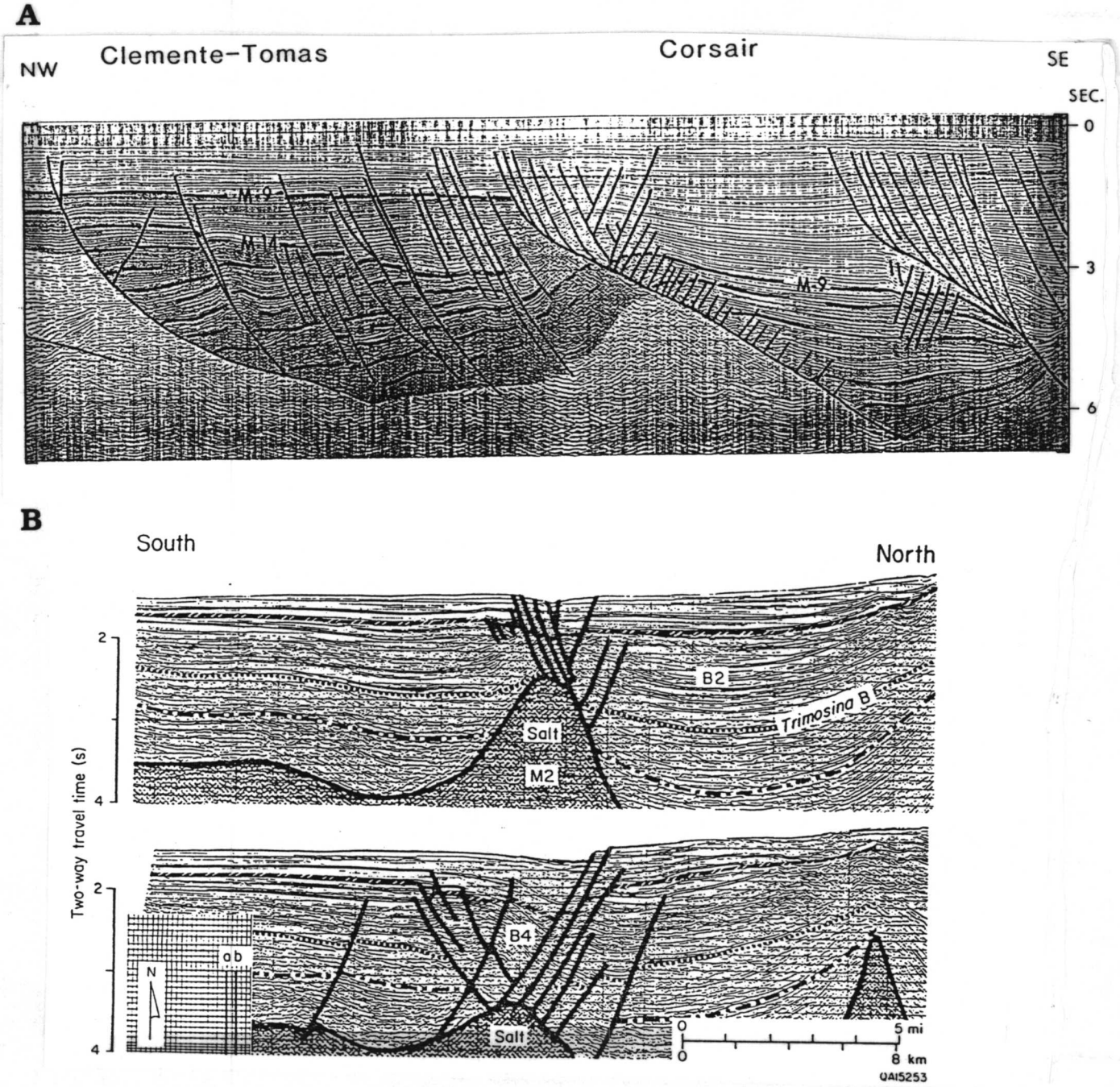


Figure 2.6 Interpreted seismic reflection records showing growth fault systems. A: the Clemente-Tomas and Corsair growth faults. Note the numerous small antithetic faults emanating from the Corsair Fault (from Worrall and Snelson 1989). B: Growth and antithetic faults over salt bodies in the Green Canyon region (from Seni and Jackson, 1992).

the hanging wall slides down the curved portion of the growth fault (Worrall and Snelson 1989).

Growth faults in the northern Gulf fall into two general categories: the "Texas" type, characteristic of onshore Texas and western Louisiana, and the "Louisiana" type, found predominantly on the Louisiana and Texas slope (Worrall and Snelson 1989). The Texas type are long (hundreds of km), deep, linear, usually listric, and parallel to the basin contours. Most of these have the seaward side downthrown, although a few, called "counter-regional" faults, face in the opposite direction. These counter-regional faults are typically located near the toe of the allocthonous salt mass. Texas style faults are thought to be regional fracturing caused by the lateral movement and extension of the salt/sediment mass making up the slope. However, these faults usually appear to have no direct association with salt. Louisiana type faults are shorter (less than about 50 km), arcuate, listric, usually shallower in extent, and can face either seaward or landward. These faults often appear to root into salt bodies or form at their boundaries. They are thought to be caused by differential sediment loading, salt withdrawal, and the downbuilding of intrasalt basins. Modeling experiments indicate that such faults would form radially around diapirs in the absence of regional stress. However, in an extensional stress field like that in the northern Gulf of Mexico shelf and slope, the faults extend laterally and line up perpendicular to the axis of maximum stress (Figure 2.2; Jackson and Galloway 1984).

Faults stimulate hydrocarbon seepage in two ways (Behrens 1988; Kennicutt and Brooks 1990). First, they act as a tap, breaking through an impermeable sediment layer that would otherwise form a reservoir cap. Second, they provide an upward-trending conduit so that the hydrocarbons can get to the seafloor. Despite this relationship, the fluid transmission

properties of faults are undetermined. Clearly normal faults allow the passage of fluids such as hydrocarbons, at least to a limited extent. However, they are also known as traps, blocking the passage of hydrocarbons (Weber and Daukoru 1975; Jackson and Galloway 1984). Indeed, the oil industry has made good use of the latter property in drilling commercially viable oil and gas reservoirs along normal faults.

The apparent conduit/trap discrepancy can probably be explained by complications in fault geometry, stress regime, and sediment composition. Jackson and Galloway (1984) note that it is the larger (throw greater than about 150 m) growth faults that appear to be conduits. A large-throw fault should have a wider fault zone with more gouge and disruption. It would also be more likely to completely offset impermeable layers, uncapping a reservoir. On the other hand, a sizable growth fault is more likely to create a large rollover of layers on the hanging wall where hydrocarbons usually pool (Jackson and Galloway 1984). The larger rollover can act as an extensive reservoir, keeping much of the hydrocarbons trapped at depth. Stress regime may also play a role in trapping hydrocarbons. Many of the known seeps in the Gulf are located over salt bodies (Behrens 1988; Kennicutt and Brooks 1990; MacDonald et al. 1990a) where the salt movement may produce more extension. Similarly, some seeps are along antithetic faults, rather than their parent faults, probably because the antithetic fault releases the stress placed on the sediment wedge in the hanging wall above the growth fault (D. Cook, pers. comm., 1991).

The behavior of fluids moving along a fault conduit is also unclear. It is uncertain whether they move as sheets, waves, or tubes. Wavelength and time scale differences between less viscous gas and more viscous fluids are also unknown. Observations of seeps suggests that they can extend laterally

either as wide-spread gas columns (Watkins and Worzel 1979; Addy and Worzel 1979) or pervasive oil-staining fluids (Behrens 1988). Furthermore, salt dome growth is episodic, so fault movement and fluid flow along the fault is probably episodic as well (Roberts et al. 1990b). However, these variations in salt dome growth and fault movement are typically large scale and extend over thousands of years, whereas fluid flow time constants may be much shorter.

2.3 Geologic Features Associated with Seeps

On a large scale, seeps have been associated with salt bodies and large normal faults (Behrens 1988; Pratsch 1989; Kennicutt and Brooks 1990). Seeping faults are usually growth faults rooted in or bounding salt structures. Either the salt or the fault has penetrated an impermeable layer which formed a reservoir cap and has allowed the hydrocarbons or other fluids to use the fault as a conduit. Irregular topography, particularly over salt bodies, is often a clue to active faulting that may allow seepage (Kennicutt and Brooks 1990).

There are several smaller scale geologic features often associated with hydrocarbon seeps. Carbonate mounds form by the precipitation of $CaCO_3$ where CO_2 is released by microbial degradation of hydrocarbons in shallow sediments or at the surface (Behrens 1988; Roberts et al. 1990a). These are typically irregular in shape, a few meters to a few tens of meters in diameter or height. Mud volcanoes are usually conical mud domes with a central vent (Hovland and Judd 1988). They form by fluid flow and entrainment of muddy sediments and are often found at fault zones that were probably the conduit for the fluid flow (Newton et al. 1980; Hedberg 1980). Pock marks are shallow depressions, often a few meters in depth and a few tens of

meters across or less. Although usually subcircular in plan view, pock marks can be irregular or elongated. They are thought to form by the release of gas, perhaps explosively, from shallow subsurface accumulations (Hovland and Judd 1988). Seepage of brines formed from dissolution of the silt stack may cause pockmarks to fill with a stable volume of hypersaline fluid (MacDonald et al., 1990c) or may cut rivulets in surface sediments (MacDonald et al., 1990a). Giant gas domes are large mounds, up to 100 m in height and 2 km in diameter, reported from the Gulf of Mexico slope between the depths of 600 and 2400 m (Kennicutt et al. 1985; Brooks et al. 1986). Samples from these mounds have included gas hydrates, bitumen, and authigenic carbonates, attesting to pervasive hydrocarbon seepage. Their origins are unclear, but Hovland and Judd (1988) suggest that they form somewhat like mud volcanoes, extruding onto the seafloor and building upwards.

Many of the markers of hydrocarbon seepage are acoustic signatures seen on seismic reflection records. Acoustic "wipe-outs", in which the subseafloor signal is attenuated, are characteristic of shallow gas (Behrens 1988). The gas probably disrupts the sediment layering and either absorbs much of the acoustic energy or reflects it away with its large acoustic impedance (Hovland and Judd 1988). Behrens (1988) recognized two types of wipe-out: type 1 has normal or lighter reflections at the seafloor and is transparent below, whereas type 2 has a strong return at the seafloor and strong, chaotic echoes below, sometimes called "acoustic turbidity". The former probably is caused by gas whereas the latter may be the result of precipitated material such as carbonate nodules. "Pagoda structures" are acoustic features probably related to biogenic gas. They appear as columnar

zones which alternate horizontally between normal reflection properties and acoustic wipe-out (Hovland and Judd 1988).

Gas does not always cause a wipe-out; indeed, sometimes it can cause a reflection to be stronger. Reflector enhancements are small segments of strong echoes from a buried, but usually shallow, seismic reflector. Their source is unclear, but may be gas (Hovland and Judd 1988) or some material precipitated by seepage (Behrens 1988). Similar bright-spots are seen on multi-channel seismic profiles but are not restricted in section depth (Jenyon and Fitch 1985). These are clearly a result of the acoustic impedance contrast between gas-charged and normal sediments.

Gas hydrates create a unique seismic reflector (Brooks et al. 1984). They cause a slight attenuation of the shallow subsurface acoustic signal and make a bottom stimulating reflector (BSR), or a strong reflection from the bottom of the hydrate layer (Hovland and Judd 1988). Because hydrate is only stable at temperatures close to the freezing point of water, its bottom layer typically follows the ocean floor, since sediments quickly become too warm with depth to retain hydrates. Pressure is also needed to form gas hydrates, so they are usually only found in depths greater than about 500 m. Hydrates can form an impermeable cap, blocking the flow of fluids from deeper formations or routing them to certain areas. Thus a hydrate layer could help to concentrate a seep.

Seepage effects can also be detected with side-scan sonars. These devices typically use much higher frequencies than seismic reflection systems, so the acoustic energy is returned from "backscattering" at the seafloor interface (Johnson and Helferty 1990). Two types of reflection character have been noted that may be useful in seep recognition. One is strong seafloor backscatter from areas around faults (T. W. C. Hilde, personal

communication 1991) and carbonate mounds, which possibly are from authigenic carbonates disseminated through the sediments (Laswell et al. 1990; in preparation). The second is low backscatter from brine pools, such as Orca Basin. Low backscatter would occur because the sea water/brine interface has few scatterers to return acoustic energy to a side-looking source.

3.0 Authigenic Carbonates at Hydrocarbon Seeps: A Review of Published Material

W.W. Schroeder

The formation of authigenic carbonate is intimately linked to the microbial oxidation of methane and oil. Although oxidation of hydrocarbons does occur under aerobic conditions, it is believed that oxidation of hydrocarbons seeping at or near the sea floor coincides with sulfate reduction under anoxia (M.C. Kennicutt, personal communication; J. Morse, personal communication). The abundant sulfur in the system confirms the fundamental process:

$$\begin{array}{ccc} & & H_2O, FeS_2 \\ & & \uparrow \\ 2CH_4 + 2SO_4^{-2} \Rightarrow 2HS^- + 2HCO_3^- + 2\,H_2O & \Rightarrow & Ca_3 + H_2CO_3 \\ & & \uparrow \\ & & Ca^{-2} \end{array}$$

The evidence for the linkage to fossil carbon is the presence of ^{13}C-depleted $CaCO_3$ (Kennicutt et al. 1989). The abundant supply of HCO_3^- from the oxidation of methane drives the equilibrium reaction to completion. The carbonic acid would remain largely undissociated due to excess bicarbonate generated during sulfate reduction. As long as a sufficient supply of calcium is also available, calcium carbonate will form a solid.

Research during the past half decade has clearly established that authigenic[1] carbonate deposits are a regular component of hydrocarbon seep sites on the outer shelf and continental slope of the northern Gulf of Mexico

[1]Formed or generated in place; specially said of rock constituents and minerals that have not been transported or that crystallized locally at the spot where they are now found, and of minerals that came into existence at the same time as, or subsequently to, the formation of the rock of which they constitute a part.

(e.g. Roberts et al. 1987, 1990b; Kennicutt and Brooks 1990). Sea floor lithification in this region of the Gulf was first observed on high resolution seismic profiles over areas of complex bathymetry associated with salt diapirs (Roberts et al. 1987, 1990b). These records consist of pinnacle- and mound-shaped features of unknown origin as well as low topographic relief areas of highly reflective and rough sea floor.

The first direct sampling of carbonates was reported in a paper describing liquid petroleum and natural gas in cores from the upper slope of the northern Gulf of Mexico in lease block Green Canyon 234 (Anderson et al. 1983). (This hydrocarbon seep area is one of the study sites for the MMS Chemosynthetic Study.) Anderson et al. reported that the abundance of ^{13}C-depleted carbonate material in their cores was the result of microbial oxidation of organic matter to CO_2, which was then precipitated as calcium carbonate. They also stated that the presence of large lumps of ^{13}C-depleted carbonate in the upper section of the cores indicated biodegradation late in the migration pathway, as oil approached the seawater-sediment interface.

The second group to remark on the presence of carbonate material at a hydrocarbon seep was **Brooks et al. (1984)**. They discovered thermogenic gas hydrates in the vicinity of Green Canyon 184/185 (Bush Hill). This is also a now well-known seep area and a study site of the Chemosynthetic Study. The material, obtained in piston cores, was described as carbonate rubble. Motivated by interest in the effect of chronic exposure to oil seepage upon benthic fauna, **Kennicutt et al. (1985)** collected two benthic trawl samples in the Green Canyon lease area (approximately 27°-28° and 90°-92°). These trawls recovered substantial quantities of "vent-type" taxa including vestimentiferans and vesicomyid clams. Stable carbon isotope analyses subsequently suggested that these organisms were chemosynthetic and derived

their energy from hydrogen sulfide and/or hydrocarbons. Although collection of hard substrate was not reported in the publication, Kennicutt (personal communication, 1992) confirmed that carbonate materials, ranging in size from small rubble to large slabs, were present in both trawls.

Behrens (1988) presented the first detailed documentation of the geology of an oil seep on the Gulf of Mexico continental slope as a follow-on to the initial report on the oil seep in Green Canyon 234 (Anderson et al. 1983). Behrens, who was the original discoverer of the oil seep and a co-author on the earlier work, presented geophysical data consisting of high-resolution and multichannel seismic reflection profiling, and chemical analyses of replicate piston cores. He reported that seepage occurred over a relatively shallow salt ridge that was manifested at the surface by a graben in strike section and by a half-graben in dip section. Faulting over the crest of this feature was commonly associated with zones in which reflective energy was markedly reduced—called acoustic "wipe-outs". He described two wipe-out types, one characterized by reduction or no change in the reflection from the sediment-water interface and a second type in which the bottom echo was strong and prolonged. Oil and gas was found in most of the cores taken in the wipe-out zones of the second type. The cores also commonly contain carbonate material identified as having been derived from microbial degradation of hydrocarbons. Behrens suggested that the ^{13}C-depletion of the carbonate and its negative correlation with porosity may be subtle indicators of seepage at sites where oil and gas are not evident. In addition, he noted pore-fluid salinities in excess of 200 ppt in the upper 20 cm of piston cores, indicating the presence of brine despite the absence of obvious caprock or salt.

Harry H. Roberts, of Louisiana State University, and his colleagues began publishing on the carbonate geology of the Louisiana continental slope in 1987

and maintain an active research program in this field. Their initial work was chiefly concerned with the engineering challenges associated with both hydrocarbon exploration and production in slope water depths. It included a review of the regional geologic framework from Treadwell (1949) and Gealy (1955); who had attributed irregular bathymetry to faulting, slumping, and other mass-movement processes. Roberts et al. (1987) also discussed contributions resulting from the advent of seismic reflection profiling (e.g., Moore and Curry 1963; Antoine and Bryant 1969; Martin 1980), and the more recent high-resolution seismic surveys of the slope (Bouma et al. 1980, 1981; Coleman et al. 1986, Bouma 1982, Bouma and Coleman 1986).

Roberts et al. (1987) stressed that although the sediments on the slope are principally terrigenous clays (Suter and Berryhill 1985; Roberts et al. 1986), carbonates are a significant component, occurring as 1) highly calcareous hemipelagics, 2) carbonate-cemented clays, 3) shell hashes, 4) hardgrounds, 5) mounds, and 6) biotherms. They emphasized the growing evidence suggesting that numerous small scale topographic features are calcareous and are linked to the precipitation of carbonate (dominantly aragonite). These zones of lithification appear to range from small localized nodules and cemented burrows to mounds (up to tens of meters in diameter and 10 m in relief). Seeps and associated calcareous hardgrounds provide a setting for carbonate-secreting organisms that require a hard substrate and perhaps a hydrocarbon-related nutrient source, thus encouraging the buildup of carbonates into significant topographic features.

Roberts et al. (1987) state that the crude oil and associated light hydrocarbons were generated outside the realm of their surface host sediments. The source of crude oil in the slope was believed to be organic-rich source rocks of lower Tertiary or Cretaceous age (Nunn and Sassen 1986). The

diagenetic environment of the crude oil seeps where these products are forming is similar to the cap rock setting of shallow Gulf Coast salt domes, where crude oil biodegradation and mineral deposition have occurred simultaneously. Cap rocks of such salt domes are characterized by enormous volumes of isotopically light calcite, elemental sulfur, sulfide minerals, and hydrogen sulfide, which are the result of microbial activity (Sassen 1981). Precipitated carbonates with light carbon isotope ratios have also been reported from other marine environments (Allen et al. 1969; Hathaway and Degens 1969; Roberts and Whelan 1975; Davis and Kirkland 1979: Kocurko 1986).

Roberts et al. (1988) continued to look into the origin of the hydrocarbons found at various seep sites and to examine the relationship between hydrocarbon oxidation and the formation of authigenic carbonates. They concluded that:

- The hydrocarbons at seep sites have two main origins: 1) *in situ* biogenic production of methane and 2) migration of thermogenic gas and crude oil from great subsurface depths, presumably by way of large growth fault systems, to the surface.

- Isotopic signatures of the carbonates ($\delta^{13}C$ values to -48‰ PDB) reflect a link to the hydrocarbons in the carbonate-forming process. Much of the isotopic variability of the carbonates is probably related to the varied pool of carbon made available by microbial degradation of a spectrum of hydrocarbons, from biogenic and thermogenic methane to crude oil.

Roberts and Coleman (1988) addressed the lithofacies characteristics of surface and shallow subsurface (condensed and expanded) sequences on

Louisiana's distal shelf and upper slope, produced during high-frequency sea-level fluctuations of the late Pleistocene-Holocene. Germane to the topic of carbonate geology is the following summary (Roberts and Coleman 1988 p. 291):

> Condensed sections accumulate at rates of 5.0-30.0 cm/1000 years and are highly calcareous. High-relief areas of the slope are dominated by carbonate sediments and mound-like buildups. Carbonates in these areas include cemented hemipelagics, shell hashes, hardgrounds, isolated nodules, and large mounds. Many of the diagenetic carbonates, including the mounds, are isotopically light (-20 to -48 ppt PDB) and are linked to methanogenesis. Aside from the above diagenetic products, condensed-section carbonates are typically unstratified, highly burrowed, and pelleted.

Roberts et al. (1989a) introduced the use of direct observations from manned submersibles in describing carbonate deposits on the upper Louisiana slope in Green Canyon Blocks 52-53. Water depths in this region range from approximately 90 m to over 300 m. They confirmed that authigenic carbonates were responsible for producing a variety of seafloor features including the following:

Carbonate Mounds - Submersible observations indicate that these "mounds" (constructed from ^{13}C-depleted carbonate) are much more complex than the simple parabolic forms seen on high-resolution (3.5 kHz) seismic profiles. Mound flanks are much steeper and, in some areas, chimney-like structures frequently rise abruptly from the seafloor. Well-defined crevasses (~0.6-3 m) and cracks commonly cut through the larger mounds. The authors

interpreted these features as surface expressions of faults and joints. This is based on their sighting of thick white and yellow bacterial mats covering the walls of the crevasses, which they felt indicates that hydrocarbons are seeping to these sites via fault/joint pathways. This position is further strengthened by observations of gas bubbles venting to the water column from some of these sites.

Underwater photographs are used to illustrate important biological attributes of these mounds. For example, the population density gradient of organisms (e.g. octocorals, crinoids, antipatharian sea whips) range from very low on the sides to high on top and the numerous small cavities and pits on the mounds suggest active bioerosion by organisms such as boring sponges. Also, because this site occurs at the limits of the photic zone, coralline algae appear abundant, but hermatypic corals were not identified. Only in rubble eroded from the mound top were hermatypic corals found. These specimens are thought to represent the remains of a previous low-sea-level period reef community.

Small-Scale Buildups - In addition to large mounds, they observed extensive areas of seafloor, associated with dome crests, that were covered with small relief (~0.3-2 m) carbonate buildups. The seafloor in these regions is covered with cobble- and boulder-sized carbonate (depleted in ^{13}C) debris or clasts. In many cases it appears that the "small-scale" features are accumulations of these clasts that have been cemented into substantial structures. As with the larger mounds, these features also harbor organisms requiring hard substrate.

Upturned and truncated bedding is common on the crests and upper flanks of domes and are the areas where Roberts et al. observed these buildups. Sediment erosion and concentration of clasts as a lag deposit is

consistent with analysis of high-resolution acoustic data and direct observations. Continued seepage of hydrocarbons through these areas likely results in selective cementation of lag deposits into low-relief seafloor features.

Sediment Induration - Downslope of the diapir crest mounded zones are vast areas of seafloor covered by hemipelagic sediments with a high carbonate content (up to 70% carbonate), primarily derived from foraminifera. Within these surficial layers, carbonate cements, depleted in $\delta^{13}C$, are being deposited to form isolated nodules. It is the opinion of the authors that this penecontemporaneous cementation is evidence of an ongoing process related to persistent percolation of hydrocarbons through sediments associated with shallow salt diapirs.

In addition, seismic profiles across diapirs and their flanking deposits frequently show high-amplitude reflection events that could represent subsurface cementation zones. Submersible observations of the bottoms and sides of small crater-like features in both Green Canyon 52-53 and 184-185 areas support this contention. Thin "shingles" or "slabs" of carbonate-cemented sediment were frequently found protruding from the crater walls. The origin of the craters is problematic, but their low-relief, cone-like morphologies, coarse sediment lags, and occasional ejection rims suggest formation by episodic and perhaps violent gas emissions.

In the second publication, Roberts et al. (1989b), continue to utilize data obtained from manned submersible operations during the summer of 1988. This paper focuses on research results from the deeper of the two sites (Green Canyon lease blocks 140, 184 and 185), where water depths range from about 200 to 600 m. Their conclusions generally reinforce findings that have been presented in previous publications. The one subject area they did expand upon dealt with identifying the "origins" of the carbonates collected from both the

shallow (Green Canyon 53) and deep (Green Canyon 140, 184 and 185) water study areas. By plotting ^{13}C values from the four Green Canyon sites against whole sample mineralogy they were able to identify three groupings that suggest different origins of the carbonates. Positive ^{13}C values from the shallow Green Canyon 53 site represent cemented biogenic debris from a low sea-level reef that formed over a ^{13}C-depleted carbonate substrate. The coexistence of positive and very negative $\delta^{13}C$ values at this site supports the low-stand reef interpretation. Isotopically negative aragonites and Mg-calcites from the deeper sites at Green Canyon 140, 184 and 185 probably represent authigenic carbonate phases formed in a surface to very near-surface setting. These samples were ledges protruding from unconsolidated bottom sediments. In contrast, Mg-calcite/dolomite samples were collected from massive mound-like structures that appeared to be exhumed subsurface features.

Two other papers published in 1989 dealt with the topic of carbonates and hydrocarbon seeps, Kennicutt et al. (1989) and Brooks et al. (1989). Kennicutt et al. (1989) provided a general overview of the relationship between hydrocarbon seepage, gas hydrates, and authigenic carbonate in the northwestern Gulf of Mexico. Most of the information provided had been previously reported.

Brooks et al. (1989) broke new ground by summarizing visual observations of chemosynthetic communities from *Johnson-Sea-Link* submersible dives and surveys made aboard U.S. Navy submarine *NR-1* on the Louisiana-Texas continental slope over the period 1986-1988. Geologic descriptions are provided for five chemosynthetic community sites; Green Canyon 184/185 (Bush Hill), 234 and 272, Garden Banks 388, and East Breaks 376. Other sites surveyed, for which there was no geological information, were located in Green Canyon lease blocks 29/31, 52, 185 and

195. The geologic settings and associated communities of the five described sites varied greatly. The following are summaries of these descriptions (Brooks et al. 1989 p. 664-666):

(1) Bush Hill (Green Canyon 184/185) occurs over a salt diapir that rises about 40 m above the surrounding sea floor to a minimum water depth of 540 m. As one progresses up slope, carbonate outcroppings generally become more common, ranging in size up to prominent boulders. Large vestimentiferan bushes, which are the most obvious biological component, occur both among the carbonate outcroppings and on soft sediments away from surficial rubble. Along the western side of the carbonate cap, the outcroppings form an escarpment, which rises about 15 m at its steepest margin. Attached to the hard substrate are large colonies of both gorgonians and the scleractinian coral Lophelia sp.

(2) The mussel and lucinid clam site in western Green Canyon 234 is a region of level topography along the 980 m isobath with a few low, rocky outcroppings, while the vestimentiferan site in the northeastern sector of the block occurs in an apparent graben fault zone. Rocky outcroppings are predominant and frequent, ranging from small boulders to house-size structures.

(3) The northeastern corner of Green Canyon 272 is characterized by slopes in excess of 30° and by a highly irregular micro-relief consisting of exposed carbonate. The carbonate varies in form from a rubble to spire-like boulders and broad, perforated plates. The occurrence of clams and mussels is apparently correlated with the substrate; clams are restricted to areas of soft sediments, while

mussels are attached to low-relief carbonate material often in shallow depressions.

(4) Topography in the Garden Banks 388 seep site, in 670-700 m, is undulating with several areas of rough terrain. Scattered throughout the area are large carbonate boulders, surface faults, and craters (blow-out pockets). Three types of gas seeps were observed in these areas of rough terrain: those associated with bacterial mats; those found along surface faults; and those emanating from craters.

(5) The East Breaks 376 site occurs on a 90 m topographic high in surrounding water depths of 620 to 625 m. A general survey of the region, conducted by *NR-1*, revealed a mostly flat, featureless, mud bottom except for several areas of exposed carbonate material distributed in a linear, east-west orientation. The rocks were from one to a few meters across and up to 2.5 m high. Tube worms and clam shells were mostly associated with the boulder fields, while sea fans and corals were attached to the larger boulders.

In 1990, Geo-Marine Letters, an international journal of marine geology, produced a special issue (Volume 10, Number 4) on the northern Gulf of Mexico continental slope. This issue contained eight articles, including Roberts et al. (1990b), which addressed the complex and widespread nature of sea floor responses to hydrocarbon seeps, with special emphasis placed on authigenic carbonates and the mounds that result from their accumulation. Other articles in the issue dealing tangentially with carbonates included Kennicutt and Brooks (1990), Bouma et al. (1990), and **MacDonald et al. (1990a)**.

Roberts et al. (1990b) began with a review of "indicators" of seeps, which include direct observations of hydrocarbons (e.g., biogenic and thermogenic

gases, crude oil and gas hydrates), chemosynthetic communities (e.g., mussel beds, tube worms, bacterial mats) and authigenic carbonates (e.g., cemented sediments, hardgrounds, and small to massive mounds). They also discussed the process of carbonate precipitation involving microbial oxidation of hydrocarbons and then went on to re-examine the linkage between carbonate stable isotope signatures (e.g. ^{13}C and ^{18}O values), and the different carbonate mineralogies (aragonite through a range of Mg-calcite to dolomite) in order to identify the source of the hydrocarbons being acted on by the microbial communities and the sites of carbonate precipitation (seafloor or shallow subsurface).

In addition, Roberts et al. (1990b) presented detailed geologic descriptions of three basic sea floor mound types they had identified on the Louisiana continental slope. The first mound type, found primarily on the shallow upper slope and distal parts of the continental shelf, is similar to the banks, biotherms, and reefs described by Rezak et al. (1985) because the presence of living organisms on their surfaces give them a reef-like appearance. The mounds observed and sampled by Roberts et al. (1990b) were found in Green Canyon lease blocks 52, 53, 99, and 143, and had active micro-seepage associated with them. Of particular importance was the observation that surface configurations suggested that authigenic carbonates had been encrusted by coralline algae and other carbonate-secreting organisms during a period of greater light intensity, indicating a period of lower sea level. Isotopic analyses confirmed this relationship when ^{13}C-depleted carbonates were found beneath biogenic veneers on large samples collected during submersible dives.

The second mound type is associated with the crests of salt domes in water depths greater than 300 m. These mounds are numerous, have diameters up to 150 m, and vertical relief on the order of tens of meters. They

often occur in linear patterns and are cut by steep-sided crevices, both being considered products of faulting. Their basic design appears to be that of a cone of cemented blocks arranged around a central vent. Inspection of larger clasts indicated that many of the blocks were composed of numerous smaller clasts welded by internal sediment and carbonate cements. The mounds are believed to be the cumulative result of both authigenic carbonate production at long-term seep sites and sediment stripping from the dome crest (Roberts et al. 1989a).

The third mound type was described from a deep site in Alaminos Canyon visited by DSV *Alvin* in April of 1990 (Brooks et al. 1990). These mounds are composed of fine grain sediment and authigenic carbonates, both as nodular masses and as lithified ledges that protrude from the sediment cover. This latter characteristic is also typical of hydrate mounds. Carbonates were also observed around the bases of tube worm clumps and in mussel beds. According to the authors, the origin of these mounds is still problematic.

Brooks et al. (1990) published a report based on twelve dives with the submarine *Alvin* made in 1990. The dives were made in support of the long-term studies addressing the relationships between salt, seepage, seafloor configuration and deep-ocean symbiosis at the seafloor of the Gulf of Mexico. Four sites were visited: Alaminos Canyon, Orca Basin, Green Knoll (Sigsbee Escarpment), and an underwater blow-out crater in the De Soto Canyon region. Major accomplishments from these dives included (Brooks et al. 1990 p. 1772-1773):

(1) First direct observations of an exposed salt dome on the deep Gulf of Mexico seafloor.

(2) Best collection of rocks from deep waters of the Gulf.

(3) Confirmation that seafloor cementation by seep-associated carbonates is taking place from the edge of the continental shelf to the basin floor.

(4) Confirmation that the occurrence of carbonate buildups, or "false Reefs", as they appear on high-resolution seismic records, is directly related to hydrocarbon seepage, which in turn can be associated with faulting of the seafloor and the sedimentary units beneath it.

As of this report one other contribution has been made to the body of literature dealing with the subject of carbonates associated with hydrocarbon seep sites. Roberts et al. (1990a), publishing in the "Proceedings of the Ninth Annual Research Conference - GCS/SEPMF", reviewed this topic through the existing literature. They presented very little in the way of new material or novel thinking.

4.0 The Origins of Petroleum in the Northern Gulf of Mexico

M.C. Kennicutt II

The origins of the vast petroleum reserves found in the northern Gulf of Mexico still remain an open question. As our understanding of the geological history of the basin and the geochemistry of fluids and source rocks has improved, various generation models and correlations have been proposed. These are compiled in a recent SEPM publication (edited by Schumacher and Perkins 1990). In the onshore area, geographically and geologically restricted accumulations of hydrocarbons have allowed for convincing oil-to-oil and source rock-to-oil correlations (Jones 1990). However, in the offshore area, few, if any, high quality mature source rocks have been penetrated to provide definitive correlations. For the offshore accumulations, source rocks of nearly all ages have been invoked including Mesozoic and Cenozoic strata. Various correlations have been postulated based on simple oil characteristics as well as on more complex biological marker compositions. In general only limited suites of oils were analyzed; however, regionally consistent correlations were possible. Linkage between reservoired fluids and potential source rocks are either direct or argued intuitively from chemical compositions.

Displacement of oil generated in shales to adjacent reservoir sands can be illustrated in a few onshore locations (Claypool and Mancini 1989; Sassen 1989). In the offshore, it has been shown that the present stratigraphic position of pooling is too immature to have produced significant amounts of petroleum (Bissada et al. 1990). Consensus has therefore grown that most offshore oils are significantly displaced from their location of generation. The primary issue of contention in the offshore region is whether to invoke Cenozoic or Mesozoic source rocks as the major source of petroleum and gas (Jones

1990). These alternate scenarios have been developed on the basis of several critical assumptions. Basin modeling suggests that Miocene and older Tertiary sections are presently in the oil generation phase throughout much of the Gulf Coast (Bissada et al. 1990). Deeper Mesozoic sections are inferred to be at a post-generative stage across most of the basin and thus are considered gas sources at the present time. In contrast, only immature, non-source rock quality Tertiary sections have been recovered in the offshore, which suggests little or no source potential for these younger sections, with the possible exception of the Paleogene.

Those invoking a significant Cretaceous or Jurassic source rely mainly on analogy with other prolific oil-producing basins world-wide and onshore Gulf of Mexico oil correlations (Thompson and Kennicutt 1992; Comet et al. 1992). Mesozoic strata are the source of a large portion of known world-wide reserves, and an equivalent source is often envisioned in the Gulf Coast. As mentioned above, the primary objections to a Mesozoic source are 1) the deep position of the strata - particularly in the offshore- at a presumed post-generative phase, and 2) their unknown source rock potential and character. In order for this scenario to be feasible, the generated fluids must continually escape the zone of thermal destruction, thus leading to a dissociated or decoupled source rock-oil system (Bissada et al. 1990).

Until recently, Paleogene strata were generally included in the Cenozoic scenarios. Recent investigations of the Late Paleocene/Early Eocene, in particular the Wilcox, have demonstrated a significant oil and gas generation potential in southern Louisiana (Sassen et al 1988; Sassen 1990a; Sassen and Chinn 1990). Sassen and co-workers have suggested that the Eocene may be an unrecognized source of significant amounts of petroleum, including fluids reservoired in offshore areas (Sassen et al. 1988, 1990a). Wilcox, Frio, and

Jackson correlations have been made by several authors for onshore accumulations (Sassen 1990a; Sassen and Chinn 1990; Tanner and Fuex 1990). It should also be noted that the well-described Jurassic Smackover oils, as well as oils generated from Cretaceous source rocks (Tuscaloosa, Hosston), can be geochemically differentiated from Wilcox oils reservoired in southwestern Louisiana (Wenger et al. 1990).

The initial control on the distribution of oil and gas in the northern Gulf of Mexico is provided by the areal extent of potential source rocks. The evolution of the basin after Louann salt deposition and rifting proceeded during a clockwise rotational movement of the Yucatan block (Hall et al. 1982). Normal ocean-floor spreading processes produced the sediment distributions presently observed. The basin is encircled by carbonate reefs or banks that date to the early Cretaceous at least (Moore et al. 1978). Sea level fluctuations drowned the reefs and deep water sedimentation was common throughout the Upper Cretaceous (Mitchum 1976; Worzel and Bryant 1973). The depocenter of basin filling migrated in an eastward clockwise direction throughout the Cenozoic. Sediment supply was provided by rivers draining the Sierra Madre Mountains during the Paleogene. During the Neogene, sediment was primarily delivered by rivers draining the Rocky Mountains, with a lesser input from the Appalachians (Moore et al. 1978). The events developed a series of prograding sequences of terrigenous clastic sediments. This orientation in drainage provides limits on the areal extent of potential source rocks and sets the paleooceanographic conditions for depositional environments. A primarily marine setting in the Jurassic and Cretaceous was followed by more terrigenous-influenced deposition throughout the Paleogene, although a strong marine influence continued. A decreasing terrigenous influence can be recognized in an easterly direction across the basin in Paleogene strata.

Cenozoic deposition accelerated petroleum formation and provided secondary control on the distribution of oil and gas. The placement of Cenozoic sediments dictates the present day geographical distribution of oil and gas by providing the thermal stress needed to generate oil, though Jurassic strata were probably generating oil during Cretaceous times in some parts of the basin (Nunn and Sassen 1986; Sassen 1990b). While prospective source rocks of various ages are widespread throughout the basin, many have been buried to depths conducive to oil destruction. At the same time, younger strata become mature and continue to generate large volumes of liquid. The present day distribution of petroleum ages and a rim of fluids of Jurassic age around the edge of the basin reflect this interplay of source rock distributions and thermal history (Curtis 1989).

Younger Cretaceous-sourced fluids covering a broad expanse adjacent to this basin across eastern Texas and central Louisiana. The Cretaceous is buried to a depth of primarily gas production or is spent in the offshore, though vestiges of condensate liquids can be recognized. In the central portion of the basin, Paleogene sources predominate and account for a major portion of the reservoired fluids. In many offshore areas, even Paleogene strata are presently at high maturity and a mechanism for preserving liquid hydrocarbons is necessary (Dow et al. 1990). Salt tectonics are critical in producing reservoirs and conduits for transporting fluids out of the zone of thermal destruction and for providing a location for pooling (Bissada et al. 1990). In the central basin, as well as offshore, the underlying Cretaceous is still important, or was in the past, as a source of gas and condensate, giving the basin its overall gassy character. The continued injection of deep-seated gas has also contributed to enhancing upward migration and promoted alteration of reservoired fluids by evaporative fractionation throughout the offshore portion of the basin

(Thompson 1987, 1988; Thompson and Kennicutt 1990; Walters 1990).

In areas of offshore Texas, thermal condensate and gas are reservoired directly above the thickest accumulations of Cenozoic sediments along the northern Gulf Coast (Thompson et al. 1990). The most likely scenario is that these condensates represent the over-mature end-member of the Paleogene oils. Due to the mature nature of these fluids, definitive typing is difficult. This location is also the most likely location for Neogene strata to generate petroleum. However, the generally poor source quality of Neogene sediments suggests only minor amounts of fluid would be generated, though "immature" condensates cannot be ruled out.

The onshore sequence of Mesozoic source strata again becomes important in the deep water Gulf of Mexico where Cenozoic sediments thin. Oils from carbonate-influenced marine sequences reappear in areas seaward of the present day shelf break in a region where older strata are believed to be viable sources (Comet et al. 1992; Bissada et al. 1990). The seaward extent of the repetition of the onshore Mesozoic trend is still uncertain. Studies of seeps have suggested that significant petroleum accumulations are expected to the east and southwest in water depths as great as 10,000 ft. (Kennicutt, unpublished data). In general, these fluids are most similar to Flexure Trend oils, suggesting that the Jurassic/Lower Cretaceous potential extends over a wide region of the deep water Gulf of Mexico.

Based on a review of the published literature, putative source rocks and the ages of known reservoirs are presented in Table 4.1. Mesozoic strata are important at the rims of the immense pod of Cenozoic deposition.

Table 4.1 Summary of the occurrence and potential sources of Gulf Coast oil families.

Oil Family	Suspected Age	Potential Sources	Age of Reservoirs	References
Smackover Oils	Jurassic	Smackover	Upper Jurassic Lower Cretaceous Upper Cretaceous	(2), (3), (4), (5) (13)
Florida Oils	Lower Cretaceous	Lower Sunniland Lime	Lower Cretaceous	(12)
Flexure Trend	Upper Jurassic/ Lower Cretaceous	(Smackover?) (Hosston?) (Pine Island?)	Pleistocene	(1), (8), (9) (14), (15)
Cretaceous Oils	Upper Cretaceous	Tuscaloosa Eagle Ford (Austin Chalk)	Lower Cretaceous Upper Cretaceous Plio-Pleistocene	(1), (2), (4)
Paleogene Oils	Paleogene (Eocene?)	Wilcox Frio Jackson Sparta	Plio-Pleistocene Paleocene/Eocene	(2), (4), (6), (7) (11)
Texas Condensates	Paleogene (Miocene?)	? (all of the above??)	Plio-Pleistocene Miocene	(10), (11)

(1) Evans, 1987
(2) Claypool and Mancini, 1989
(3) Sassen, 1990b and references therein
(4) Wenger et al., 1990
(5) Oehler, 1984
(6) Sassen, 1988; Sassen et al., 1988; Sassen and Chinn, 1990
(7) Tanner and Fuex, 1990
(8) Thompson et al., 1990
(9) Bissada et al., 1990
(10) Dow et al., 1990
(11) Curtis, 1989
(12) Palacas, 1984
(13) Koons et al., 1974
(14) Thompson and Kennicutt, 1992
(15) Comet et al., 1992

Mesozoic sources include shales and carbonates of both Jurassic and Cretaceous age (Sassen 1990b). The importance of Paleogene sources is consistent with previous models of the basin's evolution. In transitional areas between families of oils, mixtures of oil from more than one source are often observed. Today, the Paleogene can be mature to post-mature, depending on its location in the basin (Dow et al. 1990).

The interior salt basins and offshore diapiric belt have produced conduits for oil migration and reservoirs for accumulation. Salt tectonics provide the mechanism for fluid transfer away from the zone of oil destruction. The distribution of gas and liquids is jointly controlled by the timing of migration and trapping and the time-temperature history of multiple source rocks distributed over a range of geologic ages. Discrete strata most likely account for regional variations in oil chemistry producing changes in chemistry that are relatively abrupt. The areal extent of the source strata is a primary control of the geographic distribution of an oil family. As Jones (1990) points out, if we accept that Jurassic-sourced oils are identifiable and that Flexure Trend oils most likely have a Jurassic/Cretaceous source, Paleogene oils and shelf oils found in Neogene reservoirs must have a discrete and separate source. Various geochemical characteristics easily differentiate these oils from the surrounding oil families as a distinct group of oils (i.e., Thompson and Kennicutt 1990). The reasons for excluding Neogene sources have already been discussed in detail. The Tuscaloosa and other Upper Cretaceous sources can also be uniquely distinguished from sources of other ages. This reasoning suggests that the most likely candidate for Paleogene oils, including the Neogene reservoired shelf oils, is the Paleogene section (Jones 1990). While variations in source rock facies and maturity within a source bed can cause variations in oil chemistry, the distinctive nature of each oil family argues against these processes as

primary controls on oil chemistry. Most likely the genetic make-up of the source rock controls the oil's properties. Resolution of this question can only be accomplished by direct source rock/oil correlations. This may not be possible if the sources of offshore oils are presently at a post-generative stage. However, the use of onshore oils as analogues and future source bed penetration in the deep water Gulf of Mexico may provide the needed proof.

Within a family of oils, organic facies and lithofacies changes are seen as gradual changes in oil geochemistry. The preservation of oil across the basin is secondarily controlled by the interaction of the time-temperature history of that particular portion of the basin and the availability of migration conduits out of the zone of oil destruction. The volume of gas and liquids generated is controlled by the distribution of organic matter over geologic time, its composition, and its thermal history.

The northern Gulf Coast is one of the world's most prolific petroleum basins due to the presence of multiple source rocks and appropriate reservoirs emplaced over geologic time. The timing of subsidence and Cenozoic salt tectonics allowed for the preservation of large amounts of liquid hydrocarbons that would have otherwise been thermally cracked to gas. The liquids that did not migrate vertically and the residual organic matter were cracked to gas, providing the generally gas/condensate nature of the northern Gulf of Mexico.

5.0 Preservation of Seep Communities in the Paleo-record

E.N. Powell

5.1 Introduction

Our knowledge of taphonomy is based primarily on descriptive studies of the processes and products of taphonomic alteration, including decomposition, dissolution, abrasion, bioerosion, fragmentation, and the biological and hydraulic reworking of skeletal remains (Brett and Baird 1986; Powell et al. 1989). Taphonomic rates measured in the field are rare, although numerous laboratory studies have been conducted (see Powell et al. 1989 for a review). The majority of field measurements have been limited to shallow, nearshore settings (e.g. Driscoll 1970; Tudhope and Risk 1985), although rates of inorganic carbonate dissolution have been measured (Berelson et al. 1990). Lutz et al.'s (1985, 1988), Rio and Roux's (1984) and Herrera-Duvault and Roux's (1986) measures of dissolution at hydrothermal vents are an important exception. Taphonomic rates for molluscan remains in continental shelf and slope settings remain relatively obscure.

One important set of slope biofacies are seep biofacies. These communities form around areas of local trophic enrichment typically produced by the *in situ* formation of hydrogen sulfide or methane and their subsequent oxidation by chemosynthetic symbiotic bacteria present in the seep biota (Kennicutt et al. 1985, 1988; MacDonald et al. 1990b). The reasons for local enrichment are multitudinous, including petroleum seepage (e.g. Brooks et al. 1987), biogenic methane production (Paull et al. 1985, 1989), and the seepage of sulfurous brine (Paull and Neumann 1987). In all cases, seep communities can be recognized by the abundance of large bivalves, typically Lucinidae,

Vesicomyidae and Mytilidae, which depend upon symbiotic chemosynthetic sulfur or methane-oxidizing bacteria for much of their carbon source.

Seep communities are now recognized to be a widespread and important type of deep water community in the recent and fossil records (Goedert and Squires 1990; Squires and Goedert 1991; Callender and Powell, in press). Modern communities are dominated by a variety of clams and mussels. The dominant molluscan fauna of petroleum seeps off Louisiana and Texas includes three lucinids (*Lucinoma* sp., *Lucinoma atlantica*, and *Thyasira oleophila*), a mytilid, and several vesicomyid clams (*Vesicomya cordata* and *Calyptogena ponderosa*). Callender et al. (1990, in press) and Callender and Powell (in press) studied the taphonomic alteration of chemoautotrophic molluscan-dominated assemblages on the Louisiana upper continental slope. These studies focused primarily on characterizing the taphonomic signature of autochthonous assemblages, of which seep assemblages are an important recent example. Live mussels dominate many seep sites (MacDonald et al. 1990a; Hessler et al. 1988a), but Callender et al. (1990) observed few dead shells. In contrast, live clams were usually present in low numbers, but dead clam shells typically covered wide areas. Callender et al. (1990) identified dissolution as the primary taphonomic process by taphofacies analysis and suggested that mussels are less likely to be preserved.

To determine taphonomic rates on the continental slope and to test the hypotheses that preferential loss of mussels occurs, nylon net bags were filled with lucinid and mytilid shells and deployed on the Louisiana upper continental slope. Eight nylon net bags (1x2 cm mesh) were filled with shells of a lucinid, *Codakia orbicularis*, and a mytilid, *Mytilus edulis*. The lucinid shell is constructed of prismatic and crossed-lamellar aragonite; the mussel of mixed fibrous and prismatic calcite and aragonitic nacre (Majewske 1969;

Alexandersson 1979). Actual shells from the continental slope petroleum seeps were not used because only a small number of these shells were available and also because the majority of shells collected from this region of the slope were already severely taphonomically altered (Callender and Powell, in press). The two shell substitutes cover the range in degree of taphonomic alteration observed in species from petroleum seeps.

Seven shell bags were deployed in mid-August 1988 by the Pisces II submersible at a site known as Bush Hill (27≤ 46.9' N, 91≤ 30.4' W) on the Louisiana slope. Each was deployed on the sediment surface in 550 m of water. One bag was stored in the laboratory as a control. Three shell bags were recovered during a series of Johnson-Sea-Link dives in late September 1991. Shell bags 4 and 6 were placed and collected immediately adjacent to each other near a live mussel bed. Shell bag 2 was deployed and collected near another live mussel bed approximately 10 m from the location of the other two bags.

5.2 Taphonomic Processes

Since the continental slope has the reputation of being a relatively quiet, benign place and most of the assemblages are autochthonous, we expected the shells to be well-preserved (Callender and Powell, in press); however, both mussel and lucinid shells left on the sea floor for 3 years were radically altered by a variety of taphonomic processes:

- significant dissolution and edge rounding (nearly all shells);
- carbonate crusts (some lucinid shells);
- discoloration (both species);
- periostracal breakdown (all of the mussels); and
- some fragmentation and biological alteration.

These alterations occurred despite burial. After three years, all three bag samples were covered by at least 1 to 2 cm of sediment. As many of these taphonomic processes can be expected to have occurred most rapidly while the shells were still exposed on the sea floor, the rates we observed after three years must represent minimal values (Figure 5.1).

Among the taphonomic processes affecting the shells, dissolution was the process most likely to affect their long-term preservation. Callender and Powell (in press) showed that dissolution is an important process at all petroleum seep sites studied off Louisiana. Dissolution may be important because elevated concentrations of H_2S, typical of most seep sites (Lutz et al. 1988; Roux et al. 1989; Callender et al. 1990), are oxidized to the corrosive H_2SO_4 at the oxic/anoxic interface. This acid production drives carbonate dissolution (Boudreau 1991). Dissolution not only resulted in loss of shell weight and shell sculpture, but also produced much of the edge rounding observed. Dissolution produced feathered or rounded edges on most mussel shells, but did not affect the edges of lucinid shells. For each shell type, the intensity of these dissolution processes did not vary between sites. Feathered or rounded edges were also noted by Flessa and Brown (1983) in a laboratory study of shell dissolution.

Powell and Davies (1990) observed that discoloration was a good indication of the relative age of shells on beaches. Discoloration is known to occur rapidly in many environments (Pilkey et al. 1969). Mussel shells generally acquire a faded appearance. Lucinid shells are more frequently stained yellowish brown, sometimes gray. Exposure to liquid hydrocarbons and H_2S probably explain these discolorations. Orange stains of obvious hydrocarbon origin have been found frequently on lucinid shells from most

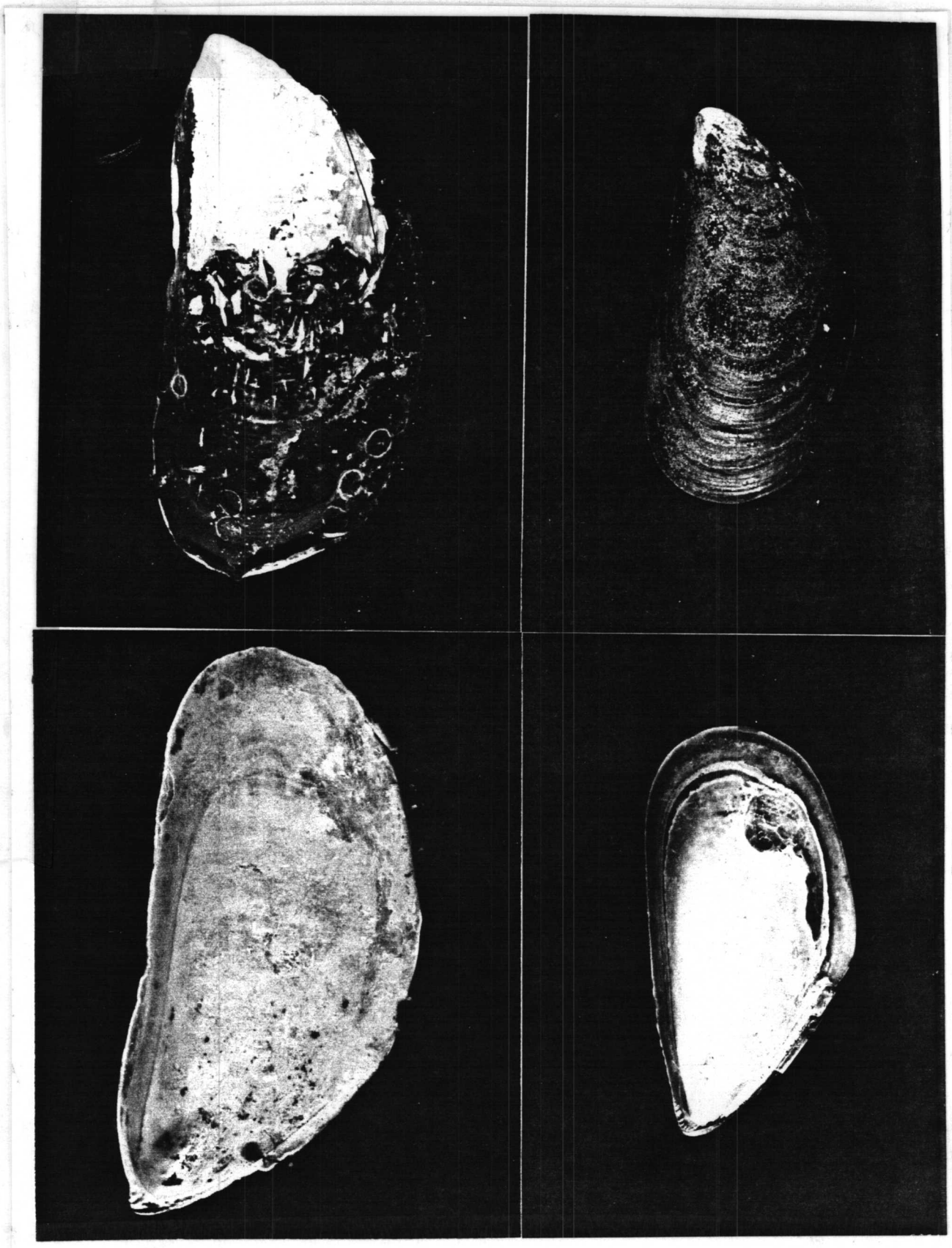


Figure 5.1 Effect of taphonomic processes on a *Mytilus edulis* shell (left) recovered from the hydrocarbon seep at Green Canyon 184/185 (Bush Hill) following a three year deployment in a nylon bag. Photographs on right show a control shell.

seep sites (Powell and Davies, unpubl. data). An alternative explanation is that the yellowish brown color came from the oxidation of sulfide minerals. Blackened mussel shells collected from an anoxic brine at nearby Green Canyon lease block 233 turned reddish orange less than one hour after being brought to the surface (Powell and Davies, unpubl. data).

A number of mussel shells were fragmented. Callender and Powell (in press) suggested that some fragmentation at petroleum seeps was due to loss of shell integrity as dissolution proceeded rather than to any physical or biological breakage. In our three-year study, mussel shells had been so weakened by dissolution that only the continuing presence of periostracum maintained the shell in a recognizable condition. The life span of a recognizable mussel shell on the sea floor, certainly less than ten years, is probably controlled in large measure by the rate of degradation of the periostracum.

Authigenic carbonate production is an important feature of seep sites (e.g. Han and Suess 1989). This process obviously can occur rapidly. About 25% of the mussel shells in our three- year study had recognizable carbonate crusts. None of the lucinid shells did. As the lucinid shells were much less affected by dissolution, the implication is that the carbonate crust required a surface affected by dissolution. However, carbonate crusts were only observed on the inner shell surface where dissolution was less severe and most commonly in the shell center rather than around the margin. Consequently, microenvironment was important in authigenic carbonate formation. Certainly, dissolution and precipitation occur within microenvironments of close proximity because all shells with carbonate crusts also showed clear evidence of dissolution, and the deployment site where carbonate crusts occurred most frequently was also characterized by mussel shells that had lost the most weight through dissolution.

5.3 Species-Specific Rates

With the exception of staining and some aspects of biological alteration, mussel shells were degraded significantly more rapidly than lucinid shells in three years. Mussels have a higher surface-to-volume ratio which should make them more susceptible to rapid degradation (Aberhan and Försich 1991). However, the rate of degradation was much faster than what might be expected based on a simple relationship with surface area, and small individuals were affected no more significantly than large ones. Probably some other aspect of shell construction, such as its organic content, was important. The estimate of the life span of a mussel shell was 3 to 15 years at the most affected site, whereas a lucinid shell was indefinitely preserved.

Although the mussel shells were significantly more degraded, the process of degradation was similar in many respects between the two species. In both cases, the dorsal and umbonal area of the shells' outer surfaces was most seriously affected, as was the ventral margin; the ventral and inner surface was less seriously affected. Precipitation was an obvious exception: the differences then were more in degree than in kind and probably represent those areas first affected by taphonomic processes during life. The dorsal, umbonal area of the shell's outer surface is likely to be the site of periostracum degradation during life and thus the shell surface is likely to be more easily exposed to taphonomic assault in this area after death.

The more rapid deterioration of the mussel shells lends credence to the belief that the species composition of fossil seep assemblages is biased in favor of the more robust clams. Furthermore, the relatively good preservation of the clams should not be taken as an indication of an unbiased preservation of the fossil assemblage any more than should its autochthonous nature (Callender and Powell, in press). Some lucinid shells were still in mint condition after

three years on the sea floor. All of them would have been described as well preserved. It is likely that mussels were a dominant component of most fossil seep communities, but the record of their presence has been very poorly preserved compared to lucinids, which were well-preserved.

5.4 Spatial Scale of the Taphonomic Process

Callender and Powell (in press) suggested that one of the important characteristics of autochthonous assemblages like those at petroleum seeps was the importance of small-scale variability in the preservational process. In our case, shells deployed within 10 m of each other suffered considerably different degrees of taphonomic attack. The source of this local variation is unclear. Processes as divergent as discoloration, dissolution and biological alteration were more important in bag 2 than in bags 4 and 6. One likely explanation is that bag 2 was buried more slowly than the bags at the other deployment site; however, we have nothing but the circumstantial evidence associated with the shells themselves to support this belief.

5.5 Conclusions

Petroleum seep shell assemblages on the continental slope are significantly and rapidly altered by most of the same taphonomic processes just as are their shallow-water counterparts, although the rates differ. The presence of carbonate encrustations and the relative absence of abrasion are the salient exceptions for the seep assemblages on the continental slope. The principal bias is produced by dissolution and periostracal degradation. The rates of these processes are species- and size-dependent, so that the final assemblage is heavily biased against juveniles and mytilid species.

Despite a quiet deep-water environment, taphonomic rates are rapid enough to be measured over reasonable investigator time spans. Extrapolation of the results to longer times agrees with the observations in cores from these sites and fossil assemblages of Cenozoic age. By implication, most taphonomy must occur early in the assemblage's formation while the shell is near the sediment surface and the degree of taphonomic alteration is controlled in part by the rapidity with which the shell migrates through the taphonomically-active zone (Powell, in press). Accordingly, measurement of taphonomic rates in presently-forming assemblages can be expected to have application to understanding the biases imposed by taphonomy in the fossil record. Moreover, the general agreement between the results of taphofacies analysis and the measured rates offers hope that a reasonable correlation might be found between the evidence preserved and the rates themselves.

6.0 Non-Symbiotic Microbiota as Associated with Chemosynthetic Communities

Carl O. Wirsen, Holgar W. Jannasch, and S.J. Molyneaux

6.1 Introduction

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.

In aquatic environments, including hydrothermal vents, localized dense populations of filamentous sulfur-oxidizing microorganisms are not limited to *Beggiatoa* sp., but can include non-gliding members of the genus *Thiothrix*, which generally occur in tufts (Larkin 1980; Stein 1984; McGlannan and Makemson 1990), or *Thioploca*, which occur as bundles of gliding filaments within a common sheath (Gallardo 1977; Maier et al. 1990). The *Thioploca* found off the coast of Chile and Peru contain a large central vacuole (Maier et al. 1990) very similar to that reported for the large *Beggiatoa* filaments from Guaymas Basin (Nelson et al. 1989).

Free-living chemosynthetic sulfur-oxidizing bacteria of the genus *Thiobacillus* and the genus *Thiomicrospira* have been isolated from deep-sea HTV sites and are believed to be the major primary producers at these sites (Ruby et al. 1981; Jannasch et al. 1985). These isolates consist of both obligate and facultative autotrophs, which offers the facultative use of either organic or inorganic energy sources (Jannasch and Wirsen 1985). The ability to grow as a facultative autotroph (versatile) as opposed to an obligate autotroph (specialized) can offer advantages for organisms that exist in an

environment in which the chemical milieu may change significantly (Gottschal et al. 1979; 1981). This can be especially true at HTV sites where effluents may only intermittently bathe the organisms with reduced sulfur.

The marine *Beggiatoa* at deep-sea HTVs have not been isolated in pure culture, but shipboard and laboratory experiments have established that they have autotrophic potential and can fix CO_2 (Nelson et al. 1989). Their cytochromes have also been characterized (Prince et al. 1988). Whether they possess facultative chemoautotrophic capability, as does the marine strain isolated from a salt marsh (Nelson et al. 1982), remains to be determined. Filamentous mats containing gradient organisms such as *Beggiatoa* would be dependent on an intermittent flux of reduced sulfur (sulfide) from the sediments below for autotrophy (Nelson et al. 1986). Thus the obligate autotroph may not be as competitive in these situations as one that can switch between heterotrophic and autotrophic nutrition.

Facultative autotrophy is certainly an area to investigate with respect to the pigmented (yellow and orange) and non-pigmented (white) *Beggiatoa* found at the Gulf hydrocarbon seeps. It is probable that one form is pursues an autotrophic existence where sulfide is plentiful due to sulfate reduction occurring in the hydrocarbon-rich sediment. The other form may rely primarily on heterotrophic utilization of organic compounds from hydrocarbon metabolites diffusing through the sediment and from degradation of the mat material itself.

6.2 Results of Studies Concerning Microbiota at Oil Seeps

This section deals with chemosynthetic activity measurements and observations of the bacterial mats covering areas of sediment at the Bush Hill petroleum seep site in the Gulf of Mexico (27°46'40"N, 91°30'44"W). C.O.

Wirsen participated as an observer on *JSL* Dive # 3108 to the Bush Hill site at a water depth of 1884 feet. The dive took place on August 31, 1991, commencing at 11:39 and surfacing at 14:31. The goal of this shared dive was to collect bacterial mats of both white and orange color by using slurp gun and tube core sampling procedures. The sampling was successful for the most part in that the yellow/orange bacterial mat was slurped into a Nitex mesh covered container. One tube core, taken over patchy white bacterial mat, was successfully subsampled after retrieval. A sample of blackened surface sediment from the core was also taken for bacterial direct counts. The other tube core collected over a dense mat layer degassed extensively upon surfacing, causing total disturbance of the surface sediment, thus making it of no use for surface mat collection. This core had a visibly large amount of petroleum present, and a surface sediment slurry was preserved for bacterial counts. Samples of the *Beggiatoa*-like bacterial mats were either used immediately on board ship for CO_2 fixation experiments, frozen for a later enzyme assay, or chemically fixed for microscopic examination.

6.2.1 Time Course Determinations of Chemosynthetic CO_2 Fixation

The mat filaments (white and orange) were collected separately and inoculated into volumes of a temperature equilibrated artificial seawater mix containing a known concentration of $NaHCO_3$. All flasks were spiked with radiolabeled bicarbonate (approx 0.15 μCi/ml final). The **test** flasks received 10 mM thiosulfate and 100 μM sulfide, while the **control** flasks received no amendment. A series of both orange mat material and white mat material were incubated at 22°C and at 8°C. Fixation of CO_2 was followed over time and the results are presented in Figures 6.1 and 6.2. The data are presented as nmol C fixed/mg dry weight because additional samples of inoculum were taken, dried

and corrected for salts on the filters so that the actual amount of mat material sampled at each time point could be determined. The data are presented on a linear scale in Figures 6.1A and 6.2A and on a log scale in Figures 6.1B and 6.2B. While there was virtually no fixation activity by orange mat, with the possible exception of a very slight increase in the 8°C sulfide test, there was a very significant activity by white mat in the test flask at 8°C (the white control and sulfide test samples at 22° showed some activity for the first hour but then leveled off). The fixation rate for the 8° sulfide test averaged about 57.5 nmol carbon fixed/ mg dry weight/hr. This greatly exceeds the rate noted for field-collected samples of *Beggiatoa* from Guaymas Basin sediments (Nelson et al, 1989). The rate is more linear than exponential, as seen by comparing Figures 6.1A and B. An interesting point is that this is the first notation of this level of activity for benthic bacterial mats at psychrophilic temperature (8°C), while no significant activity took place at a mesophilic temperature of 22°C. This is largely understandable in that the Bush Hill site is a cold seep area and has no hydrothermal activity. The data support the idea that the white mat material is chemosynthetically more active than the pigmented yellow/orange mat material.

6.2.2. Determination of RuBPCase Activity in Bacterial Mat Material

Samples of white, orange and yellow (the latter may be due to just having less pigment in the cells) mat material were collected and frozen in microfuge tubes containing seawater and brought back to the laboratory. They were thawed, spun for 2 seconds and then suspended in assay buffer before cell lysis. The assay procedure for RuBPCase followed that of Beudeker et al (1980) as modified for *Beggiatoa* by Nelson and Jannasch (1983). Determination of protein in the cell free suspensions was determined by the Coomassie brilliant

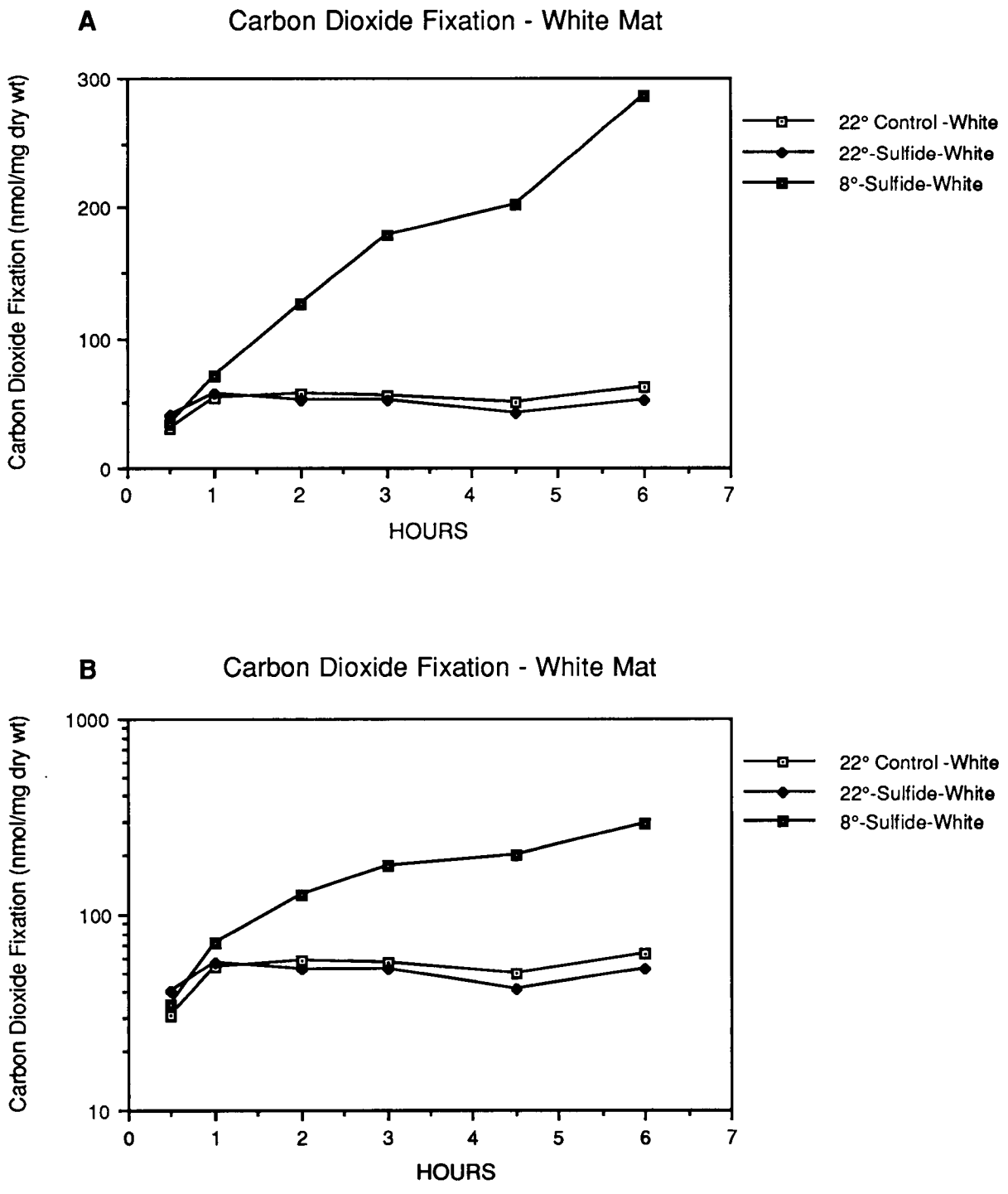


Figure 6.1 Linear (A) and log (B) scales depicting rates of CO_2 fixation by white *Beggiatoa* mat samples from GC 184/185, determined from uptake of radio-labeled bicarbonate at two temperatures. Test flasks were spiked with 10 mM thiosulfate and 100 μM sulfide; control received none.

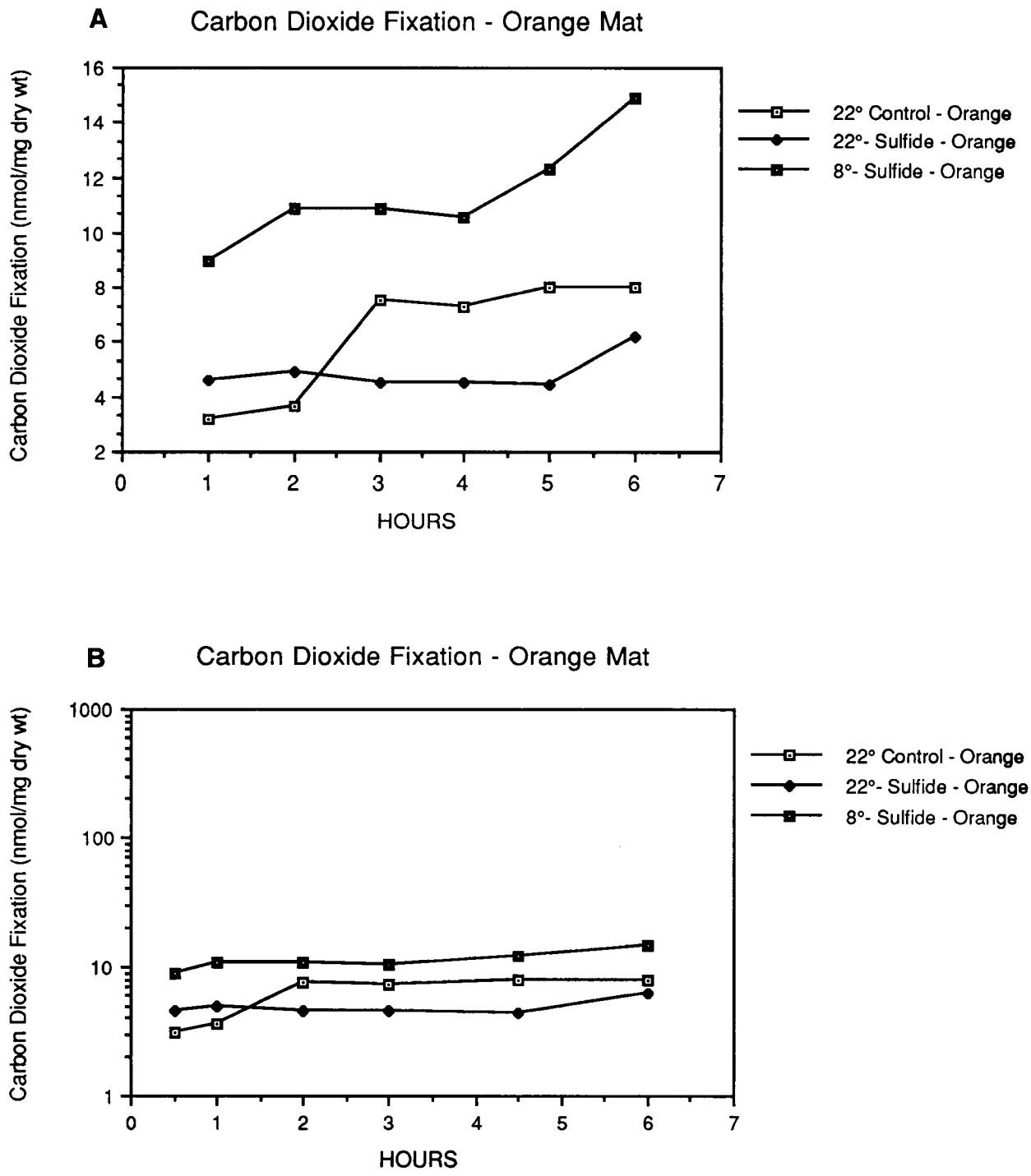


Figure 6.2 Linear (A) and log (B) scales depicting rates of CO_2 fixation by orange *Beggiatoa* mat samples from GC 184/185, determined from uptake of radio-labeled bicarbonate at two temperatures. Test flasks were spiked with 10 mM thiosulfate and 100 μM sulfide; control received none.

blue dye binding technique (Bradford, 1976) using the Bio-Rad protein assay kit. The results of the enzyme assay are presented in Table 6.1. As noted, upon examination of the DPM counts, there was no carbon fixation (enzyme activity) in any cell free extract run at the normal assay temperature of 30°C. Spinach, run as a positive control, showed very high RuBPCase activity at this temperature. Indicated questionably on the table, when a sample of white mat extract was run at 8°C there is a hint of some activity starting between 12 and 15.5 minutes. It is unknown whether this would have continued to increase so that a real rate could be determined. The value of 0.72 for carbon fixation in this sample is in all probability not a true value, but it tends to indicate, as the data in Figure 6.1 indicate, that the chemosynthetic activity of these *Beggiatoa* mats is likely to occur at the ambient temperature of 8°C. This value (0.72 nmol C/mg Protein/min) is lower than the reported RuBPCase activity values for field collected *Beggiatoa* spp. from the Guaymas Basin (Nelson et al., 1989).

The enzyme data (as well as the data in Figure 6.2) indicate that the orange/yellow mat material is again the least active with respect to chemosynthetic potential. One point that should be mentioned is that the protein values (ug/ml) in the cell free extracts (i.e. enzyme concentration) of mat material was quite low, so that fixation activity could be difficult to measure. In future experiments larger amounts of biomass should be used to obtain more concentrated cell free extracts, and they should be run at the colder temperature (8°C) for longer periods of time. Also, when the cells are originally obtained and frozen it should be as a moist pellet and not suspended in seawater. There is a possibility of significant cell lysis of these large cells when frozen in seawater and hence a loss of enzyme when the seawater is thawed and removed before the assay procedure is initiated.

Table 6.1 RuBPCase assay (carbon fixation) for white, orange, and yellow *Beggiatoa* mat material with spinach as positive control. Test and control activities were determined for 20 µl of unacidified assay mix.

Sample and temperature	DPM (50 µl) Time (minutes) 1	2	3	4	5	6	7	8	10	12	15.5	Protein mg/l	Test DPM	Control DPM	nmol C/ mg protein/min
White 30°C	8	0	0	0	0	0	-	-	-	-	-	125	169248	162665	none
Orange 30°C	16	8	0	0	15	0	-	-	-	-	-	85	191227	179108	none
Yellow 30°C	0	5	-	3	-	0	7	0	-	-	-	94	149600	130484	none?
White 8°C	3	-	6	-	4	-	0	9	21	-	-	125	150696	141913	0.72??
Spinach 30°C	19401	24075	25303	25554	25943	26069	-	-	-	-	-	10095	127892	131838	110

6.2.3. Description of *Beggiatoa* Morphologies Present in Mat Material

In our opinion, the primary cell morphology comprising both the white and orange mats covering areas of sediment at Bush Hill are of *Beggiatoa* spp. The cells occurring in filaments were seen to contain significant quantities of internal sulfur granules. The sediment below a mat slurped up by the submersible was black, indicating anaerobic sulfate reduction processes occurring beneath the mat. These processes were most probably supplying sulfide as the diffusible chemosynthetic energy source to the *Beggiatoa* cells. At some future point studies should examine the possible alternative use of CH_4 as an energy source by these populations.

We examined fixed samples of white, yellow and orange mat filaments. The width classes fell into primarily two size ranges (three groups were noted for Guaymas Basin *Beggiatoa* mats- Nelson et al, 1989), consisting in the large majority of approximately 30 to 50 μm diameter cells and occasionally 85 to 108 μm diameter cells. Intact filaments were seen to have the characteristic rounded tip of *Beggiatoa*. The cells pigmented orange or yellow appeared to contain this colored material within the cell because it was easy to microscopically distinguish those cells from the non-pigmented white filaments when mixed in a sample. Some of the *in situ* mats that were pigmented appeared to have fringes of the white non-pigmented cells. The pigment or pigments themselves (of unknown composition) appeared to be water soluble as they would colorize seawater following resuspension of cells. As cells lysed after extended incubation, more colorization became visible in the suspension medium. Microscopically, the cells containing the pigment did not appear as healthy as the white filaments, were more knobby or pleomorphic in shape, and, as evidenced by the fixation and enzyme data, were the least active in chemosynthetic potential. The pigmentation of these cells is not characteristic

of the pink color due to high c-type cytochrome content noted in dense suspensions of *Beggiatoa* spp. from Guaymas Basin sediments (Prince et al., 1988).

6.2.4. Cell Counts of Free-Living Microbes on Sediment Surface

Acridine orange direct counts were conducted on chemically-fixed surface sediment samples taken from tube cores. The first was blackened sediment taken from below the white mat layer, and the second was from the disturbed oily tube core that degassed upon retrieval. The numbers noted below (average of two sample counts) reveal high populations of free-living microbes in the sediment, and are indicative of relatively rich oceanic surface sediments.

1. Sediment below white mat = 2.96×10^9 cells/ml
2. Sediment from oily core = 3.96×10^9 cells/ml

6.2.5. Photomicrographs of *Beggiatoa* Filaments in Mat Material

Photomicrographs were taken using phase and bright field microscopy. Representative photos of the different morphologies and pigmented types are shown in Figures 6.3 to 6.10. Sample filaments from the white mat layer averaged between 35 to 43 μm in diameter and were fairly uniform in appearance and contained significant numbers of internal sulfur granules. Samples from the yellow mat (some of which were clumped as tufts of cells) had a wider range in size, and within these samples very wide filaments (approx. 100 μm) were occasionally seen. The large majority of the yellow filaments ranged between 27 to 50 μm in diameter and the cells containing pigment were somewhat more pleomorphic in appearance. The occasional wide filaments, which did not appear to have pigment inside but did contain sulfur granules, ranged between 90 to 108 μm diameter. Filaments from the orange mat

contained sulfur granules, but not all cells contained the pigmentation. The pigmented filaments were fairly uniform in appearance, ranging from 35 to 50 μm in diameter. White filaments mixed in with this population contained internal sulfur granules.

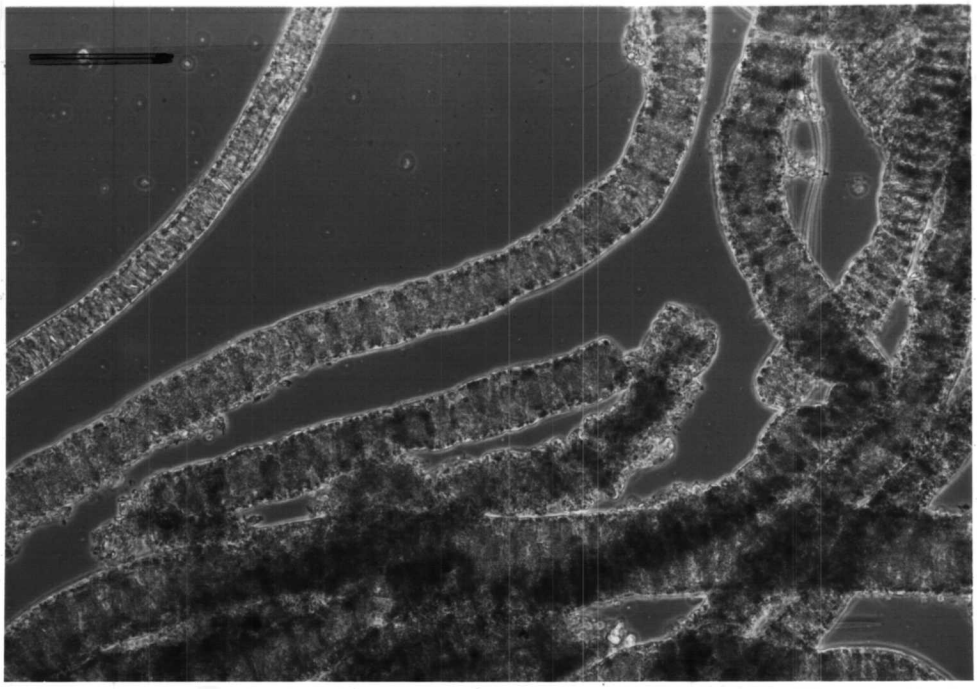


Figure 6.3 A mix of pigmented (yellow/orange) and non-pigmented (white) *Beggiatoa* filaments from the slurp gun collection of a visibly pigmented mat. The filaments containing pigment appear more opaque when examined microscopically. Bar indicates 100 μm.

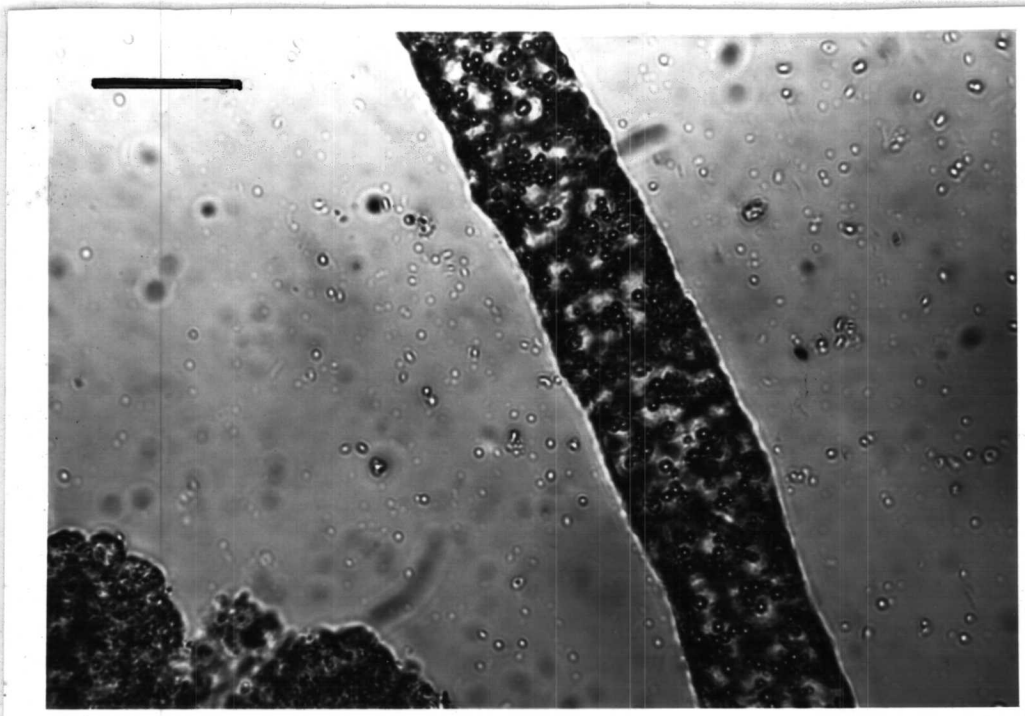


Figure 6.4 A bright field photograph of a single white *Beggiatoa* filament. Note the numerous internal sulfur granules. Bar indicates 50 μm.

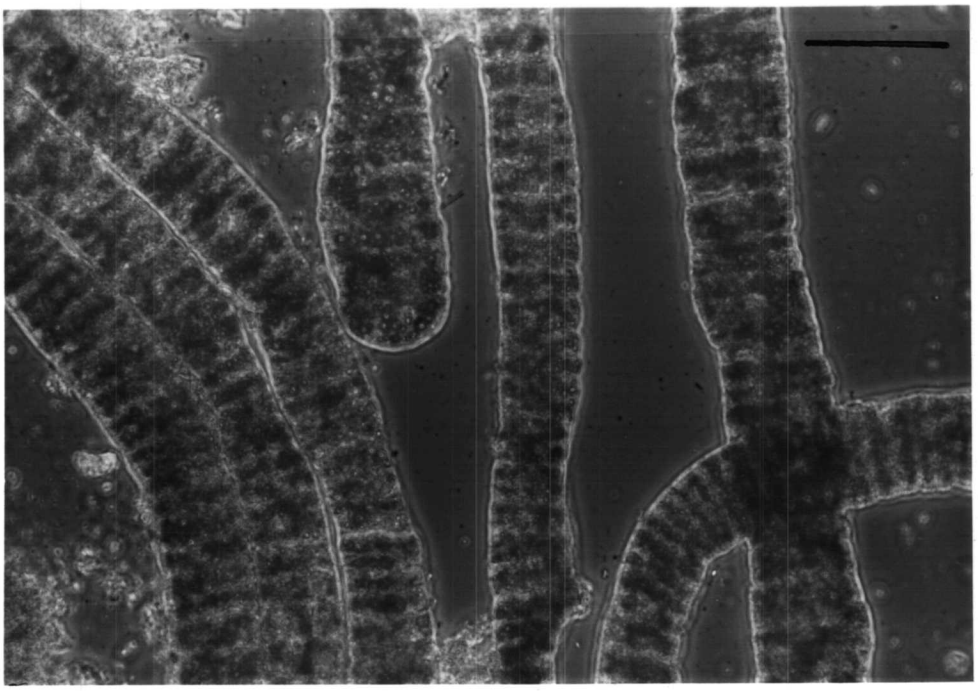


Figure 6.5 A phase contrast photograph of a group of *Beggiatoa* filaments collected from a white mat present on the surface sediment of a tube core. Note the internal sulfur granules present in the filaments and the rounded tip of one filament. Bar indicates 50 μm.

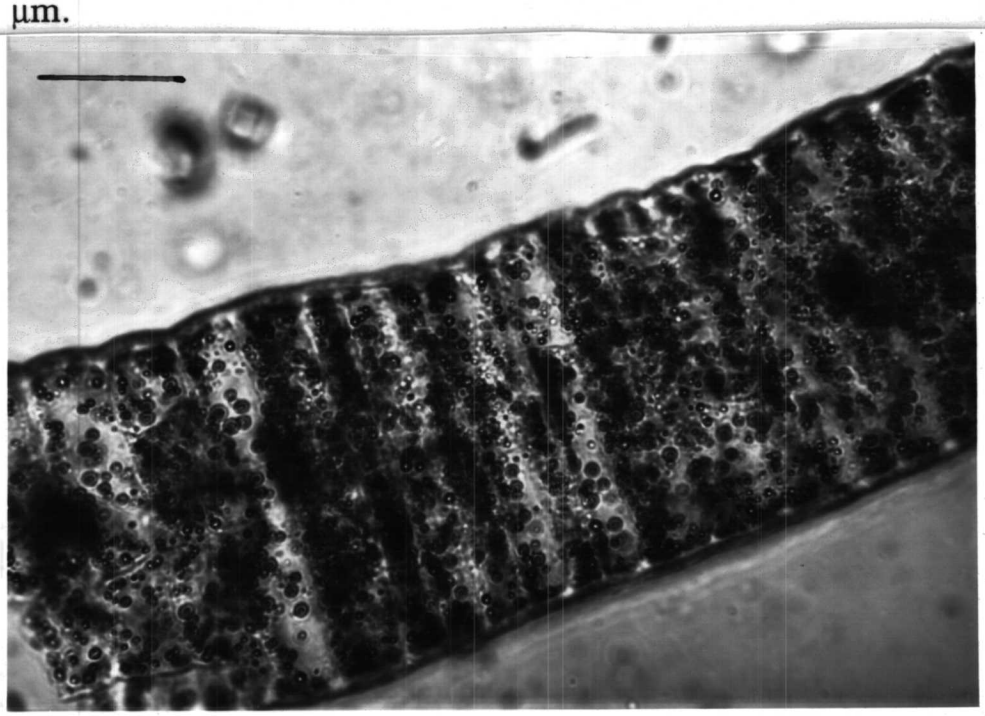


Figure 6.6 A bright field photograph of a very wide *Beggiatoa* filament seen occasionally in the collection of yellow pigmented mat. Cell septa and internal sulfur granules are visible. Bar indicates 50 μm.

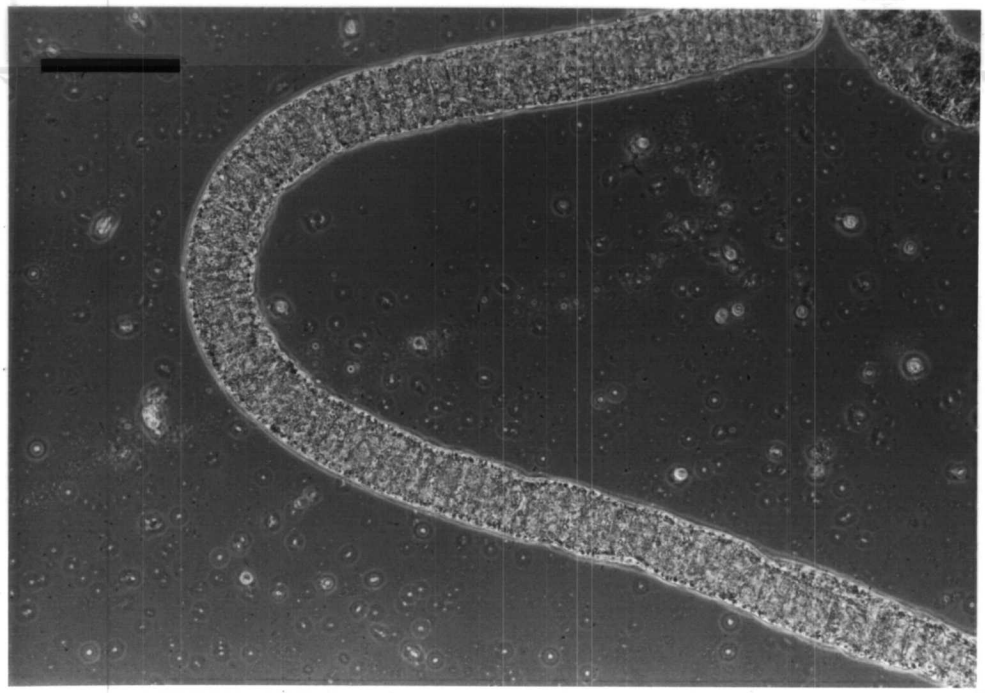


Figure 6.9 A phase contrast photograph of a single yellow pigmented *Beggiatoa* filament. Bar indicates 100 µm.

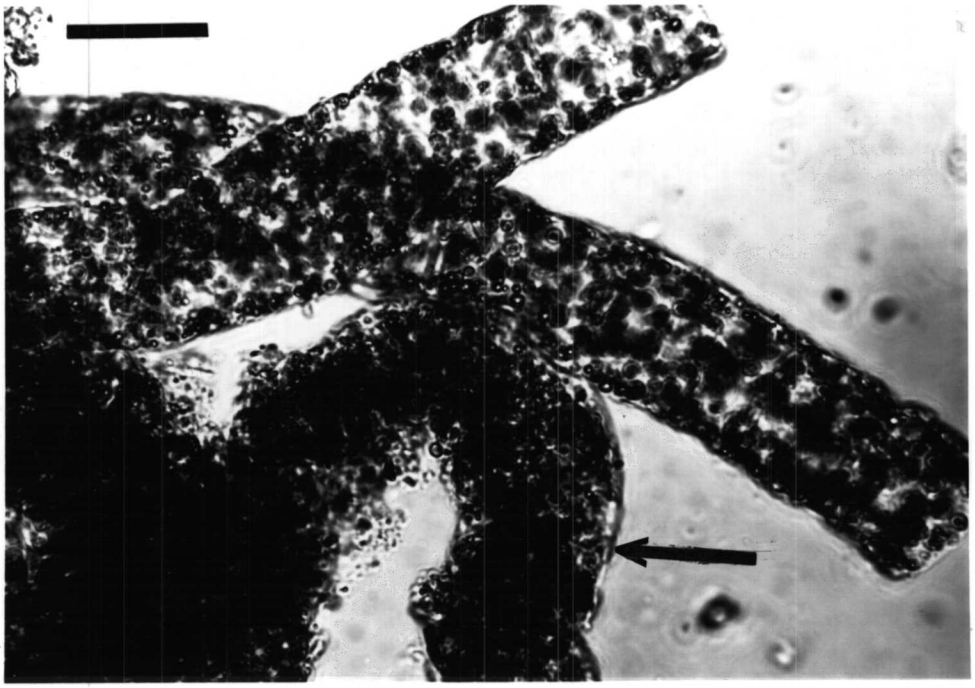


Figure 6.10 A bright field photograph of *Beggiatoa* filaments from the yellow/orange mat collection. Two of the filaments are white (non-pigmented) and sulfur granules are more visible than in the third filament (indicated by arrow) which contains pigment and is significantly more opaque. Bar indicates 50 µm.

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

C.R. Fisher

7.1 Introduction

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 1985a; 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 suggests 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. They are not covered in this portion of the literature review.

Separate sections of this review will provide a general background of the physiology, biochemistry, and ecology of the vestimentiferans, vesicomyids, and mytilids, respectively, and will outline our working models of the symbioses in each group. Although much of our knowledge concerning vestimentiferans and vesicomyid clams derives from the hydrothermal-vent species, we will detail the specific research on the Gulf of Mexico hydrocarbon seep species and will review evidence that vesicomyid clams and tubeworms function similarly to their respective

hydrothermal-vent relatives. The mytilid species from the shallow seep sites support three methanotrophic symbionts that have only been found in the Gulf of Mexico. It has proven to be an extremely tractable species for physiological studies, and is perhaps the most well-studied species of chemoautotrophic or methanotrophic symbionts. The focus of this review on either HTV or seep species will reflect the preponderance of literature.

7.2 Vestimentiferans

The most extensively studied vestimentiferan is the giant hydrothermal vent tube worm, *Riftia pachyptila* (Jones 1981). However, all vestimentiferans have a similar body plan (Jones 1985b), so most of the following discussion applies equally well to other vestimentiferan species. Vestimentifera have no mouth, gut, or anus; they possess four body regions: the obturacular region, the vestimentum, the trunk, and the opisthosome (Figure 7.1). Located at the anterior end of the worm, the obturacular region comprises a central supporting structure, the obturaculum, and an efficient gas exchange organ, the branchial plume (Jones 1981; Arp et al. 1984). The plume is the only portion of the worm's anatomy which is normally exposed to the environment (it can be withdrawn into the tube at will); the remainder of the worm in encased in a thick-walled tube composed of a chitin-like proteoglycan/protein complex (Gaill and Hunt 1986). In all known vestimentiferans except *Riftia*, the animal tissue extends all the way to the posterior end of the tube (Jones 1988). Posterior to the plume is the vestimentum, a muscular region that serves both to anchor the animal in its tube when the plume is extended and to secrete the tube as the animal grows. Below the vestimentum, the trunk makes up the bulk of the organism. Inside the trunk, between a pair of coelomic cavities, are gonads and an organ termed the trophosome (Van der Land and

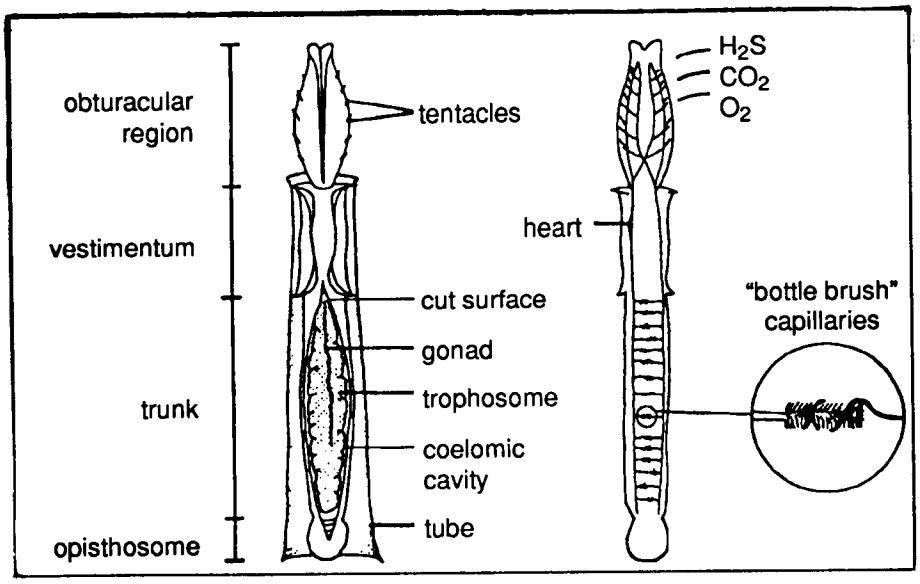


Figure 7.1 Schematic drawings of *Riftia pachyptila* showing major body regions and gross vascularization. Insert at right shows "bottle brush" arrangements of capillaries found in each lobule of the trophosome. The heart is located on the dorsal vessel (from Fisher 1990).

Nørrevang 1977). In *R. pachyptila* the trophosome accounts for about 16% of the animal's wet weight (Childress et al. 1984).

The opisthosome, a short posterior region, apparently serves to anchor the base of the worm to its tube, and in *R. pachyptila* to secrete basal partitions inside the tube. The trophosome consists primarily of symbiont-containing bacteriocytes, associated cells, and blood vessels (Hand 1987). The bacterial volume in the trophosome of *R. pachyptila* has been calculated to be between 15 and 35% of the total volume of the trophosome (Powell and Somero 1986). Activity levels of RuBP carboxylase in the trophosome, produced by chemoautotrophic symbionts in vestimentiferans, (Cavanaugh 1985; Felbeck et al. 1981), are the highest measured in any chemoautotrophic symbiosis (Felbeck 1985; Brooks et al. 1987; Fisher et al. 1988c; Fisher 1990).

Because the symbionts are isolated from the environment within the interior tissue off the trophosome, the host physiology and metabolism must

intercede to extract the required chemosynthetic substrates (H_2S, O_2, and CO_2) from the environment and transport them to the bacteria. The most likely pathway for these substrates in the HTV vestimentiferans is as follows: (1) intake from the hydrothermal effluents across the plume surface; (2) attachment of the substrates; and (3) transport to the trophosome through the vascular circulatory system. In vestimentiferans, hemoglobin is the binding protein; both the vascular hemoglobin and the hemoglobins in the coelomic fluid bind sulfide and oxygen with high affinity; binding for both substrates is simultaneous and reversible (Arp and Childress 1981; Arp and Childress 1983; Arp et al. 1987; Childress et al. 1984). The trophosome is highly vascularized so that the symbiotic bacteria are all in a position to be well-supplied with nutrients and substrates transported by the blood (Jones 1988). In fact, vestimentiferan blood appears to contribute to the creation of a chemical environment within the trophosome (i.e. large pools of sulfide present at low activity), that promotes high rates of chemoautotrophic carbon fixation (Fisher et al. 1988d; 1989). The products of either bacterial translocation or digestion can be readily transported to other host tissues from the trophosome.

Vestimentiferans in general, and *R. pachyptila* in particular, appear to be sulfide specialists; that is, interactions of animal metabolism with sulfide are minimized and the symbionts are provided with sulfide as the sole form of reduced sulfur (Childress et al. 1991a). Furthermore, only sulfide, among the reduced sulfur species tested, has been found to stimulate carbon fixation by vestimentiferan symbionts (Fisher et al. 1989, Fisher et al. 1988e, Wilmot and Vetter 1990). Diffusion of sulfide and oxygen across the plume, coupled with binding and transport through the blood, is apparently sufficient to supply the metabolic needs of the intact symbiosis even when, as is usually the case at HTV sites, the individual worm is growing rapidly

and is metabolically highly active (Childress et al. 1991a). A variety of evidence suggests that carbon limitations affect tube worms in the hydrothermal-vent habitat (Felbeck 1985; Rau 1985; Fisher et al. 1990). In *Riftia*, evidence from live animal respiration and maintenance experiments indicate that inorganic carbon is accumulated in the blood by an as-yet-unknown mechanism (Childress et al. 1991a).

7.3 Gulf of Mexico Hydrocarbon-Seep Vestimentiferans (Shallow Sites)

There are two species of vestimentiferan tube worms present at the shallow sites, *Lamellibrachia* sp. and *Escarpia* n.sp (S. Gardiner pers. comm.) The chemical environment at the hydrocarbon seeps differs substantially from hydrothermal vents. Most notably, sulfide is normally undetectable (< 3 μM) in the bottom water around the animals' plumes and siphons, although it is abundant in interstitial water in the sediments (**MacDonald et al 1990a**). Some methane gas streams have been observed and there are no significant temperature anomalies. A distinct set of adaptational strategies for the HS vestimentiferans is therefore to be expected.

The ecological physiology of the two HS species is not well enough understood to hypothesize on niche differentiation between the two species; the two species are often intermingled such that large aggregations of *Lamellibrachia* sp. include a smaller number of *Escarpia* n.sp. scattered around the periphery. Vestimentiferan assemblages at the HS take many forms. **MacDonald et al.** (1990a) have described aggregations morphologies that range from 40-cm diameter tangles, to 1-m radial arrays with basket-like centers, to 2-m domes, and finally to contiguous clusters over 9 m in diameter made up of ≥1.5 m-long individuals. This variety probably reflects a combination of different age histories for the clusters and a chemical environment that is heterogeneous at a small spatial scale. One dramatic

indicator of the variability of conditions between separate HS sites is the range in stable isotope content found in the tissues of the seep vestimentiferans (Fisher et al. 1990, Kennicutt et al in press); this probably reflects differences in the source hydrocarbons among seep sites.

The two species of vestimentiferans from the hydrocarbon seep sites have symbiont-enzyme activities and blood properties similar to those described above for HTV tube worms (Brooks et al. 1987; Childress et al. 1991b; Fisher et al. 1988a). They most likely function physiologically in a manner very similar to the HTV species. Studies with isolated symbionts from the HS escarpid have demonstrated that blood function with respect to symbiont autotrophy is exactly as outlined above for the HTV species, and that the HS species are also sulfide specialists (Fisher et al. 1988a). Stable isotope comparisons indicate that the seep vestimentiferans are most likely not carbon limited (Fisher et al. 1990), although the symbiont's apparent Km for CO_2 appears similar to HTV species (Fisher et al. 1988a).

7.4 Vesicomyid Clams

The Vesicomyidae are a deep-sea family of bivalves. The vesicomyids are characterized by a short simple gut, small labial palps, and a reduced feeding groove on the ventral margin of the gills (Boss and Turner 1980; Fiala-Médioni and Métivier 1986; Le Pennec and Fiala-Médioni 1988; Turner 1985). Thus they have greatly reduced abilities to acquire food by filter-feeding. All of the species in two genera in this family, *Calyptogena* and *Vesicomya*, apparently contain chemoautotrophic bacteria as endosymbionts in their large fleshy gills (Fiala-Médioni 1984; Vetter 1985; Brooks et al. 1987; Fiala Médioni and Le Pennec 1988; Fisher 1990). A third genus, *Ectenagena* (Boss 1968), has not been examined for symbionts. *Calyptogena magnifica* form a substantial component of the HTV

communities at the Galápagos Rift and East Pacific Rise (Boss and Turner 1980). The gills account for 13-22% of the body wet weight of *C. magnifica*, and the blood accounts for another 24-44% (Fisher et al. 1988a). The uptake of oxygen and sulfide by vesicomyids is different from that of the vestimentiferans. The blood of *C. magnifica* contains a hemoglobin with moderate oxygen affinity in erythrocytes and also contains an extracellular sulfide-binding component that can accumulate sulfide levels an order of magnitude greater than the environmental ambient concentration (Arp, Childress and Fisher 1984; Childress et al. 1991b). Experiments with *C. elongata* (a Pacific species), *C. ponderosa* and *Vesicomya chordata* (the Gulf of Mexico HS species) indicate that all three have blood properties similar to those of *C. magnifica* (Childress et al., in prep.; A. J. Arp, pers comm.).

Vent vesicomyids apparently take up sulfide from the environment across their foot, which is well vascularized and supplied with blood. Sulfide evidently attaches to an unknown binding compound (other that hemoglobin) and is then transported in the blood to the symbionts in the gills (Arp et al. 1984; Fisher et al. 1988b; Childress et al. 1991b). Oxygen and CO_2 are apparently taken up across the gills from the ambient sea water (Fisher et al. 1988b; Childress et al. 1991b). The range of habitats *C. magnifica* occupies at the warm water vents of the Galápagos are well characterized (Hessler et al. 1985). Measurements made around and adjacent to the clams indicate that their feet are inserted through fissures in the basalt into warm waters with sulfide concentrations as high as 40 μM. Their siphons, in contrast, are bathed in ambient bottom water that contains abundant oxygen but no sulfide (Fisher et al. 1988b).

Physiological studies of this group and their symbionts lag considerably behind similar studies with vestimentiferans and mussels. This is because of the inherent difficulties in extracting gill or symbiont preparations from

these clams and because they acquire sulfide and oxygen from spatially discrete pools—an arrangement not easily reproduced in the laboratory. However, recent work based on in-vitro studies has confirmed that the proposed functioning of the blood of these animals would allow living *C. magnifica* to concentrate sulfide by about one order of magnitude above ambient (Childress et al. 1991b); This tends to support the foot-to-gill transport proposed early. In the same study, the symbionts' sensitivity to sulfide was shown to be abolished by clam serum that contained the sulfide binding component.

Vesicomyid clams are found at a variety of vent and seep sites: *Calyptogena ponderosa* and *Vesicomya cordata* on the Louisiana slope associated with hydrocarbon seep sites (Brooks et al. 1987; Rosman et al. 1987); *C. elongata* in reducing sediments at the interface between deep anoxic waters and overlying oxic waters (550-570 m) in the Santa Barbara Channel (Vetter 1985); *V. gigas* at Guaymas Basin HTVs (Grassle 1985); *C. phaeseoliformis* in Monterey fan valley and the Japan Trench (Juniper and Sibuet 1987; Debevois 1989); *C. magnifica* at the Oregon subduction zone, as well as at hard substrate vents (Kulm et al. 1986; Turner 1985, reviewed in Fisher 1990), and *Calyptogena* sp. on the Laurentian Fan, western Atlantic Ocean (Mayer et al. 1988). All of these vesicomyids are apparently able to bridge the oxygen-sulfide interface by extending their foot into a reducing environment while positioning their inhalant siphon in the overlying sea-water (Fisher 1990).

7.5 Gulf of Mexico Hydrocarbon-Seep Vesicomyidae

The two species of vesicomyids found associated with hydrocarbon seeps in the Gulf of Mexico have not been studied intensively by physiologists. The presence of characteristic symbiont enzyme activities

and elemental sulfur in the gills of the hydrocarbon seep species have confirmed the presence of chemoautotrophic sulfur-oxidizing symbionts in both species of vesicomyids (Brooks et al. 1987; Fisher 1990; pers. obs.). In fact, levels of elemental sulfur and symbiont enzyme activities are similar to those found in *C. magnifica* (Fisher et al. 1988a; Fisher 1990; Childress and Fisher 1992). Limited analyses of blood samples taken from live individuals of each species indicate that their blood has sulfide-binding properties similar to those of HTV species (Childress and Fisher 1992; Somero et al. 1989; pers. comm. A. J. Arp and J. J. Childress).

Thus, physiologically, HS clam species apparently function in a manner analogous to the HTV species, accumulating sulfide across their heavily vascularized foot, transporting it to their symbionts in their gills, and obtaining oxygen and CO_2 across their gills in a "normal" molluscan manner (Fisher 1990). The habitat in which they occur at the HS sites is typically unconsolidated hemipelagic sediment perfused with oil and evidently containing high concentrations of sulfide; the clam lives with the foot thrust down into the sediment and may move across the sediments leaving distinctive furrowed trails (**Rosman et al. 1987**). This is a marked contrast to the basalt fissures that are the typical habitat of *C. magnifica* at the HTV sites (Hessler et al. 1985), but is quite similar to the aggregations of vesicomyids from the Japan Trench (Juniper and Sibuet 1987) and the Laurentian Fan (Mayer et al. 1988).

7.6 Mytilids

Deep-sea mytilids either in the genus *Bathymodiolus* or closely related to that genus are proving to be a very interesting group due to their considerable plasticity with respect to symbionts. Methanotrophic symbioses have been described in three different (undescribed) species

from the Gulf of Mexico, one of which apparently also harbors a second, minor symbiont and another which harbors a second thiotrophic symbiont (Childress et al. 1986; Cavanaugh et al. 1987; Fisher, submitted; Fisher and Childress 1992; Fisher et al. 1987; McDonald et al. 1992). Several other species of mussels have yet to be characterized or described (Hessler et al. 1988b; Van Dover et al. 1989; R. Turner (Harvard MCZ) and A. M. Danet (IFREMER, pers. comm..).

Bathymodiolus thermophilus, from both Galápagos Rift and the East Pacific Rise, is the by far the most studied of the HTV species; however, it is only poorly understood. There is considerable evidence that is consistent with chemoautotrophic symbiosis, but there are also significant findings that contradict this interpretation. Stable carbon isotope values (Rau and Hedges 1979; Fisher et al. 1988a), histological studies (Le Pennec and Hily 1984; Fiala-Médioni et al. 1986a; Fisher et al. 1987), enzyme analyses (Felbeck et al. 1981; Fisher et al. 1987; 1988a), thiosulfate stimulation of ATP production (Powell and Somero 1986) and carbon fixation (Belkin et al. 1986; Fiala-Médioni et al. 1986a) all indicate that the symbionts in this mussel are chemoautotrophic. However, the levels of autotrophic enzyme activities, stimulated ATP production, and stimulated carbon fixation are quite low when compared to other vent invertebrates with symbiotic chemoautotrophs (See Fisher et al. 1987; Fisher et al. 1988a; Fisher 1990). Reconciliation of these low activities with the abundance of symbionts in the mussels gills is problematic. A further difficulty is the lack of elemental sulfur in the gills among all individuals investigated (Fisher et al. 1988a). Although levels of elemental sulfur are variable (undetectable to over 3% of gill wet weight) among bivalve species with chemoautotrophic symbionts, *B. thermophilis* is the only species in which elemental sulfur has not been demonstrated. Finally, carbon fixation by the symbionts in *B. thermophilis* is

stimulated by thiosulfate and not sulfide (Belkin et al. 1986), while thiosulfate remains undetected in vent waters (Johnson et al. 1986; Johnson et al. 1988).

At hydrothermal vents, *B. thermophilus* is the most widely distributed of the symbiont-containing species, both spatially and with respect to exposure to vent effluents (Fustec et al. 1987; Hessler and Smithey 1983; Fisher et al. 1988a; 1989b). Their ability to tolerate this wide range of conditions has been explained by their filter-feeding capability (Le Pennec and Hily 1984; Le Pennec and Prieur 1984), which was recently verified experimentally (Page et al. 1991). Despite their multiple nutritional strategies, these mussels are never found outside the vent field, and when collected from very peripheral environments are in a poorer nutritional state than similar mussels collected from "warmer," more central areas in the same vent site (Fisher et al. 1989; Fisher et al. 1988e; Smith 1984).

Taxonomy of the symbiont-containing deep-sea mytilids remains unresolved; only one species has been assigned a specific name to date (*Bathymodiolus thermophilus* from hydrothermal vents), and there are at least four other related species in the Gulf of Mexico. However, geneticists and taxonomists working on these mytilids have divided them into several groups on the basis of both variations in the allozyme banding patterns at 24 presumptive gene loci and differences in shell morphology (Pers. comm. C. Craddock, R. Vrijenhoek, R. Lutz, R. Turner). Table 7.1 lists the taxonomy and known range of these related mytilids from the Gulf of Mexico. Each group represents a population which is recognizable from the others. Unique Roman numerals indicate differences minimally at the species level and different letters indicate differences minimally at the sub-species level.

7.7 Gulf of Mexico Hydrocarbon-Seep Mytilids (Ia and III, Shallow Sites)

Seep mytilid III has only recently been recognized from collections at the shallow hydrocarbon seep sites. It is rare there, and constitutes less than 1% of the mussels collected from those sites. All of the 10 specimens collected to date are much smaller (up to about 5 cm total shell length) than the largest, or even the average, individuals of species Ia, with which it co-occurs. Thus, it constitutes an insignificant portion of the biomass of the shallow mussel communities. Species III does contain symbionts which are apparently chemoautotrophic sulfur-oxidizers and not methanotrophic (based on enzyme activities, stable isotopes, and symbiont ultrastructure) (Fisher, submitted). Since Seep Mytilid Ia harbors methanotrophic symbionts, Seep Mytilid III is not competing directly with it for an energy source. On the other hand, the two may be competing for oxygen in the dense mussel beds, because species Ia has quite high respiratory demands (Kochevar et al. 1992), and species III seems to occur on the bottom of the beds (Fisher, pers. obs.). Interestingly, species III harbors a commensal scale worm which appears similar to the commensal scale worm, *Branchipolynoe symmytilida*, found in both *B. thermophilus* and Seep Mytilid Va from the Florida Escarpment. The other mytilids from the shallow seep sites and Alaminos Canyon do not harbor similar commensals (Fisher, pers. obs.).

Seep Mytilid Ia, the "methane mussel" from the hydrocarbon-seep sites, can be maintained alive for extended periods in the lab, and has been intensely investigated. This species provided the first demonstration of a methanotrophic symbioses (Childress et al. 1986). Methanotrophic symbionts were confirmed through the presence of methanol dehydrogenase in the gills of the mussels and the ability of the gills to oxidize ^{14}C-methane to $^{14}CO_2$ and ^{14}C-organics (Fisher et al. 1987). The

Table 7.1. Standardized common names for mytilid mussels found at seep sites in the Gulf of Mexico (Based on personal communication from R. Gustafson).

Common Name	Description
Seep Mytilid Ia	Common Bush Hill/Louisiana Slope mussel
Seep Mytilid Ib	Small Alaminos Canyon mussel (similar both morphologically and genetically to Seep Mytilid Ia)
Seep Mytilid II	Large Alaminos Canyon mussel
Seep Mytilid III	Rare Bush Hill/Louisiana Slope mussel (first retrieved on JSL-I Dive 3108 of 8/31/1991 at Bush Hill)
Seep Mytilid IV	*Idasola*-like mussel from Louisiana Slope (retrieved on JSL-I Dive of 9/29/1991 near Garden Banks - 386)
Seep Mytilid Va	Florida Escarpment mussel
Seep mytilid Vb	Rare Florida Escarpment mussel (3 known specimens)

ability of this mussel to supplement its nutritional uptake by filter-feeding on free living bacteria (~1μm diameter) has been demonstrated, although uptake rates for phytoplankton (~7μm diameter) are significantly lower than in intertidal mussels without symbionts (Page et al. 1990). Individual mussels have shown growth in shell length with methane as sole carbon and energy source (Cary et al. 1988). Symbionts do not release small molecular weight compounds concomitant with carbon fixation as in most other autotrophic symbioses, but rather accumulate carbon. This carbon accumulated by host tissues is temporally delayed from fixation by the symbionts, suggesting digestion of bacterial symbionts as a major mode of carbon transfer in this symbiosis (Fisher and Childress 1992).

Nitrogen metabolism of this species has also been studied in the laboratory. In the presence of methane, Seep Mytilid Ia will take up ammonium and free amino acids from concentrations comparable to those found in its natural habitat (Lee et al. 1992). Calculations based on environmental concentrations of methane and ammonium, and measured rates of methane oxidation and ammonium uptake indicate that this species can potentially meet its nitrogen needs by ammonium uptake alone, and that uptake of free amino acids may be a significant nutritional supplement (Lee et al. 1992).

Rates of methane consumption by mussels in the laboratory are highly dependent on external methane and oxygen concentrations, and maximal rates in individuals under optimal conditions range from 1.8 to about 14 μM methane g^{-1} h^{-1}, (Kochevar et al. 1992). The authors indicated that a methane consumption rate of 4-5 μM g^{-1} h^{-1} is "reasonable", however, they also noted rates of up to 10-13 μM g^{-1} h^{-1} in animals tested very soon after collection. Similarly, oxygen consumption rates and requirements have been measured in the laboratory and the relation between methane, oxygen,

and CO_2 flux under a variety of conditions has been documented (Kochevar et al. 1992). According to the model of Kochever et al. (1992), mussels capable of consuming methane at a rate of 10 $\mu M\ g^{-1}\ h^{-1}$ under optimal conditions will consume methane at a rate of 3.2 $\mu M\ g^{-1}\ h^{-1}$ at an ambient methane concentration of 65 μM methane (a rate of at least 1.1 $\mu M\ g^{-1}\ h^{-1}$ is required to meet the respiratory demands of this size mussel).

Fisher (submitted) calculates community rates of methane oxidation based on these laboratory measurements, density estimates for young and old patches of mussels (MacDonald et al. 1990b), and the empirically determined relationship between shell length and mussel wet weight. These calculations indicate community oxidation rates of between 22.4 and 42.4 g $CH_4\ m^{-2}\ day^{-1}$ for isolated "young" patches of mussels like those described by MacDonald et al. (Fisher, submitted). In the general area of the Mussel Beach site studied by MacDonald et al. (1990b), the average calculated rates of methane consumption due to the mussels is between 5.5 and 6.9 g $CH_4\ m^{-2}\ day^{-1}$. Although these estimates will certainly be refined with better environmental measurements and when ongoing in-situ growth studies are completed, the estimates are adequate for "order of magnitude" predictions.

These methane oxidation rates are 3 to 4 orders of magnitude higher than those reported for natural soils (Mosier et al. 1991; Whalen and Reeburgh 1990; Yavitt et al. 1990) or for aquatic microbial populations (Frenzel et al. 1990; Kuivila et al. 1988). Whalen et al. (1990) report rates of 45 g $m^{-2}\ day^{-1}$ for topsoil covering a retired landfill and note that these rates drop to 6.1 mg $liter^{-1}\ day^{-1}$ when these soils are waterlogged. They interpret this drop as being due to the difference in gas-phase and aqueous molecular diffusion rates. The high calculated rates for the aquatic communities of mytilids is most likely a reflection of the high biomass in

these communities, as well as advantages inherent in the symbiotic habit, such as a regulated environment in an organ bathed in circulating sea water and specialized for gas exchange (the gills).

8.0 Regional Distribution of Chemosynthetic Fauna and Community Ecology

I.R. MacDonald and J. Ambler

8.1 Introduction

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 1.1, 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.

In this section we will comment on the methods used during submarine surveys and collections, outline how these methods have been adapted to the Chemosynthetic Ecosystem Study, and discuss approaches for combining

geophysical and geochemical data with the submarine survey results. We will catagorize the types of chemosynthetic communities that have been found in this region, together with what is known regarding the abiotic features that are associated with these communities. We will also compile all the locations of the communities that have been found in the northern Gulf of Mexico to date. Special attention will be given to describing the study sites that have been chosen for the Study. This section should provide a context for interpreting future discoveries, should indicate where these discoveries might be made, and should give a qualitative indication of the ecological importance of these communities on the continental slope.

8.2 Methods

8.2.1 Existing Data from Submarine and Surface-Ship Cruises

Since 1987, we have utilized four submarines to survey and collect samples in the Gulf of Mexico chemosynthetic communities. Additional biological and geochemical data were available from the trawl collections that targeted chemosynthetic communities (**Kennicutt et al. 1988**) and from the Northern Gulf of Mexico Continental Slope Study (Gallaway et al. 1988). Geophysical and geological data on the oil seep at the Green Canyon Block 234 have been reported by **Behrens** (1988). Geophysical data have been made available to the Program from industry sources, in particular, Conoco Inc., Enserch Exploration Inc., Exxon USA Inc., and Oryx Energy Inc. These data include selected portions of multi-channel and high-resolution seismic surveys as well as water depth maps for individual lease blocks. Although the total data set is clearly quite rich, there are often problems in reconciling information collected for different purposes during cruises widely separated in time. Below, we briefly describe the individual sources and outline the steps

we took to produce a regional description of community composition and distribution.

8.2.2 Submarine Surveys

A total of 85 days of bottom time has been spent aboard the U.S. Navy Submarine *NR-1* exploring and surveying chemosynthetic communities in the northern Gulf of Mexico. During those dives, over 830 hours of videotaped observations were collected while searching for new chemosynthetic communities or while doing detailed visual and side-scan surveys over known communities. Seismic data collected with *NR-1* included side-scan sonar records (hard-copy) and sub-bottom profiles collected with a high frequency (28 kHz) transponder. Data logs from *NR-1* also provide detailed bathymetry and position information for all these records; however, the positions were determined as offsets from a single "mark on top". This mark is a position fix obtained by LORAN C from the *NR-1*'s support ship while it was ranging the submarine. Therefore, although *NR-1*'s logged positions are internally accurate (that is, the range and bearing between logged positions is accurate), there is always some bias or offset between the total array of positions and true geo-reference.

Additional dives were conducted on the *Johnson-Sea-Link*, *Pisces II*, and *Alvin*. These 3- and 4-person submarines were used for detailed video-photographic work, close-up still photography, and sampling (push-cores, grabs, sediment cores, rock collection, organism collection, relocation experiments and placement of markers). A total of 59 dives with bottom times of two to six hours per dive were conducted from these platforms prior to the beginning of the present Study. Over 122 hours of video photography (primarily three-quarter inch format) were recorded. In addition to

photographic and observational data, numerous sediment, water, rock, and organism samples were collected. An inventory of the data collected, including organisms, on the *Sea-Link* and *Pisces II* is presented in Appendix A. Position logs were maintained for these observations and collections. Typically, the position of the submarine was determined by maneuvering the support ship to near zenith over the submarine and recording the ship's position from LORAN C. There is some slant-range error associated with each position fix obtained in this manner and there is also a consistent bias associated with individual LORAN units. The result of this latter bias is that LORAN positions for known benchmarks (markers, large rocks, etc.) recorded on successive years are offset from each other by as much as 500 m. In practice, the communities are sufficiently small and well-mapped so that bench marks and sampling locations can be relocated without major difficulty.

8.2.3 Geophysical Data

Detailed bathymetric data and high-resolution (3.5 kHz) seismic data known as "shallow hazard" surveys are routinely collected by energy companies during the exploration and test drilling in lease blocks. These maps, typically at 12000:1 scale, are collected with rigorous geo-positioning and provide the means for locating the major topographic features of communities, as well as surface faults and other shallow features—thanks to the generous industry policy of making these data available to the Study. Access to the 3.5 kHz seismic lines that cross communities, and to multi-channel 2D- and 3D-processed data, has provided an additional level of detail for sites in the Green Canyon 234, 233, 184, and Garden Banks 386 lease blocks. **Behrens** (1988 and personal communications) provided additional seismic and geochemical data for the Green Canyon 234 oil seep. Seismic data collected by the *NR-1*

provide detailed information on geophysical characteristics of chemosynthetic communities

8.2.4 Establishing Sampling Stations and Reconciling Observations

Analysis of existing data and new field efforts for the Chemosynthetic Studies Program 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 8.1 and Figure 8.1 for locations). 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 catagorization 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.

To maximize the utility of information from past submarine cruises, efforts at compiling existing data were subsequently concentrated on the information available from the six sampling sites. As noted, it is challenging to reconcile positions determined on separate cruises. Our approach has been to treat each array of positions obtained during a given submarine cruise at a given site as an integral network. The networks from separate cruises are then shifted in their entirety until marked stations or natural benchmarks coincide. The unified network is then shifted, by trial and error, on the water depth maps

for each lease block until the best fit between the recorded depth at each station and the depth predicted by the bathymetric contours is found. For example, to prepare the map for the Green Canyon 272 site (Figure 8.11), we progressively shifted all the fixes from the 1987 *Sea-Link* cruise by constant offsets until the location of a marker at fix 2066-2 coincided with the position of the same marker when it was revisited during the 1991 *Sea-Link* cruise. We then shifted the entire array of fixes and stations until we got a reasonable fit between recorded depths and the depths on the map.

8.2.5 Analysis of Videotaped Observations

The complete set of videotaped observations from the submarine cruises is being critically reviewed to eliminate observations that lack reasonable geo-position information. For the *NR-1* observations, analysis was restricted to recordings made along track-lines. For *Sea-Link* video data, analysis was restricted to what the camera recorded while the submarine was at rest at the fix points. In both cases, fauna were identified to the lowest practical taxon; generally the *Sea-Link* was considerably closer to its subjects and so obtained better identifications. The environment traversed by the *NR-1*, and the fauna encountered, was evaluated for the presence or absence of a standardized set of categories. The videotaped records were divided into 30-second intervals and all possible categories of observation were evaluated for each interval. Thus, the presence of a tube worm cluster or a rock outcrop, for example, could be assigned to a discrete portion of the survey trackline.

Table 8.1 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. 8.1; 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 3.1)	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. (1990b), 11–Boland 1986, 12–Boss (1968), Gallaway et al. (1990), Volkes (1963).

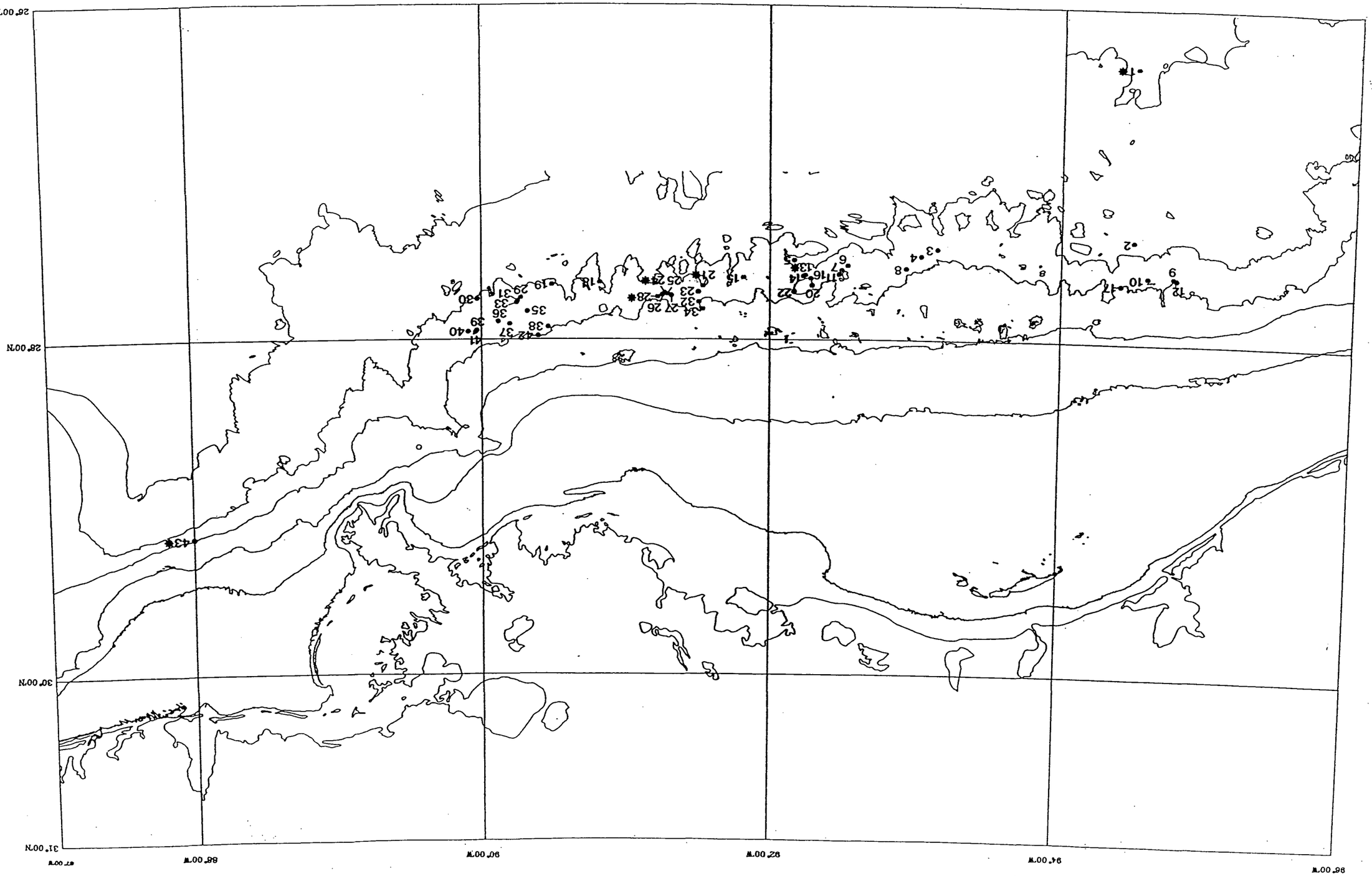

28° 00'N
30° 00'N
32° 00'N
98° 00'W
96° 00'W
94° 00'W
92° 00'W
90° 00'W
88° 00'W

Figure 8.1 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 8.1; locations marked with and asterisk (*) are Study Sites for the MMS Chemosynthetic Ecosystems Study.

The *Sea-Link* video records, while generally of higher quality, could not be geo-referenced with the same precision as the *NR-1* records because the *Sea-Link* has had no ability to record its position while under way. [Beginning in 1992, a continuous position record will be maintained for *Sea-Link* dives, according to T. Askew (personal communication).] Analysis of *Sea-Link* records is therefore restricted to observations recorded at the fix-points or along short, straight transects between reliable fixes. Each of the *Sea-Link* fix points was assigned to one of ten general categories according to its predominant chemosynthetic fauna (e.g. tube worms) and substrate characteristics (e.g. carbonate rubble); the categories and their attributes are given in Table 8.2. Presence or absence of a variety of other biotic and environmental variables was also noted.

Although the *Sea-Link* observations recorded prior to 1991 were often highly detailed, they are inherently qualitative descriptions; the areas observed and the care with which the video records were made varied greatly among fixes. For example, at one fix, the observer may have had the opportunity to pan the camera across a large area for a period of 10 to 15 minutes; at a subsequent fix, in contrast, the submarine may only have remained in place for a few moments and the observer may have been distracted with other duties. Likewise, the selection of fixes was an *ad hoc* process, subject to needs for specific collections; the observations were not randomized and cannot be analyzed using statistical techniques that require random sampling.

Table 8.3 Species list for *Johnson-Sea-Link* dives, 1987, developed from video-taped observations by J. Ambler.

Monera Kingdom

Beggiatoa sp., bacterial mats: white mats are chemoautotrophic (CO2 uptake demonstrated), but yellow and orange are not chemoautotrophic (no CO2 uptake demonstrated).

Animal Kingdom

Porifera, Sponges

sponges on vestiminiferans
sponges on rocks, white sponge field
sponges on gorgonians, bright orange, sponges on pogonophorans

Cnidaria

hydroids on tubeworms
Calogorgia, white sea fan, gorgonian
burrowing anemone
anemones on vestiminiferans and gorgonians

Pogonophorans

Galathealinum n. sp., several dark stalks from common base
solitary stick

Vestimentifera, tubeworms with thiotropic endosymbiotic bacteria. Three growth forms: individual tubeworms, recumbent tubeworms, and bushlike tubeworms.

Lamellibrachia n. sp.
Escarpia n. sp.

Arthropods, Crustaceans

Bathynomus giganteus, large isopod

Shrimp:

red and white shrimp, second antennae 3-4 times length of body
Alvinocaris stactophila (there may be two species, R. Carney)
dark red shrimp

Table 8.3 Species list for *Johnson-Sea-Link* dives, 1987 (continued).

Anomurans:

Munidopsis n. sp. (F. Galatheidae)
Eumunida picta Smith 1883 (F. Galatheidae)
Paralomis cubensis Chace (F. Lithodidae)
hermit crabs

Astacidea (clawed lobsters):

Acanthacaris caeca (A. Milne Edwards 1881)(F. Nephropidae)

Brachyurans:

Chaceon quinquedens (Smith 1879) (F. Geryonidae).
Chaceon fenneri (Manning & Holthuis 1984) (F. Geryonidae).
Rochinia crassa (F. Majidae)
Unidentified species.

Molluscs Seep mytilids, 6 species with endosymbiotic methanotropic bacteria, most are seep mytilid 1a

Acesta bullisi, scallops
Bartschia canatae, buccinidae gastropod
Cataegis cf. *meroglypta*, turban shells
Bathynerites, slipper shells
squid

Bryozoans on vestimentiferans

Brachiopods

Terebratulina sp., (big one)
small species

Echinoderms

Asteroids

Pisaster type, light pink or grey
Cube N Crackers, fatter seastar (R. Carney)
light colored burrowing seastar with thin arms
Brisingidae, filter feeding seastar

Ophiuroids

pink ophiuroids found only as epizoa on gorgonians

Table 8.3 Species list for *Johnson-Sea-Link* dives, 1987 (continued).

Holothurians

Enypniastes sp., black sea cucumber

Echinoids

Echinus sp., light colored urchin w/ long spines

Fishes

Class Agnatha (Jawless Fishes)

Eptatretus sp., (O. Mixiniformes), hagfish

Class Chondrichthyes (Cartilaginous Fishes) Only seen on transects.

Raja teevani? (O. Rajiformes), large skate
Raja garmani? (O. Rajiformes), small roundish skate
Etmopterus sp., (O. Squaliformes), shark

Class Osteichthyes (Bony Fishes)

Synaphobranchus sp. (O. Anguilliformes), cutthroat eels
Chaunax pictus (O. Lophiiformes), related to batfishes
Urophycis cirratus (O. Gadiformes), dark long hake in burrows
macrourid species c.f. *Nezumia* sp. (O. Gadiformes)
Hoplostethus sp. (O. Beryciformes)
Helicolenus dactylopterus (O. Scorpaeniformes), rockfish
Trichuriura (O. Perciformes), cutlassfishes
tilefish (O. Perciformes)
unidentified fish

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Mechanisms for growth of the posterior ends of the tubes are unknown. If all growth occurs at the anterior opening, then all burial would occur passively subsequent to attachment and might provide a gauge for the longevity of the animals. Given regional sedimentation rates of 10 to 60 cm per 1000 years (**Behrens 1988**), burial by 30 cm of sediments might indicate substantial age. [This concept was first aired in a cruise-planning meeting held in April of 1987 and attended by, among others, G.S. Boland, J.M. Brooks, R.S. Carney, J.J. Childress, M.C. Kennicutt, I.R. MacDonald, and E.N. Powell. It has subsequently been discussed in other formal and informal gatherings and was stated in print by **MacDonald et al.** (1990b) with partial attribution to C.R. Fisher.] However, the recent finding by Southward et al. (in press and personal communication) of *Lamellibrachia* sp. that were evidently buried in sacks of foodstuffs in a sunken ship suggests that some tube worms actively burrow into soft substrate.

Mytilids generally occur in single- or double-layer beds that range in size from less than 0.5 m^2 to 500 m^2 (MacDonald et al. 1990a, 1990c). The beds occur where methane and oxygen are simultaneously available, either as direct evolution of gas bubbles or dissolved in brine. The beds often define distinct boundaries of this availability.

Abundance of vestimentiferans and mytilids, respectively, has been significantly correlated with concentrations of oil in the sediment and methane in the near-bottom water (**MacDonald et al. 1989**). However, oil and methane seepage at a hydrocarbon seep are by no means mutually exclusive processes. The degree to which mytilids and tube worms form segregated assemblages depends upon the characteristics of a given seep. Brine seepage, for example, often occurs without accompanying oil seepage; brine seeps may therefore support large mytilid beds in which tube worms are either absent or

represented by a few scattered individuals. Oil-laden sediment may extend over large areas of the seafloor without any gas or brine seepage and these areas will often support "pure" stands of tube worms. Mytilids do occur with tube worms, sometimes attached to the actual tubes, where methane and sulfides are available in close proximity.

Living clams are either infaunal, in the case of the lucinaceans, or epifaunal, in the case of the Vesicomyidae. The latter often form distinctive furrow-like tracks as they plow through the surface sediment in search of sulfide (**Fisher 1990**). Areas in which living vesicomyids occur more or less continuously may be 100 to 150 m in width (**Rosman et al. 1987**). The dead shells of both groups, however, tend to accumulate on the surface sediment, sometimes producing shell "pavements" that cover very extensive areas (**Callender et al. 1990**). The shells of the two groups are often difficult to distinguish from each other visually and dead vesicomyids often occur in life position. Visual observations of shell beds may therefore indicate a community of living vesicomyids, an infaunal community of lucinaceans, or a defunct community of both.

Vesicomyid communities have been found on level or gently sloping terrain, often down-slope from tube worm or mytilid communities. The substrate is soft where the living clams are found, but occasional carbonate outcrops or the accumulation of shell material may contribute a hard component to this bottom type (Rosman et al. 1987, GERG unpublished data). Little is known regarding the chemical environment in which the vesicomyids occur. Callender (pers. comm.) has noted heavy tar immediately under the surface sediment. **Rosman et al.** (1987) and MacDonald (unpublished data) noted the absence of burrows in the vicinity of vesicomyid aggregations. Such burrows, generally formed by fish or crustaceans, are a ubiquitous component

of the slope lebensspuren (G.S. Boland in Gallaway et al. 1988) but are absent from hydrocarbon seep areas (**MacDonald et al. 1989**), perhaps because the seeping hydrocarbons render the infaunal environment less habitable.

8.3.2 Zonal Distribution of Chemosynthetic Communities in the Northern Gulf of Mexico

Because of the diversity in the surveys that have discovered chemosynthetic fauna, the best generalization among survey results is presence of the fauna at specific sites. Figure 8.1 shows the locations where the major chemosynthetic fauna have been collected or unambiguously observed. Table 8.1 lists the groups of chemosynthetic fauna found, nominal locations, depths, and the citation. Given the variety among community types described in the preceding section, the occurrence of a chemoautotrophic host can indicate a fairly wide range of environmental conditions; in all cases, however, presence is a strong indicator of active, localized hydrocarbon seepage (**Brooks et al. 1987, Kennicutt et al. 1988**). In reviewing the occurrences of chemosynthetic communities, observations separated by less than 1 NM were pooled.

Information on the areal extent of the individual communities shown in Figure 8.1 is uneven; clearly, trawl samples will not provide reliable data of this type. An analysis of clustering frequencies for tube worms at GC234 found significant clustering at spatial scales of about 5, 20, and 75 m (MacDonald 1990), which may be indicative of clustering due to formation of tube worm "bushes" at the smaller scale, and to the size and spacing of fault zones at the larger scales. A review of the occurrence of chemosynthetic fauna along the *NR-1* track-lines tends to confirm a characteristic size of about 100 m for vestimentiferan and mytilid communities and 100 to 300 m for clam communities. We therefore have some support for speculation that

communities separated by less than 300 m probably share a common hydrocarbon reservoir. Multi-channel seismic data from the GC184/185 lease blocks (Conoco, Inc. unpublished data) provided information on the spacing of reservoirs and migration pathways at this site. From these data, it appears that communities separated by greater than 1 NM are not supported by seepage from a common reservoir.

Chemosynthetic fauna were found in a ~700 km-long corridor between 88°W and 95°W and between the 290 m and 2200 m isobaths. Distribution was not uniform; the greatest number of communities were found between 91°W and 93°W between the 500 m and 700 m isobaths. These observations were strongly influenced by the limits of exploration; the envelope of occurrence suggests that the potential number of communities is much larger than those found to date. There was a gap in occurrences where the Mississippi Canyon intersects the corridor. Although this area has not been exhaustively explored for communities, geochemical exploration shows a general absence of oil-stained sediments from the Canyon, which suggests that the hiatus in community occurrence may be real (GERG, unpublished data).

The distribution of HS communities shown in Figure 8.1 and their characteristics contrast with the distribution of HTV communities in a number of ways. Although HTV communities occur over a large geographic region in the Pacific Ocean, their occurrence is limited to the geothermal fields associated with spreading ridges or back-arc basins (Tunnicliffe 1991). These fields tend to be about 20 km in length and separated by approximately 100 km on slow-spreading ridges and 150 km on more active ridges (Crane 1985). Within the geothermal fields, HTV communities tend to be small (50 m in length), spatially discrete, and ephemeral on a scale of years (Crane and Ballard 1980; Hessler et al. 1985, 1988). These characteristics reflect the

relatively focused discharge of hydrothermal fluid through fractured basalt and the tendency for vents to choke off as precipitates build up in the fluid pathways (Haymon and MacDonald 1985). The hydrocarbon source rock that is the definitive nutrient supply for HS communities and the salt layer determines whether hydrocarbon trapment and leakage occur pervade the entire slope in the northern Gulf of Mexico (see the Origins of Petroleum and Salt Tectonics sections of this report). The seeps tend to be diffused through the overlying sediment and the HS communities are correspondingly larger in area than HTV communities. Although precipitation of authigenic carbonates will undoubtedly alter seepage patterns, all preliminary evidence indicates that hydrocarbon seeps and the HS communities persist in the same areas over much longer time scales [E. Powell (unpubl. data) has dated a lucinid shell from the GC184/185 Site to 2000 y BP].

The easternmost community, in the Viosca Knoll block 826, was found by investigations initiated by the Oryx Energy Company (Gallaway et al. 1990). Interestingly, this area was trawled in 1955 by the U.S. Fish and Wildlife Service M/V *Oregon*. The resulting collections provided the holotype for the original description of *Calyptogena cordata* (Boss 1968) and a paratype for the original description of *Acesta bullisi* (Volkes 1963). The photograph of this paratype shows the unmistakable shell deformation that is caused by the commensal interaction with a vestimentiferan. The Viosca Knoll site represents early, unrecognized evidence for hydrocarbon seep communities in the northern Gulf, as well as a recent range extension.

Each chemosynthetic community supported by hydrocarbon seepage depends on a reservoir of hydrocarbon and a migration pathway or pathways through which these fluids reach the seafloor. Implicit in the distribution shown in Figure 8.1, or in a larger scale mapping of community distribution, is

a determination of what spatial separation is required to consider two occurrences as distinct communities. The number of communities in a given area should be indicative of the number of hydrocarbon reservoirs, the number of migration pathways (i.e. faults), the characteristic size of the faults, and interaction of the unconsolidated sediments, hydrates, or carbonate with seepage. This determination is also important for estimating the numbers of the communities and for management concerns regarding the potential zone of impact for a seafloor activity.

8.3.3 Seismic Wipe-out Zones Associated with Chemosynthetic Communities

The attenuation of seismic energy due to absorption or scattering by gas bubbles in sediment produces a marked loss of subbottom reflection (**Behrens 1988**). So-called seismic "wipe-out" zones are therefore a common feature in hydrocarbon seeps and may be used as an indicator for the presence of chemosynthetic communities (**Kennicutt et al. 1985**). Some caution is appropriate, however, because Behrens identifies two distinct types of wipe-out: in type I, loss of subbottom reflection is accompanied with constant or weakening reflection from the sediment-seawater interface; in type II, the bottom echo is strong and prolonged. J. Corthay (pers. comm.) suggests that events such as sediment slumping can reduce the reflection from subbottom strata in the absence of seepage.

A detailed examination of the distribution of vestimentiferan clusters and wipe-out zones at GC234 demonstrated that the tube worms are consistently associated with Behrens type II wipe-out zones (**MacDonald et al. 1990**b; MacDonald 1990). Figures 8.2 and 8.3 illustrate this relationship based on reproductions of the *NR-1* 28 kHz subbottom profile records. In Figure 8.2, tube worm clusters are visible as a fuzzy outline on the left-hand portion of the

record. The subbottom profile beneath the clusters conforms to Behren's type II wipe-out. The subbottom in the right-hand portion of the record, where tube worms are absent, conforms to the type I wipe-out. Figure 8.3 shows several additional examples of tube worms clusters over type II wipe-outs, as well as the transition to normally stratified subbottom.

8.3.4 Descriptions of Chemosynthetic Studies Program Sampling Sites

The following sections describe the sampling sites of the Program. The descriptions are based on preliminary results obtained during the 1991 cruise with *Johnson-Sea-Link*, on the analysis of video taped observations from the 1987 *Sea-Link* cruise, and on reports from the 1990 *Alvin* dives in Alaminos Canyon. The descriptions are generally more complete for the sites at Green Canyon 272, 234/233, and 184 because the communities in these areas have received the greatest attention during previous research. Figures 8.4 through 8.9 summarize the video-taped observations made during the 1987 *Sea-Link* dives at these sites. Figure 8.10 shows the regional bathymetry and the locations of the study sites with respect to the MMS lease block boundaries. Site maps and lists of sampling stations are referenced in the individual sections.

8.3.5 Green Canyon 272

The 1987 *Sea-Link* dives visited a total of 45 fixes (Table 8.4A and Figure 8.11) in GC272. The site was distinguished from the other sites by the presence of vesicomyid clams at a number of locations and by extensive areas of shell pavement (**Callender et al. 1990**, Figure 8.9). The northeastern corner of the lease block was characterized by slopes in excess of 30° and by a highly irregular micro-relief of exposed carbonate, varying in form between low rubble, prominent, spire-like boulders, and broad perforated plates (Figure 8.4). Oil-

and brine-seepages were observed (Figure 8.4). At one fix, a large brine seep (7 x 10 m) was covered with white and orange mats of *Beggiatoa*. Mussels were not observed along the seep shoreline, except at one end where the seep tapered. Animal tracks and shell hash were prominent features of the biogenic environment because of the extensive occurrence of vesicomyid clams (Figure 8.7).

This site supported an extensive chemosynthetic community that was dominated by seep mytilids and vesicomyid clams (Figures 8.6 and 8.7) The occurrence of clams and mytilids in this area was apparently correlated with bottom type: mytilids predominated where the bottom features included carbonate outcrops, whereas clams were restricted to areas of soft surficial sediment. Tube worms were relatively uncommon and were stunted individuals when they did occur (Figure 8.6).

The 1991 *Sea Link* cruise revisited the site in an effort to establish sampling stations where living vesicomyid clams predominate. Five stations were established, four associated with clam-growth experiments and a fifth associated with a substantial mytilid bed that was sampled in 1987 (Table 8.4B)

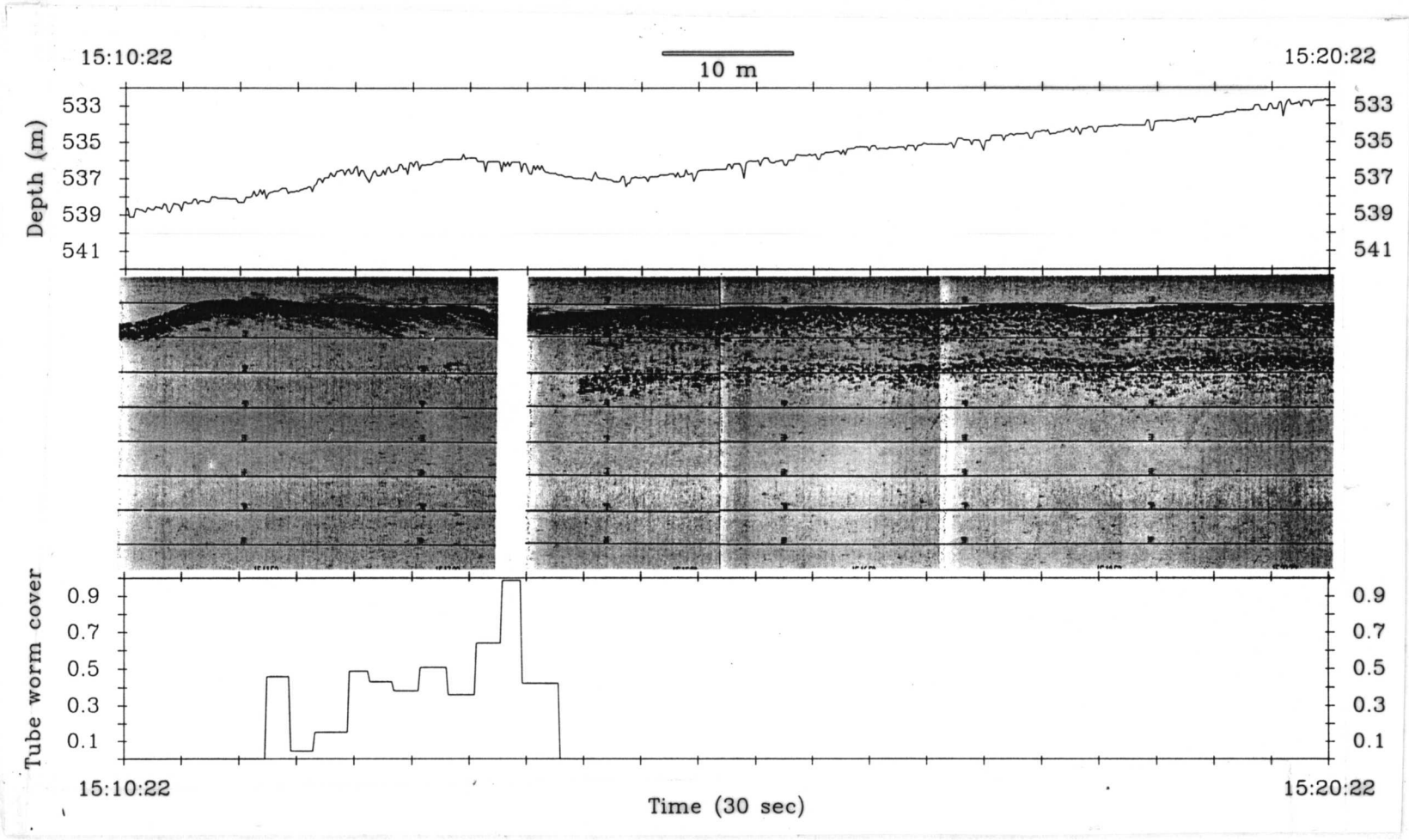

Figure 8.2 *NR-1* depth records from approximately 70 m portion of a track-line (upper panel) across a chemosynthetic community of predominantly tube worms (GC234). Sub-bottom profile of this track (middle panel) shows a type I wipe-out zone on the right hand section of the profile and a type II wipe out zone on the left-most section (see text for definition of wipe-out types). Abundance of tube worms (lower panel) show restriction to the type II wipe-out. A faint trace of the tube worms is also visible in the sub-bottom profile just above the mudline.

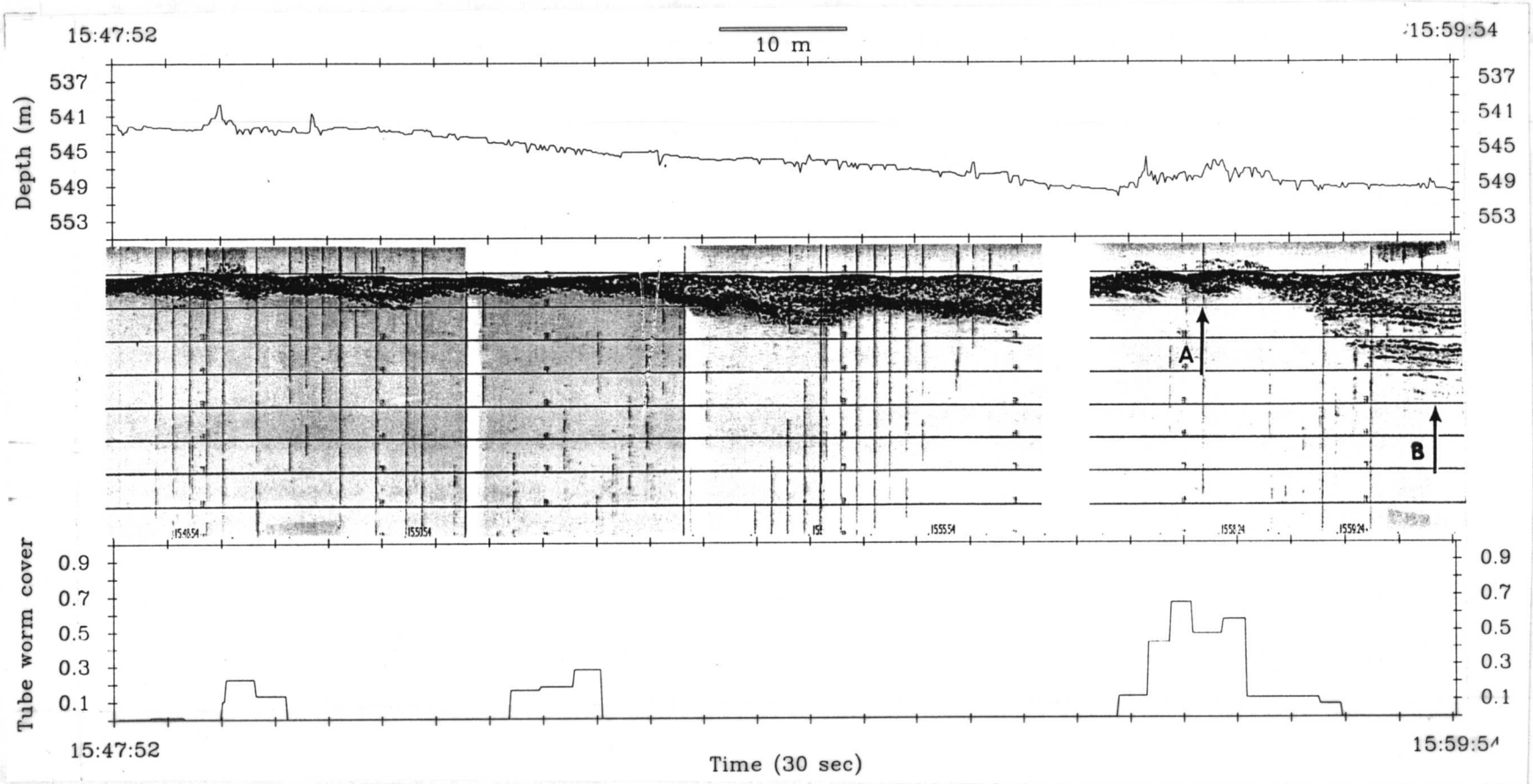

Figure 8.3 *NR-1* records of depth (upper panel), sub-bottom profile (middle panel) and tube worm abundance (lower panel) show restriction tube worms to the type II wipe out areas and the transition to normally stratified sediment in the right-most portion of the profile.

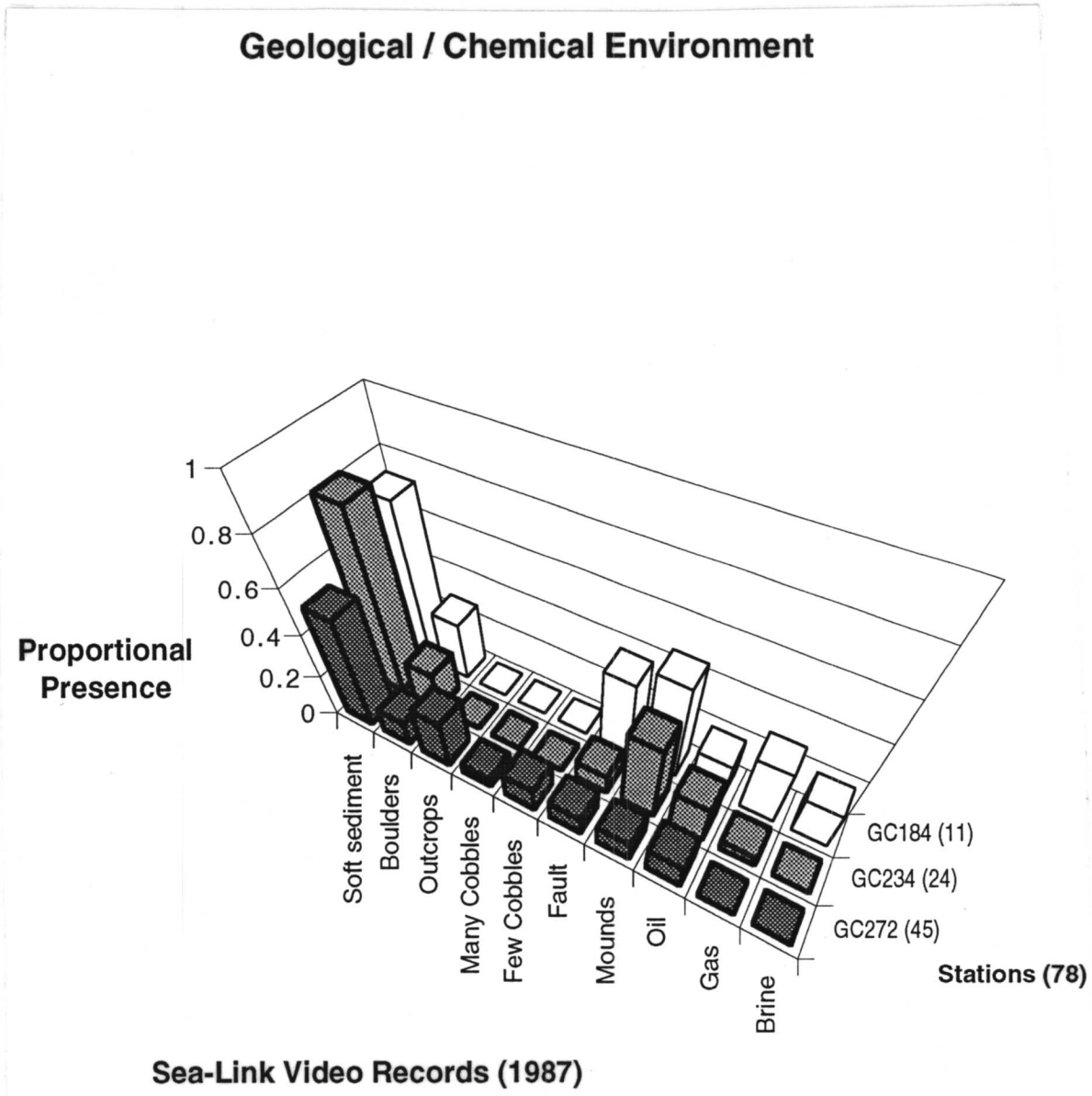

Figure 8.4 Summary of video-taped observations from the 1987 *Sea-Link* dives at the GC272, GC234, and GC184/185 Study Sites. The display indicates the proportion of stations (fix points) at which each component of the geological and chemical environment was recorded by the video camera.

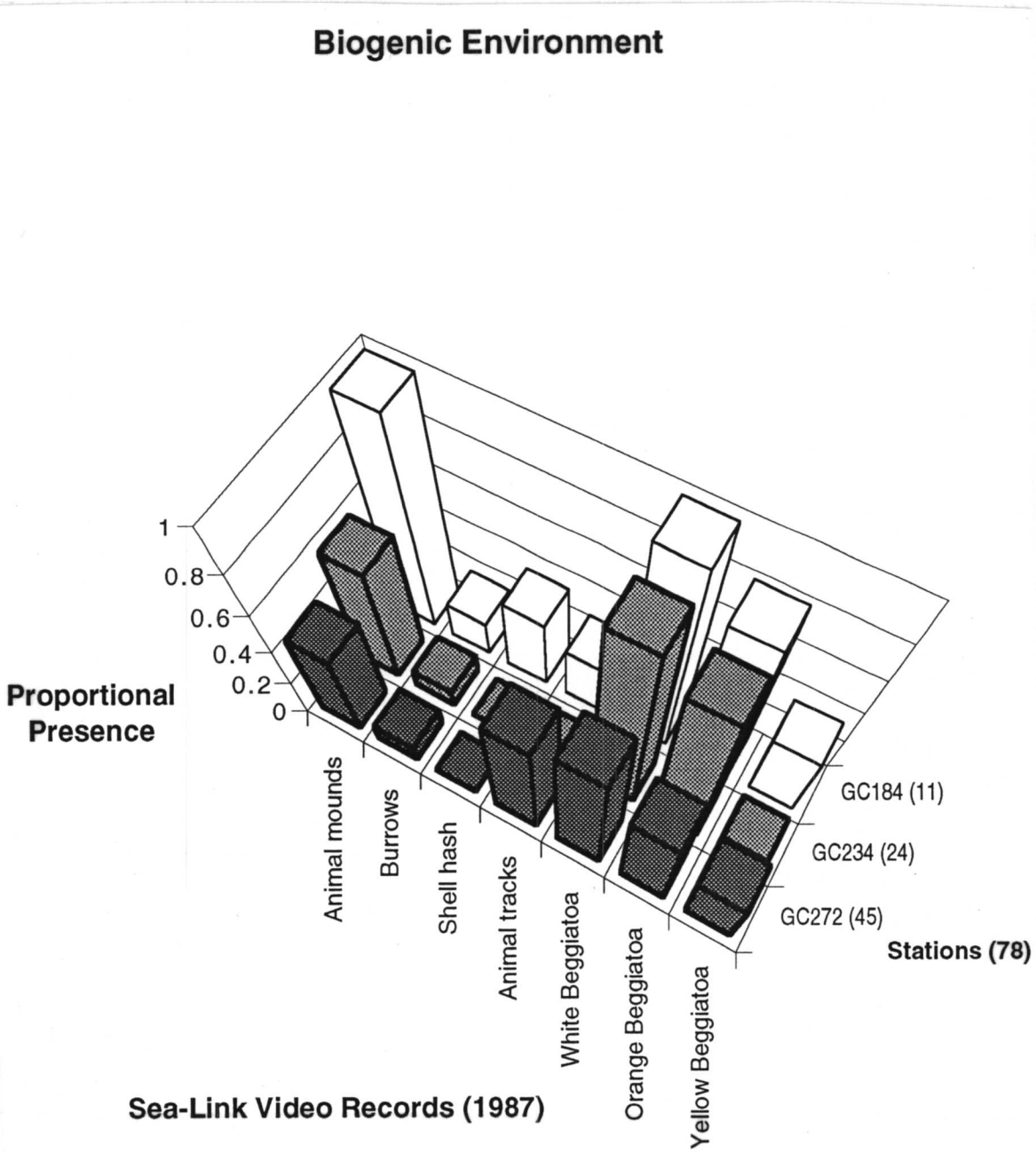

Figure 8.5 Summary of video-taped observations from the 1987 *Sea-Link* dives at the GC272, GC234, and GC184/185 Study Sites. The display indicates the proportion of stations (fix points) at which each category of the biogenic environment was recorded by the video camera.

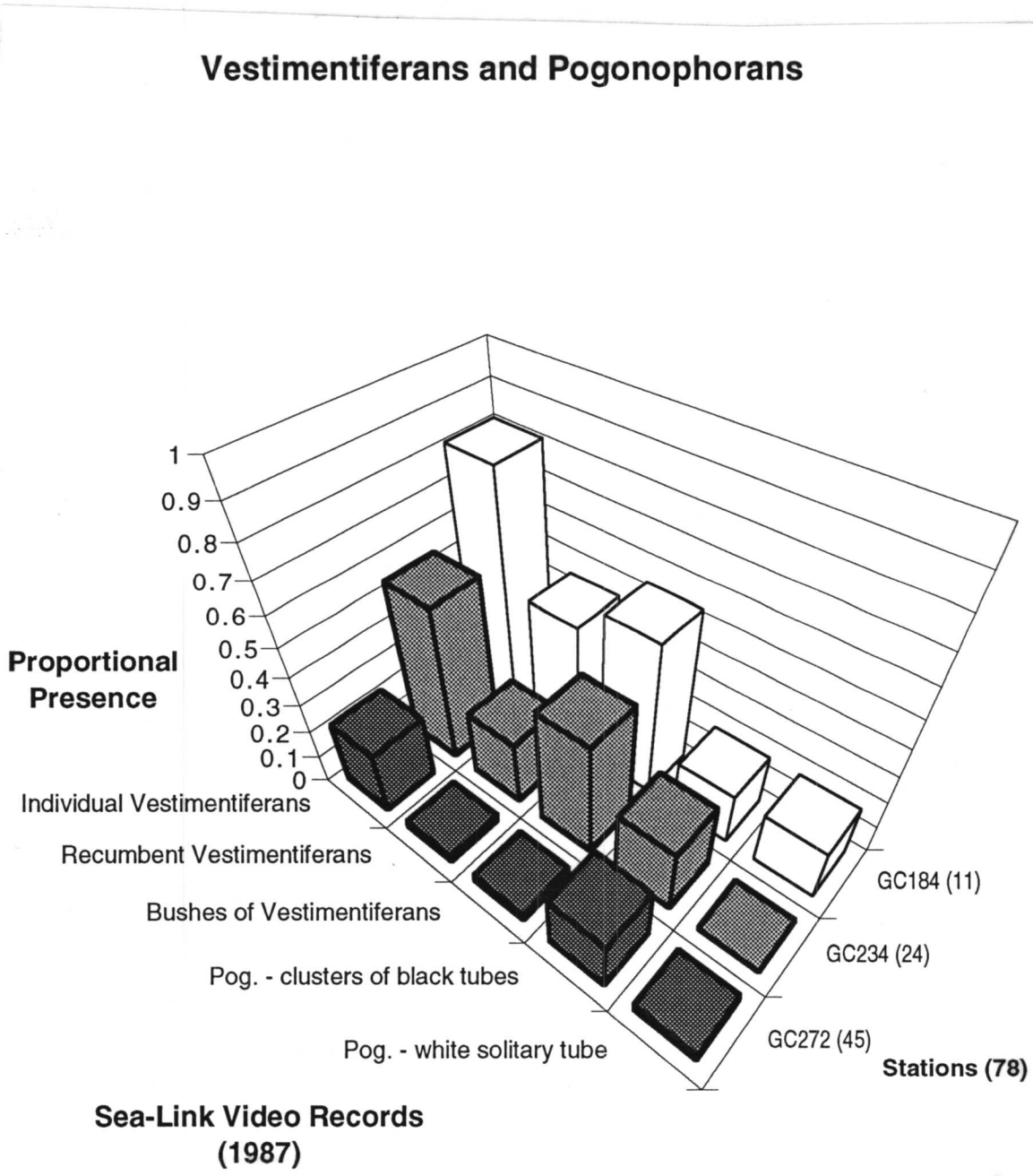

Figure 8.6 Summary of video-taped observations from the 1987 *Sea-Link* dives at the GC272, GC234, and GC184/185 Study Sites. The display indicates the proportion of stations (fix points) at which each category of tube worm was recorded by the video camera.

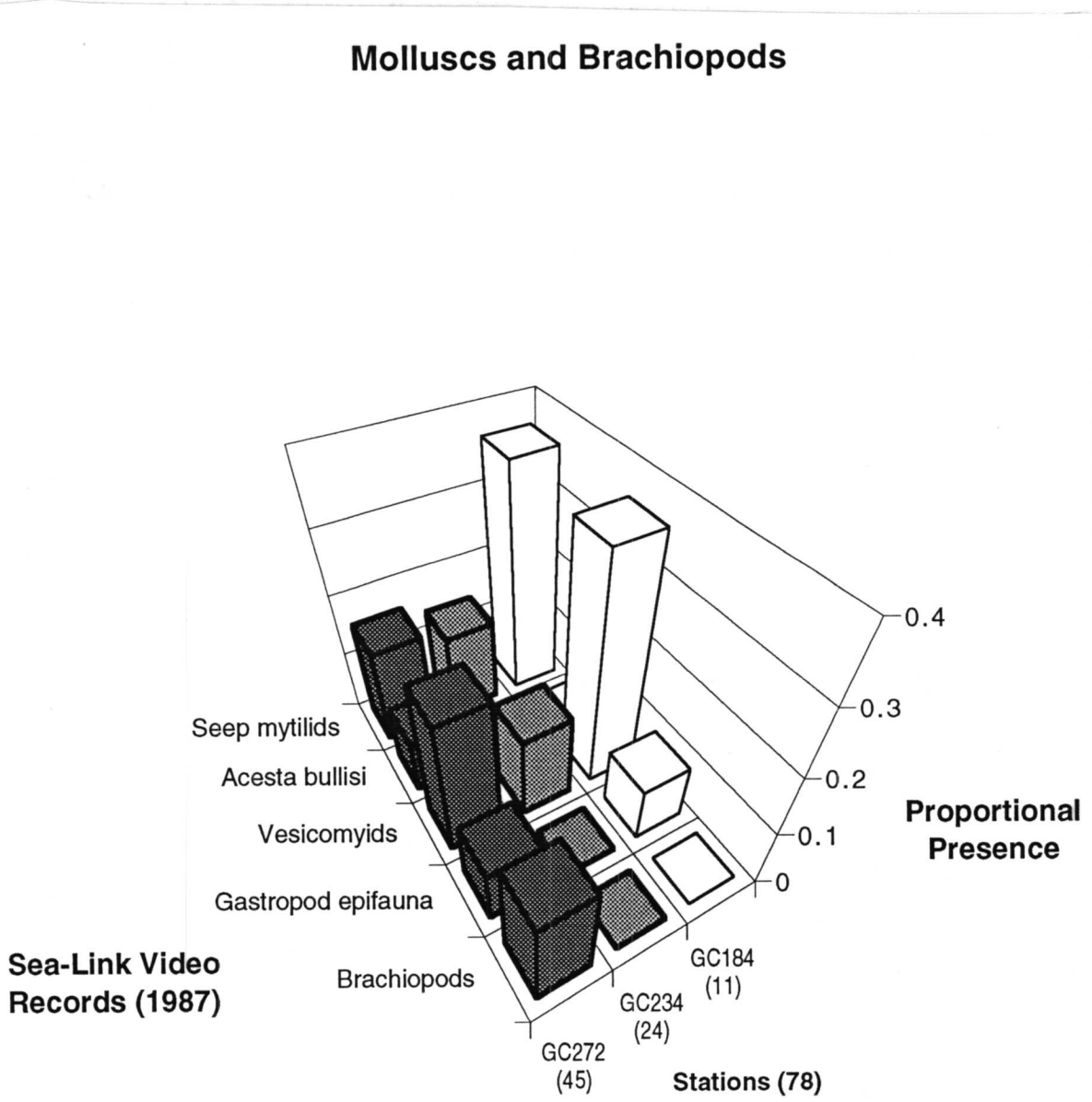

Figure 8.7 Summary of video-taped observations from the 1987 *Sea-Link* dives at the GC272, GC234, and GC184/185 Study Sites. The display indicates the proportion of stations (fix points) at which identifiable molluscs and gastropods were recorded by the video camera.

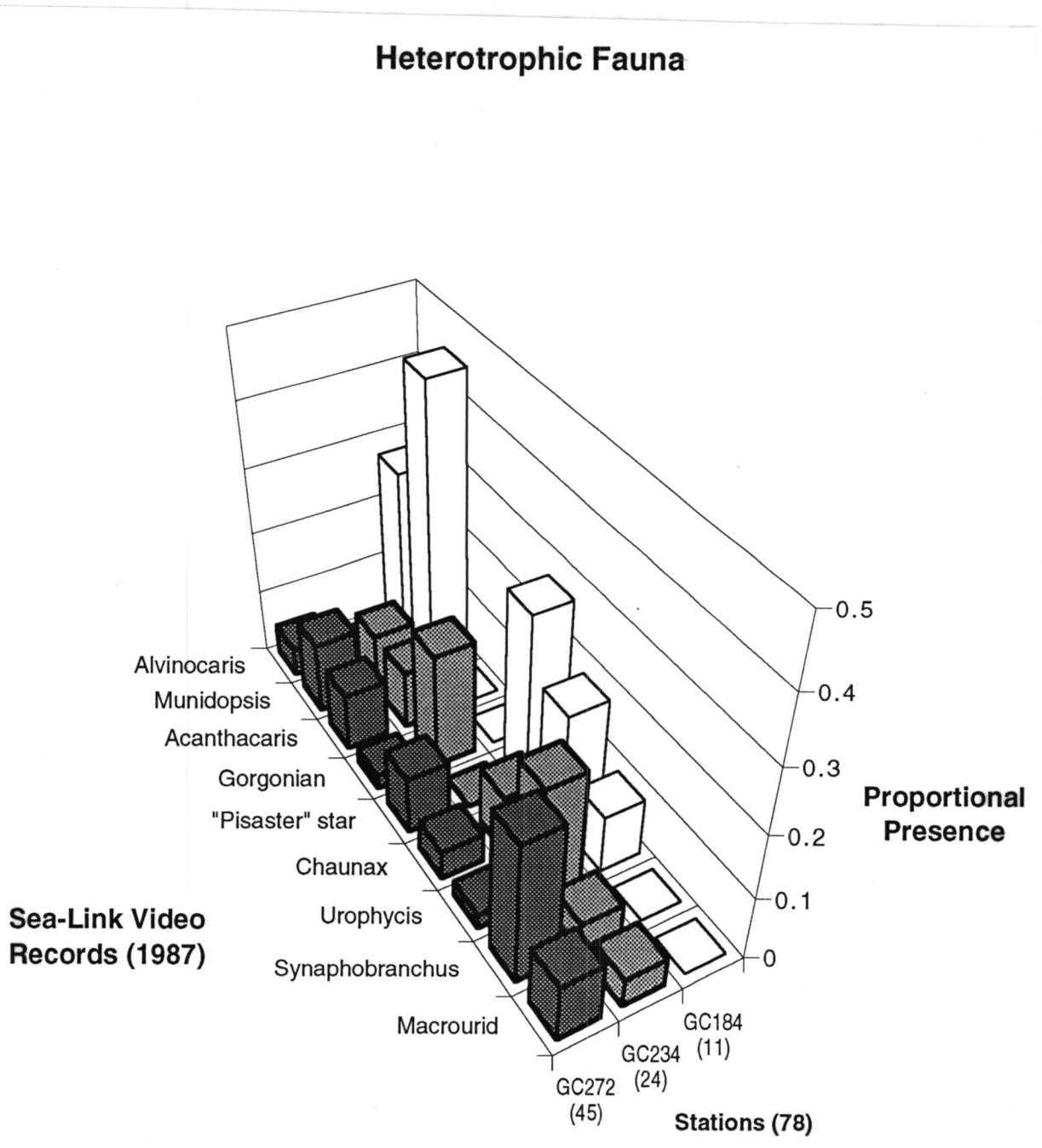

Figure 8.8 Summary of video-taped observations from the 1987 *Sea-Link* dives at the GC272, GC234, and GC184/185 Study Sites. The display indicates the proportion of stations (fix points) at which selected identifiable heterotrophic fauna were recorded by the video camera.

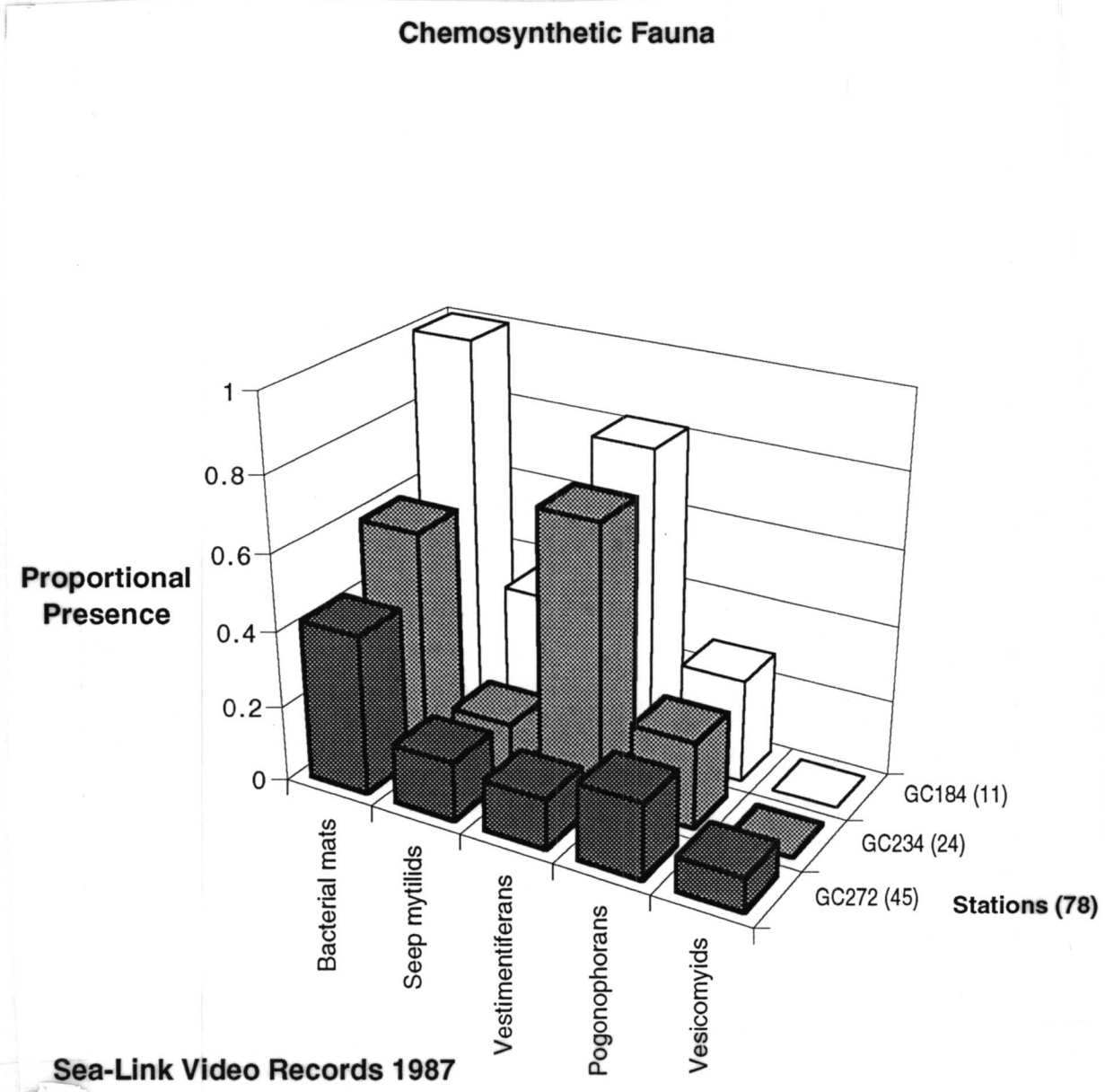

Figure 8.9 Summary of video-taped observations from the 1987 *Sea-Link* dives at the GC272, GC234, and GC184/185 Study Sites. The display indicates the proportion of stations (fix points) at which each component of the chemosynthetic fauna was recorded by the video camera.

Table 8.4A Position data for fixes in Green Canyon 272 during *JSL* submersible dives. Type is community type defined in Table 8.2. Fauna refers to presence of chemosynthetic bacterial mats (B), vestimentiferans (V), seep mytilids (M), and vesicomyid clams (C).

Dive-fix	Type	Depth (m)	Latitude (North)	Longitude (West)	Fauna Present
2065—3	HCD	735	27°41.31'	91°32.52'	
2066—1	SSM	732	27°41.36'	91°32.48'	B M
2066—2	HSM	716	27°41.30'	91°32.50'	V M
2066—3	SSO	744	27°41.34'	91°32.61'	
2066—4	HST	724	27°41.36'	91°32.55'	V
2066—5	SCD	716	27°41.35'	91°32.49'	
2066—6	SCL	735	27°41.28'	91°32.52'	B C
2067—2	SSO	738	27°40.85'	91°32.36'	
2067—3	SSO	708	27°41.11'	91°32.48'	
2067—4	SCD	733	27°41.30'	91°32.54'	
2067—5	HSO	708	27°41.33'	91°32.47'	
2067—7	HCD	735	27°41.30'	91°32.55'	
2068—2	HCD	744	27°41.35'	91°32.63'	
2068—3	HSM	739	27°41.35'	91°32.59'	B M
2068—4	HSO	739	27°41.34'	91°32.59'	
2068—5	HSO	732	27°41.38'	91°32.56'	
2068—6	SSO	746	27°41.37'	91°32.65'	
2071—2	SCD	692	27°40.99'	91°32.30'	B
2071—3	SSM	687	27°40.94'	91°32.28'	B V M
2071—4	SCL	695	27°41.19'	91°32.39'	B C
2072—1	SSO	715	27°41.34'	91°32.48'	
2072—2	HSM	735	27°41.32'	91°32.55'	B M
2072—3	SCD	718	27°41.34'	91°32.50'	
2072—4	HSO	715	27°41.37'	91°32.50'	
2073—1	HST	739	27°41.32'	91°32.55'	V
2073—3	SCL	695	27°41.23'	91°32.37'	B V C
2073—5	SCL	685	27°41.18'	91°32.32'	B C
2075—1	SCD	690	27°40.90'	91°32.28'	
2075—2	SSB	693	27°40.92'	91°31.97'	B
2075—3	SSO	692	27°40.91'	91°31.81'	
2075—4	SSB	690	27°40.95'	91°31.98'	B
2075—5	SCD	686	27° 41.00'	91°32.20'	B
2075—6	SCD	687	27° 41.02'	91°32.24'	
2075—7	SCD	710	27° 41.02'	91°32.39'	B
2075—8	SCD	691	27° 41.20'	91°32.37'	B
2076—2	HSO	740	27° 41.37'	91°32.65'	
2076—6	SSM	739	27° 41.32'	91°32.57'	B M
2077—10	HSO	741	27° 41.35'	91°32.61'	
2077—11	HCD	703	27° 41.41'	91°32.60'	B
2077—12	HSO	739	27° 41.34'	91°32.59'	
2077—13	HSM	739	27°41.34'	91°32.56'	B M
2077—15	SSO	724	27° 41.46'	91°32.60'	
2077—16	HST	696	27° 41.47'	91°32.48'	B V
2077—18	SCD	715	27° 41.24'	91°32.48'	B

Table 8.4B Sampling Stations established during the 1991 *Sea Link* dives at GC272. Codes refer to the locations plotted in Figure 8.11 and to data listed in Appendix A.

Code	Latitude (North)	Longitude (West)	TD1	TD2	Depth (m)
CF03	27° 41.25'	91° 32.40'	11557.1	27169.4	705
CF04	27° 41.26'	91° 32.41'	11557.0	27169.5	704
CF05	27° 41.23'	91° 32.39'	11557.1	27169.4	700
CF06	27° 41.24'	91° 32.41'	11557.0	27168.2	708
CF90	27° 41.17'	91° 32.45'	11557.2	27168.5	699
CF08	27° 41.30'	91° 32.52'	11556.5	27168.5	725

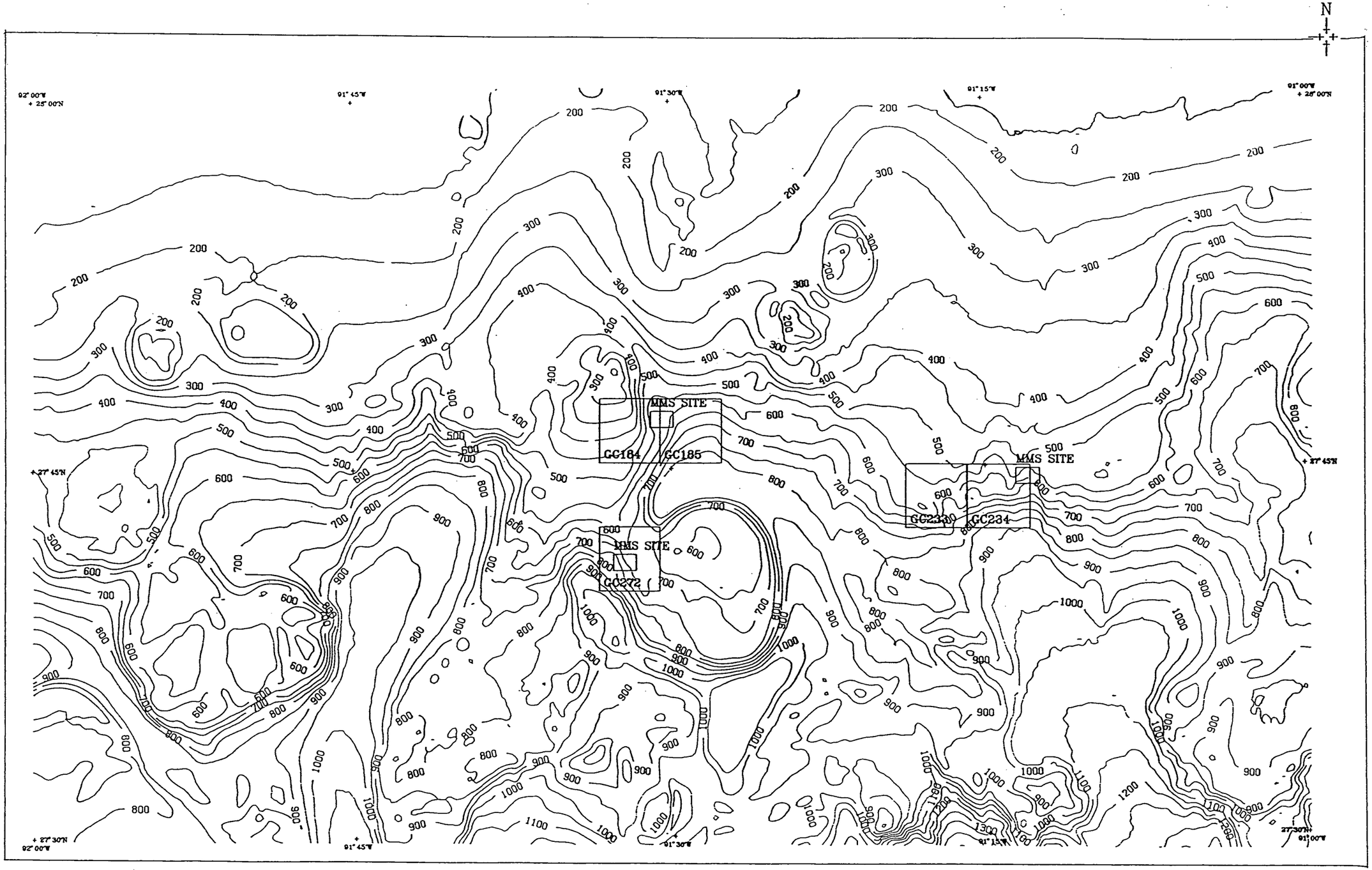
N
92° 00'W
+ 25° 00'N
91° 45'W
91° 30'W
91° 15'W
91° 00'W
+ 28° 00'N
MMS SITE
GC184
GC185
MMS SITE
GC233
GC234
MMS SITE
GC272
+27° 45'N
+27° 30'N
+ 27° 30'N
91° 45'W
91° 30'W
91° 15'W
91° 00'W

Figure 8.10 Sampling Sites in the Sweet Bank region of the Green Canyon leasing area. Large rectangles show lease block boundaries, inner rectangles show Site boundaries. The Site boundaries correspond to the map limits in Figures 8.11, 8.12, and 8.13.

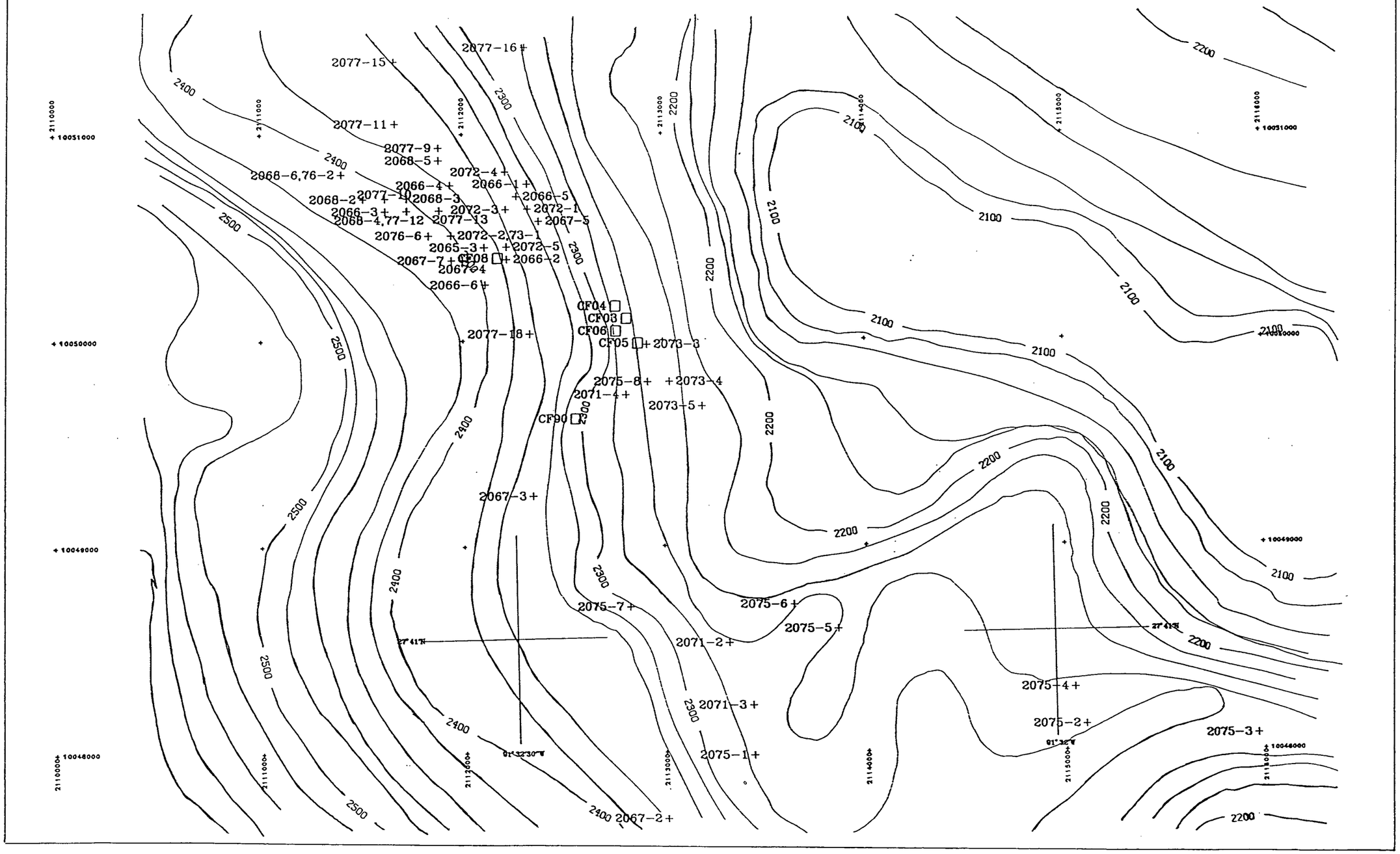
2077-16+
2077-15+
2077-11+
2077-9+
2068-5+
2068-6,76-2+
2072-4+
2066-4+
2066-1+
2077-10
2068-2+
2068-3
+2066-5
2066-3+
+2072-3+
+2072-1
2068-4,77-12
2077-13
+2067-5
2076-6+
+2072-2,73-1
2065-3+
+2072-5
2067-7+
CF08
+2066-2
2067-4
2066-6+
CF04
CF03
CF06
2077-18+
CF05
+2073-3
2075-8+
+2073-4
2071-4+
2073-5+
CF90
2067-3+
2075-7+
2075-6+
2075-5+
2071-2+
2071-3+
2075-1+
2067-2+
2075-4+
2075-2+
2075-3+
2400
2500
2300
2200
2100
+10051000
+10050000
+10049000
+10048000
+2110000
+2111000
+2112000
+2113000
+2114000
+2115000

Figure 8.11 Study Site in the Green Canyon 272 lease block. Locations of fix points in 1987 *Sea-Link* dives at this site (+) are labeled with dive and fix number (See Table 8.4A). Locations of the Sampling Stations established during the 1991 *Sea-Link* dives at this site ( ) are labeled with Station code (Table 8.4B). Station squares are 15 m^2.

8.3.6 Green Canyon 234

The study site was ~75 ha area located in the northeast quadrant of the Green Canyon lease block number 234 at water depths of ~500 to ~600 m (Figure 8.12). The 1987 *Sea-Link* dives occupied 22 fix points at this site and the 1991 *Sea-Link* cruise established three marked sampling stations (Table 8.5A and 5B).

The geological environment was predominantly soft sediment with mounds, although some large boulders were observed (Figure 8.4). Gas venting could be observed at several points among the tube worms. Experience with the *Johnson-Sea-Link* showed the sediments to be heavily oil-stained. Several push cores collected from this site contained thermogenic gas hydrates, so the occurrence of hydrates immediately below the surface is evidently common.

A massive tube worm community occurred in an extensively faulted area of variable relief on the northeastern side of the lease block. The tube worms were uniformly straight, upright, and at least 2 m in length. Contiguous clusters ranged in size from ~1 sq m to 500 sq m or greater, which made this the largest tube worm site yet described in this region. Seep mytilids were present but less abundant than tube worms (Figures 8.6 and 8.7). A time-lapse camera was deployed at Station GC02 and was trained on a prominent bed of mytilids surrounded by tube worms. On the eastern and western ends of the tube worm area, there was an extensive field of large (up to 2 m high) gorgonians arrayed in perfectly linear ranks with 2 to 3 m separation between rows (Figure 8.8). Heterotrophic species associated with the vestimentiferans and mytilid beds included *Alumocans stactophilus*, *Munidopsis* n.sp., *Pisaster*-type starfish, *Acesta bullisi*, *Hoplostethus* sp., the rockfish *Helicolenus dactylopterus*, and the hake *Urophycis cirratus*.

8.3.7 Green Canyon 233

This site, also known as Brine Pool *NR-1*, was found approximately 285 km southwest of the Mississippi Delta (27°43'24"N, 91°16'30"W) near the location where Anderson et al. (1983) collected sediment cores that contained crude oil. The pool lay at a water depth of 650 m among a series of slump terraces at the head of a broad graben that deepened to the southeast. A salt diapir, the top of which was ~500 m below the sediment-seawater interface, was evident at this site as a seismic anomaly and hyperbolic reflector. Normal faults extended from the diapir and an anticlinal feature could be seen on the surface to the south of the brine pool. Shallow gas saturation in the near-surface sediments was indicated by a high amplitude feature at the sediment surface and signal attenuation beneath the pockmark.

Brine filled a 22-m long, 11-m wide, elliptical crater that was situated atop a mound with a height of about 6 m and a basal diameter of about 130 m. Because 25 kHz profiles typically show sedimentary strata to depths of ~20 m subbottom, the highly reflective layers on the periphery of the pool suggested that gas-rich sediments and possibly diffuse hydrates occurred near the mudline at this site. Directly beneath the pool the sedimentary column appeared chaotic. Streams of fine bubbles were seen rising from the center of the pool and appeared as a slight trace in the 25 kHz record. No bubbles were observed at the pool edges or in the mussel bed.

Chemosynthetic mussels surrounded the open brine in a continuous band, approximately 3 m wide on the narrowest side, the northwest edge, and 7 m wide on the southeast edge. The mussel bed was elevated only a matter of centimeters above the brine-seawater interface; its total area was ~540 m^2 whereas the area of the open brine was ~190 m^2. Transition from the mussel

Table 8.5A Position data for fixes in Green Canyon 234 during JSL submersible dives. Type is community type defined in Table 8.2. Fauna refers to presence of chemosynthetic bacterial mats (B), vestimentiferans (V), seep mytilids (M), and vesicomyid clams (C).

Dive-fix	Type	Depth (m)	Latitude (North)	Longitude (West)	Fauna Present
2060—1	SSO	n/a	27° 44.71'	91° 13.37'	
2060—2	SSM	539	27° 44.85'	92° 13.27'	B V M
2060—3	SSO	532	27° 44.78'	91° 13.29'	
2060—4	HST	526	27° 44.75'	91° 13.42'	B V
2060—5	SSB	555	27° 44.67'	91° 13.35'	B
2060—6	SST	535	27° 44.76'	91° 13.33'	V
2060—7	HST	557	27° 44.69'	91° 13.24'	V
2063—2	SST	552	27° 44.70'	91° 13.37'	V
2063—3	HST	518	27° 44.71'	91° 13.48'	V
2063—4	SSB	551	27° 44.66'	91° 13.38'	B V
2063—5	SST	532	27° 44.55'	91° 13.50'	B V
2063—6	SSO	526	27° 44.76'	91° 13.23'	
2063—7	SST	541	27° 44.76'	91° 13.23'	B V M
2069—1	SSO	646	27° 44.16'	91° 12.72'	
2069—2	SST	573	27° 44.33'	91° 12.73'	B V
2069—3	SST	556	27° 44.38'	91° 12.72'	B V
2069—4	SST	553	27° 44.55'	91° 12.71'	B V
2069—5	SST	549	27° 44.59'	91° 12.71'	B V
2070—3	SST	573	27° 44.34'	91° 12.73'	B V
2070—4	HST	573	27° 44.33'	91° 12.70'	B V
2070—5	SSB	562	27° 44.36'	91° 12.66'	B

Table 8.5B Sampling Stations established during the 1991 *Sea Link* dives at GC234. Codes refer to the locations plotted in Figure 8.12 and to data listed in Appendix A. Stations GC98 and GC99 have no marker.

Code	Latitude (North)	Longitude (West)	TD1	TD2	Depth (m)
GC01	27° 44.75'	91° 13.27'	11619.0	27375.6	545
GC02	27° 44.73'	91° 13.22'	11619.2	27376.1	544
GC98	27° 44.80'	91° 13.45'	11618.2	27374.1	507
GC03	27° 44.78'	91° 13.40'	11618.5	27374.5	512
GC04	27° 44.69'	91° 13.44'	11618.6	27373.7	518
GC99	27° 44.71'	91° 13.43'	11618.5	27373.9	516

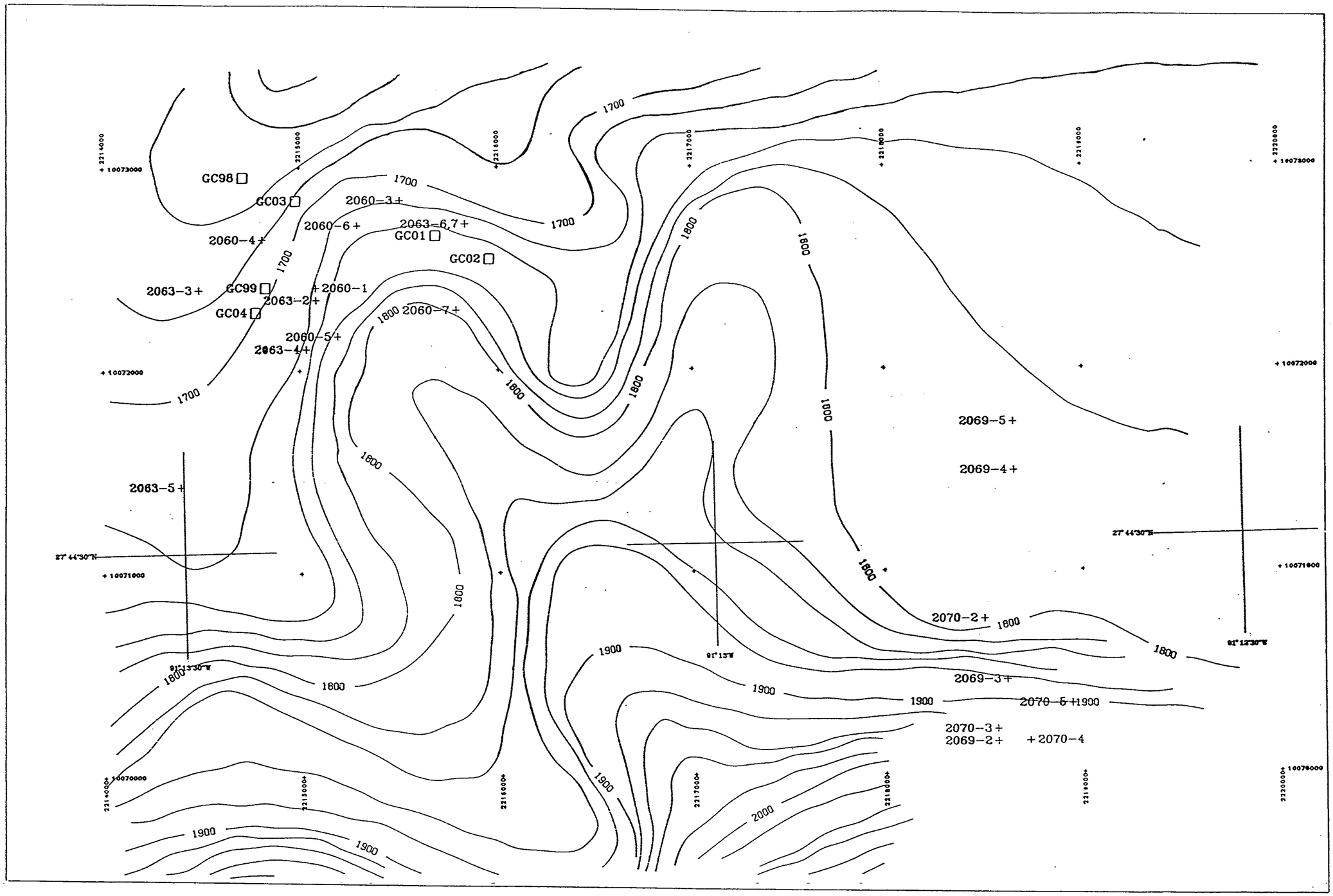
GC98
GC03
GC01
GC02
GC99
GC04
2060-3+
2060-6+
2063-6,7+
2060-4+
2063-3+
+2060-1
2063-2+
2060-7+
2060-5+
2063-4+
2063-5+
2069-5+
2069-4+
2070-2+
2069-3+
2070-5+
2070-3+
2069-2+
+2070-4
1700
1800
1900
2000
27°44'30"N
91°13'30"W
91°13'W
91°12'30"W
+10073000
+10072000
+10071000
+10070000
+10078000
+2214000
+2215000
+2216000
+2217000
+2218000
+2219000
+2220000

Figure 8.12 Study Site in the Green Canyon 234 lease block. Locations of fix points in 1987 *Sea-Link* dives at this site (+) are labeled with dive and fix number (See Table 8.5A). Locations of the Sampling Stations established during the 1991 *Sea-Link* dives at this site ( ) are labeled with Station code (Table 8.5B). Station squares are 15 m^2.

bed to bare sediment was abrupt on the north, west, and east, but more gradual to the south, where the berm was reduced or absent. To the south, gaps of stained sediments appeared as the continuous bed gave way to curvilinear stringers, intermingled with patches of disarticulated mussel shells, which were mostly broken and pitted, and filamentous colonies of white bacteria. Shells continued to dot the sediments 20 m south of the bed. There was no sign of a brine-outflow channel through the bed. We inferred that the irregular southern edge of the mussel bed resulted from lateral percolation of brine through surface sediments.

Brine Pool *NR-1* was an extremely regular habitat with respect to the controlling gradient of methane dissolved in the brine. In contrast to the highly heterogeneous distribution of seep mussels that have been seen at other HS communities, the mussels at this site maintained a relatively uniform density over an exceptionally large area. For this reason, it was an ideal location to study growth of mussel and recovery of mussel beds from mechanical disturbance. Mussels can be transplanted from one portion of the mussel bed to another with reasonable certainty that they are being placed in an equivalent environment. Likewise, denuded portions of the bed can be monitored with reasonable certainty that the supply of methane in the cleared patch is not disturbed by the removal of the mussels. The stability of brine pools remains an open question, but one which the existing data set (photomosaics, permanent markers, seismic data) is well suited to study.

8.3.8 Green Canyon 184/185

This site, also known as Bush Hill (**MacDonald et al. 1989**) occurred over a salt diapir that rose about 40 m above the surrounding sea floor to a minimum water depth of 540 m (Figure 8.13). The feature was located ~210

km south-southwest of Grand Isle, LA, at 27°47'N, 91°30.4'W. It lay in the Green Canyon offshore leasing area between blocks 184 and 185. Available data on the site included videotaped observations from 11 fix points occupied during the 1987 *Sea-Link* dives (Table 8.6A) and four marked sampling stations established in the 1991 *Sea-Link* dives (Table 8.6B). The sediment in this area consisted of silty clay of considerable thickness; however, much of the sedimentary facies of Bush Hill itself have been wiped out by rising gas and liquid and by *in situ* formation of authigenic carbonate and sulfides (Brooks et al., 1986; Behrens, 1988).

Streams of bubbles, primarily methane, could be observed escaping from the substrate, both within the mussel beds and in their immediate vicinity. Some of these bubble streams were intermittent releases; others continued throughout the period of observation. Disturbance of the bottom in the vicinity of methane streams caused the release of large oil globules, which floated upward. Such releases of oil could also be observed in other locations, usually as a result of some disturbance of the bottom.

Two species of vestimentiferan tube worms were collected from Bush Hill and other Louisiana Slope seep communities; these were identified as *Lamellibrachia* sp., family Lamillibrachidae and *Escarpia*-like species, family Escarpiidae (M.L. Jones, pers. comm.). The escarpid, which could be distinguished in the 35 mm photographs by the distinctive flaring of its tube opening, generally forms sparse clusters of recumbent individuals. The *Lamellibrachia* sp. forms bush-like clusters in numbers ranging from a few tens to many thousands of individuals. Although *Lamellibrachia* sp. was clearly dominant, mixed clusters of *Lamellibrachia* sp. and the escarpid did occur. A mytilid mussel, *Bathymodiolus* n.sp. (R.D. Turner, pers. comm.) formed discrete beds on both soft sediments and among carbonate outcroppings.

Mussels and tube worms had been observed together; however, the larger mussel beds usually contained only stunted tubeworms, if any. The beds were irregular in shape, often in close proximity to each other, and ranged in area from less than 1 sq m to approximately 20 sq m.

Animal burrows and mounds were usually present (Figure 8.5). Geological activity was the most apparent at this site where faults and mounds were frequently seen (Figure 8.4). Heterotrophic organisms frequently found on the mussels included *Pisaster*-type starfish, *Munidopsis* n. sp., *Alvinocaris stactophilus*, and gastropod epifauna. *Acesta bullisi* were attached to the vestimentiferans, the large brachyuran *Chaceen fenneri* climbed over tube worm bushes, and the small galatheid *Munidopsis* n.sp. climbed individual tubeworms. A school of *Hoplostethus* sp. was observed near large boulders while traveling between fixes, but a school of these fish was never observed at the fixes or the other sites.

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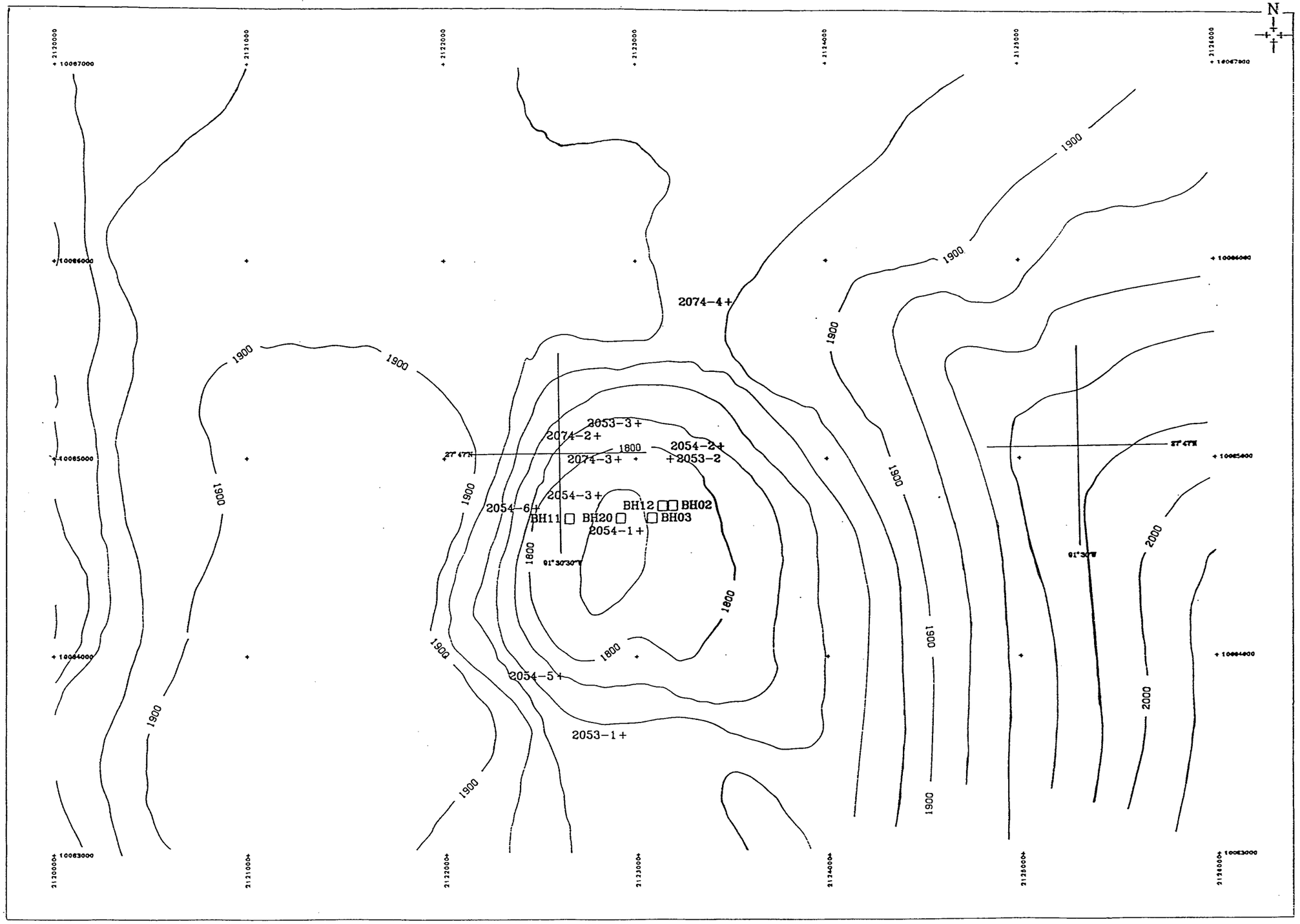
N
2074-4+
2053-3+
2074-2+
2074-3+
1800
2054-2+
+2053-2
2054-3+
2054-6+
BH12
BH02
BH11
BH20
BH03
2054-1+
2054-5+
2053-1+
1900
2000

Figure 8.13 Study Site in the Green Canyon 184/185 lease block. Locations of fix points in 1987 *Sea-Link* dives at this site (+) are labeled with dive and fix number (See Table 8.6A). Locations of the Sampling Stations established during the 1991 *Sea-Link* dives at this site ( ) are labeled with Station code (Table 8.6B). Station squares are 15 m^2.

Table 8.6A Position data for fixes in Green Canyon 184 during JSL submersible dives. Type is community type defined in Table 8.2. Organisms refers to presence of chemosynthetic bacterial mats (B), vestimentiferans (V), seep mytilids (M), and vesicomyid clams (C).

Dive-fix	Type	Depth (m)	Latitude (North)	Longitude (West)	Fauna Present
2053—1	SST	564	27° 46.76'	91° 30.44'	B V
2053—2	SST	553	27° 46.99'	91° 30.39'	B V
2053—3	SSM	547	27° 47.02'	91° 30.42'	B V M
2054—1	SST	546	27° 46.93'	91° 30.42'	B V
2054—2	SSB	558	27° 47.00'	91° 30.34'	B
2054—3	HST	541	27° 46.96'	91° 30.46'	B V
2054—5	SST	553	27° 46.81'	91° 30.50'	B V
2054—6	SSM	541	27° 46.95'	91° 30.52'	B V M
2074—2	HSM	550	27° 47.01'	91° 30.46'	B V M
2074—3	HSM	548	27° 46.99'	91° 30.44'	B V M
2074—4	SSB	571	27° 47.12'	91° 30.33'	B

Table 8.6B Sampling Stations established during the 1991 *Sea Link* dives at GC184. Codes refer to the locations plotted in Figure 8.13 and to data listed in Appendix A.

Dive-fix	Type	Depth (m)	Latitude (North)	Longitude (West)	Fauna Present
BH20	27° 46.94'	91° 30.45'	11547.8	27213.1	546
BH03	27° 46.94'	91° 30.42'	11547.8	27213.2	545
BH11	27° 46.94'	91° 30.50'	11548.0	27213.4	543
BH02	27° 46.95'	91° 30.40'	11547.9	27213.5	549
BH12	27° 46.95'	91° 30.41'	11547.9	27213.4	547

8.3.9 Viosca Knoll 826

The Viosca Knoll site had not been explored by the Program investigators prior to the 1991 *Sea-Link* cruise. Results of the first three Program dives are reported in detail below.

In August 1991, three *JSL* submersible dives were undertaken to investigate the chemosynthetic community at Viosca Knoll 826. The VK-286 lease block is located on the upper De Soto slope approximately 110 km south of coastal Alabama. Chemosynthetic fauna were found in the southwest corner of VK-826 and the southeast corner of the adjacent western lease block (VK-825) during an analysis of a video survey conducted in late August and early September 1990 (Gallaway et al. 1990). This represented the first documentation of a chemosynthetic community associated with hydrocarbon seep activity east of the Mississippi River Delta.

Living chemosynthetic fauna were represented by vestimentiferan tube worms (*Lamellibrachia* sp. and *Escarpia* sp.) and possibly lucinid clams. Numerous zones of disarticulated bivalve shells (lucinid and vesicomyid) were also present. Bacterial mats (*Beggiatoa*) were principally observed in the fissures or joints of exposed carbonate plates or associated with pockets of unconsolidated sediment and shell debris located within extensive carbonate covered areas. Conspicuous heterotrophic fauna included the ahermatypic scleractinian coral *Lophelia prolifera*, the soft coral *Callogorgia* sp., the antipatharian coral *Leiopathes glaberrima*, the asteroids *Odontaster setosus* and *Schlerateriας contorta*, the bivalve *Acesta bullisi*, and a large galatheid yet to be identified.

The areas surveyed during *JSL* dives were generally on the upper regions of a low-relief mound (centered at approximately 29° 09.5'N and 88° 01.0'W) that rose between 60-90 m (197-295 ft) above the surrounding sea floor to a

minimum water depth of 429 m (1407 ft). The first two dives, *JSL* 3096 and 3097, generally traversed the top southeastern (3096) and western (3097) flanks of the mound, while the third dive, *JSL* 3098, investigated the south to southwest flank.

AREA I (JSL 3096) - Top and southeastern flank.

The southern rim of the top of the mound ranged in depth from 444-457 m (1458-1500 ft). It had an overall moderate slope and consisted of a combination of locally hummocky terrain made up of carbonate knolls and ridges, some with abrupt vertical relief, relatively flat terraces built from carbonate substrate (large plates and slabs, moderate to small boulders, and various forms of small rubble), and unconsolidated soft sediments with patches of disarticulated clam shells and shell gravel. The lateral extent of these terraces appeared at times to run for a considerable distance around the along-isobath trend of the mound. In some areas the carbonate outcrops were covered with extremely large colonies of *Lophelia prolifera*. Along the edges of the carbonate and shell/sediment interfaces were clusters of tube worms, small bacterial mats and occasionally bubbles from seeping methane. A five gallon "marker bucket" was deployed at 29° 09.74'N and 88° 01.08'W in a water depth of 447 m (1467 ft) to identify a major sampling area.

To the east and southeast the bottom leveled off into a relatively flat area consisting mostly of soft, unconsolidated sediment and patches of carbonate outcrops, many covered with colonies of *Lophelia prolifera*. The slope, consisting of fine, unconsolidated silt and clay, then began to increase rapidly below depths of 457 m (1500 ft) reaching an angle of up to 30° to 40°. The available bathymetry for this area combined with the observations made during *JSL* 3096 suggested that there may have been a collapsed southern wall on this

flank of the mound. The maximum depth achieved on this dive was 505 m (1658 ft) on the southeast slope.

AREA II (JSL 3097) - Top and western flank.

The eastern rim of the top of the mound ranged in depth from 443 to 457 m (1454-1500 ft). The bottom had a more gradual slope into deeper water on this side of the crest of the mound compared to the south side. However, just as on the south rim this area consisted of a combination of carbonate knolls, resulting in a hummocky topography, and relatively flat, terrace-like features consisting of various carbonate structures, shells and shell gravel, and soft unconsolidated sediment. Here again the lateral extent of these terraces was not known but they often appeared to run along the isobath trend for some distance. Scattered throughout the area were colonies of *Lophelia prolifera*, clusters of tube worms and bacterial mats similar to those observed on JSL 3096. A "marker bucket" was deployed at 29° 09.86'N and 88° 01.00'W in a water depth of 447 m (1468 ft) and a photo mosaic survey was made of the immediate area. General biological and geological collections were made in areas away from the photo survey site.

On the west side of the mound, in water depths shallower than 457 m (1500 ft), the bottom had a moderate slope. At 457 m (1500 ft) the slope began to increase dramatically, reaching 35° around 466 to 469 m (1530 to 1540 ft) and 40° to 45° at 491 m (1610 ft). The slope consisted of a series of ridges/hummocks and swales of unconsolidated fine sediment. These features were oriented along the isobath and had a vertical relief of 1 to 3 m from crest to trough. Carbonate outcrops occasionally occurred on the ridges and supported colonies of *Lophelia prolifera*, clusters of tube worms, bacterial mats and, more rarely, soft corals. The maximum depth reached on the western flank was 496 m (1628 ft).

At this depth, we observed a furrow that cut into the soft sediment and that extended out of sight both up- and down-slope. This disturbance in the bottom was traced back up-slope (generally to the east-southeast) to see what damage it may have caused in areas of carbonate deposits. The furrow continued up-slope, changing from a clean, narrow cut (10 cm) into the bottom to a complete disruption of the surface over a 2 m swath: sediments were overturned and either piled up in small ridges/mounds or scraped away, forming trenches/depressions. The cause of this feature was surmised to have been a wire cable suspended above the bottom that either hit the bottom once, or struck the bottom more than once, and/or was moved laterally across the bottom. No extensive areas of carbonate were affected by the furrow; however, it did cut through numerous colonies of *Lophelia prolifera*, inflicting severe damage. The dive ended at a depth of 475 m (1560 ft) before the end of the furrow was located.

AREA III (JSL 3098) - Southern and southeastern flank.

JSL 3098 started with a reconnaissance survey of the south side of the mound. The area investigated had a steep to very steep (up to 45° to 50°) slope covered with fine, unconsolidated sediment and small, terrace-like features built of exposed carbonate outcrops. The outcrops provided substrate for both *Lophelia prolifera* and *Leiopahtes glaberrima*. A relatively flat terrace consisting of both carbonate and soft sediment was encountered at the easternmost point reached during this dive. This feature appeared to broaden and extend further off to the coast. This is the only site where one of the most conspicuous members of the epibenthic fauna was a small white "glass" sponge attached to the carbonate substrate.

The region in the depth range of 442-526 m (1650-1725 ft) on the southwest flank of the mound was generally extremely steep-sided (45° to 50°).

The bottom in this area appeared to take the shape of a small, steep-sided valley (i.e. the isobaths were concave into the side of the mound) and may have formed as a result of slumping activity. At the base of the "slump zone?", 527-532 m (1729-1744 ft), the bottom flattened out into at least one terrace-like feature that was covered with large, mostly irregular-shaped blocks (up to 3-4 m tall by 1-2 m wide) and slabs (4-5 m across) of carbonate material. Some of the blocks were pillar-like while others were mushroom shaped with large overhangs at their tops. Rubble debris was scattered throughout the area. Additional evidence for a slumping event was the number of these large blocks that were chaotically strewn about the area. Most of the surfaces of the carbonate were barren; however, large isolated colonies of *Lophelia prolifera* and soft corals as well as clusters of tube worms, various sponges, the bivalve *Acesta bullisi* and numerous small shrimp were observed at this site. A "marker bucket" was deployed at 29° 09.46'N and 88° 01.31'W in a depth of 531 m (1743 ft) on top of a large carbonate boulder. A random photo survey was undertaken in the immediate vicinity of the "marker".

8.3.10 Alaminos Canyon 645

This site, the deepest (2200 m) and most remote of the known communities, was of considerable interest because its existence expanded the depth range of HS communities in the Gulf by three-fold. The depth of the site necessitated the use of *Alvin* or its equivalent; it was not included in the original proposal because the means for occupying it were not then available. However, six dive days with *Alvin* have been made available to Program investigators, so prospects for eventual inclusion of the Alaminos Canyon community are improved to the point where it is appropriate to discuss

information regarding this sight in this report. The following description of the communities at this site is excerpted from Brooks et al. (1990):

The chemosynthetic fauna in Alaminos Canyon included six distinct aggregations of seep mytilids and/or vestimentiferan tube worms at apparent hydrocarbon seeps along the base of a carbonate ridge. The largest aggregation, "Neptune's Garden" (26° 21.30'N; 94° 29.81'W), was a lush mixture of tube worm clusters and mussel beds spanning ~30 m and flanked by carbonate outcrops. Abundant galatheid crustaceans and a few fish were also observed. Other aggregations consisted of either mixed patches of tube worms and mussels, or of solitary tube worm clusters. All were associated with authigenic carbonate outcrops.

The Alaminos Canyon site is intermediate in depth between the Louisiana slope communities and the Florida Escarpment (3000 m) communities. Although the three regions are taxonomically distinct at the species level or higher, the preliminary results from Alaminos Canyon demonstrate that there are notable ecological characteristics common to the Gulf of Mexico chemosynthetic communities. The Seep mytilids discovered at the deep-water Alaminos Canyon site are a new species and have very light stable carbon isotopic compositions ($\delta^{13}C$ = -45 ‰) suggesting that they may contain endosymbiotic methanotrophic bacteria like seep mytilids found at previously-known Louisiana oil seep and Florida Escarpment sites. The carbon isotopic composition of the mussels is similar to values seen in Louisiana slope mussels and may reflect the thermogenic nature of the seeping hydrocarbons (**Brooks et al., 1987**). Two species of vestimentiferan tube worms found in the oil-seep areas of Alaminos Canyon were different from those found at the Louisiana slope seeps. At least one of the vestimentiferans is apparently a new species.

8.3.11 Garden Banks 386

The major objective for this sampling site was the clam community. Observations from *NR-1* indicated that extensive beds of clams were distributed across the plateau. The dive schedule proposed for the 1991 cruise therefore included a total of 10 dives to this site, including deployment of clam growth experiments. The HS community was dominated by vesicomyid clams with subsurface lucinid clams. Sparse tube worm clusters and occasional beds of mussels also occurred. The community was concentrated on a plateau approximately 25 ha in area and raised above the surrounding sea floor by approximately 10 m. The plateau was distinctive; flat-topped with steep and rocky walls on all sides, it was also underlain with unusual structural features (J. Corthay, personal communication). Closer inspection with the *Sea-Link* revealed that these beds were in fact shell pavements consisting exclusively of dead shells. The sampling objectives for this site were curtailed sharply because of this finding. A marginal tube worm cluster was photographed and a limited suite of water and sediment samples were collected. The sampling objectives that required extensive clam communities were transferred to the GC272 site.

8.4 Summary

Chemosynthetic fauna occur across most of the continental slope in the northern Gulf of Mexico. Their distribution is more homogeneous over larger geographic and depth ranges than is the case for hydrothermal vent communities. Seep communities tend to be dominated by vestimentiferans, seep mytilids, or vesicomyid and lucinid clams, but intergradations among these community types are the rule, particularly between vestimentiferans and

mytilids. The communities are associated with specific geological processes and features such as faulting and brine seepage. The communities are also associated with a characteristic seismic signature, the so-called wipe out zone. There is some variety among wipe out zones; however, their causes and the consequences for community formation have not yet been determined.

The MMS Chemosynthetic Ecosystems Study encompasses a series of study sites which were selected from the known list of communities on the basis of community type and geographic location. One of the preselected sites (GB386) turned out not to be as suitable as had been hoped and an alternative (GC272) was selected. Another site (AC645) has been proposed as an optional area to provide representation across the known depth range of HS communities.

9.0 Heterotrophic Fauna Associated with Chemosynthetic Communities

R.S. Carney

9.1 Introduction

With the increased interest in oil and gas reservoirs beyond the edge of the continental shelf, management decisions concerning development of these resources must consider the potential for anthropogenic impact upon the chemosynthetic communities associated with deep-sea hydrocarbon seeps. Therefore, there are information needs which require that the basic ecology of these seep communities be understood. Since the discovery and subsequent study of deep-sea chemosynthetic communities more than a decade ago, progress has been markedly greater in studying the organism-level processes of chemosynthesis and chemoautotrophy than in determining the basic community ecology of seeps (Grassle 1986; Tunnicliffe 1991). Fundamental questions, such as the trophic interaction of seeps with the surrounding environment and the role of biogenic factors in regulating seep community structure, remain unanswered. This section will determine what is currently known regarding heterotrophic fauna associated with chemosynthetic communities, will place the preliminary findings of the Gulf of Mexico seeps into that perspective, and will suggest a conceptual framework within which to synthesize future findings.

We contend that the determination of heterotrophic activity in seep communities and the interaction with the surrounding environment requires comparative study. Deep-sea seep and vent communities are so strikingly different from typical deep-fauna that questions immediately arise as to the types of interaction between these dramatically dissimilar systems. Considering the seep community first, we can pose the following question: How is a spatially discrete and restricted seep system, which is characterized

by high biomass and low diversity, affected by the low biomass and high species diversity environment surrounding it? For example, does extensive predation and scavenging by a food-limited typical deep-sea fauna exert significant biogenic control on seep productivity and population structure? Considering this topic from the opposite perspective, we can pose the complementary question: How is the non-seep deep-sea environment, which is vastly greater in spatial scale, affected by the seep community?

A fundamental concern is whether there is a measurable flux of carbon and/or energy between hydrocarbon seeps on the Gulf of Mexico slope and the surrounding deep-sea ecosystem. There have been attempts to estimate such a flux directly by means of stable carbon- and sulfur-isotope techniques. Spies and DesMarais (1983), for example, demonstrated incorporation of chemosynthetically derived carbon into the heterotrophic infauna via *Beggiatoa* sp. at a shallow water (15-m depth) hydrocarbon seep off Santa Barbara, California. Their approach, however, required a targeted harvest of infaunal biomass that is beyond the capabilities of the present program. Our alternative is to examine patterns in the distribution of benthic fauna, and the degree to which these patterns are altered by hydrocarbon seepage, to generate hypotheses, and then to test these hypotheses with available data.

9.2 Basic Heterotrophic Non-Seep Patterns in the Deep-Sea

In the following brief review of basic deep-sea faunal patterns, we shall argue that the interaction of a seep or vent community with the surrounding biota can be expected to change with depth. This is especially important in the Gulf of Mexico, because the depth range over which seep systems are known to occur in this region will expose seeps to distinctly different adjacent heterotrophic species, to different diversities of adjacent species, and to

different abundance of detritus-based heterotrophic fauna. Therefore, seeps must experience different levels of foraging by heterotrophs, different complexities of interaction, and different levels of carbon exchange with the surrounding seafloor.

9.2.1 The World Ocean

The deep-sea environment in which vent and seep communities are found is characterized by vast expanses of unconsolidated sediment and a fauna dominated by detritus feeders. Three general principles of deep-sea ecology are of particular relevance for comparison of seep to non-seep areas: first, the taxonomic composition of the deep-sea fauna changes with depth; second, the standing stock biomass of the fauna decreases with depth, and third, the diversity of the fauna increases with depth over some part of the shelf to abyss depth range. [Gage and Tyler (1991) is the most recent of many comprehensive reviews of the deep-sea literature that have been produced in the last decade; it makes extensive and critical use of the previous literature.] Taken together, these patterns suggest that the interaction of seeps and the surrounding seafloor will be dependent upon depth.

9.2.2 Taxonomic Patterns

The fact that faunal composition changes with depth is probably the oldest generalization about deep-sea biology, but it eludes quantification due to a host of problems associated with the taxonomy of many phyla and methods for analysis of faunal similarity (Carney et al. 1983; Gage and Tyler 1991). The key elements of the faunal pattern, however, are self-evident without precise quantification. First, benthic fauna changes with depth at a rate such that the dominant species at 500 m depths will be rare or absent at depths greater than

2000 m, and will have been replaced by a new suite of species. Second, there is a shift in the relative abundance of certain higher taxa with increasing depth. Generally, decapod crustaceans decrease with depth, echinoderms increase, and other groups usually have family-level groups that are largely unique to the deep-sea. Causes for deep-sea faunal replacement has been discussed extensively. Physiological restraints were once the most popular explanation, but depth related food supply must now be more seriously considered.

9.2.3 Diversity Patterns

The main feature of the deep-sea diversity patterns and their changes with depth is that the deep-sea has an unexpectedly diverse fauna. This was first noted by Murray as a general conclusion of the Challenger Expedition (Murray 1895), and then rediscovered by Sanders et al. (1965). The species diversity in the deep-sea can be judged to be the most enigmatic of patterns on the basis of the many speculative publications on the subject. The unexpectedness of this high diversity stems from prevalent concepts of speciation and competitive coexistence based upon genetic isolation and resource partitioning. Both of these factors are difficult to identify in the relatively uniform and connected deep-sea benthos. Numerous hypotheses and explanations have been suggested to explain the high diversity (Grassle 1989). Unfortunately, some of these explanations are circular, and few lead to postulation of falsifiable hypotheses; thus, they do not lend themselves to verification.

Whatever the cause, a series of collections made along a transect of increasing depth will commonly display two diversity maxima, one at the mid-depth range and the second at greater depths. Diversity can be unimodal with a maximum at abyssal depths, or with a maximum at bathyal depths (Gage

and Tyler 1991). However, point sampling, in the absence of a full transect, at even greater depths has shown even deeper diversity maxima. The actual pattern at any given place must depend upon local conditions as well as the faunal components being considered.

9.2.4 Biomass and Influx Patterns

Generalities about the relationship between detritus influx and deep-sea faunal feeding have been reviewed by Carney (1989) and considered theoretically by Jumars et al. (1990). The basic pattern is quite simple; the flux of carbon detritus from the photic zone through the water column to the deep-sea floor decreases markedly with depth (Suess 1980). The biomass and abundance of benthic fauna show a similar decrease (Rowe 1983).

While it is self evident that deep-sea heterotrophs must be dependent upon detrital influx from the photic zone, determination of the exact nature of this coupling is hindered by conflicting observations. It is now evident that detritus influx to the deep-sea is seasonal and rapid. Coupled with the observation that the metabolic demand of deep-sea communities equals or exceeds the apparent flux rate of carbon (Smith 1987), this suggests rapid consumption in the benthos and food limitation. However, there are two crucial observations which do not support such a suggestion. First, incorporation of the atmospheric bomb testing fission ^{14}C spike into abyssal fauna was a slow process spanning decades rather than weeks (Rau et al. 1986). Second, carbon arriving at the seafloor becomes increasingly refractory with depth and should not be readily available for metazoans assimilation (Carney 1989). While bacterial biomass is invoked as a means of converting refractory carbon into useful food, the metabolic cost of bacterial conversion is

so great (90-80% loss) that available food would be about an order of magnitude less than apparent demand.

Development of a conceptual model of interaction between seep autotrophs and a surrounding heterotrophic system is inherently difficult. Our understanding of deep-sea trophic structure is so poorly developed that few statements about trophic interactions on scales as small as seep communities are possible. Even the most basic observation, that the deep-sea is predominantly a detritus feeding system, does not lead to useful speculation since there is no useful theory concerning resource utilization and partitioning among detritus feeders (Lopez et al. 1989).

9.3 Basic Deep-Sea Patterns in the Gulf of Mexico

The basic patterns of heterotrophic fauna distribution in the Deep Gulf of Mexico has been addressed by the sampling program of Willis Pequegnat (Pequegnat 1983) and by the Northern Gulf of Mexico Continental Slope Study (Gallaway 1988; Pequegnat et al. 1990). Findings from the Gulf of Mexico are rarely considered, however, in review volumes.

9.3.1 Taxonomic Patterns

The Gulf of Mexico is the largest of a series of basins which comprise the Gulf of Mexico-Caribbean extension of the Atlantic ocean. While the taxonomic uniqueness of the Gulf of Mexico's deep-sea fauna has never been comprehensively analyzed, the existence of various sized basins isolated by deep sills suggests that both isolation and species-area phenomena might be acting to produce some degree of endemism. The deep Gulf of Mexico seems to have a mixture of northern Atlantic species and endemic species. Species composition changes with depth such that both macrofauna and megafauna

species suites at the shelf break (~400 m depth) are highly unlike the suites found at~3000 m depths (Pequegnat et al. 1990). Large decapods are common on the upper slope, but decrease with depth. Echinoderms become increasingly abundant with depth. There is considerable diversity within the deep-sea gadiform fishes.

9.3.2 Diversity Patterns

The depth-diversity pattern of the Gulf of Mexico are unlike those found in the North Atlantic. There is a diverse macrofauna, but depth trends are indistinct with an apparent, but modest and shallow, diversity maximum at about 1000 m. The lack of a distinct deeper diversity maximum may be related to a species-area phenomena (Abele and Walker 1979). Unlike open ocean basins, the depth of maximal area of the Gulf lies at bathyal rather than abyssal depths.

9.3.3 Biomass and Influx Patterns

The deep macrofauna biomass pattern of the Gulf of Mexico is basically similar to that found in the Atlantic (Rowe et al. 1983). First, there is a fairly consistent decrease in abundance with depth, but the overall abundance appears to be less than in the North Atlantic. At the shelf break depths (~400 m), abundances as high as 4000 individuals per m^2 are encountered, while at 2600 m depths, the number has declined to 1000 individuals per m^2 (Gallaway et al. 1988). Megafauna are typically sampled by non-quantitative trawling, which makes determination of all but qualitative abundance patterns unjustified. Densities are greatest in the eastern Gulf and decline with depth.

There is considerable uncertainty attached to estimating the influx of labile carbon based upon observations of the density of macrofauna per square

meter; however, we take this step for its heuristic value. Assuming that there is a linear relationship between macrofauna density and detrital influx, it appears the seafloor of the Gulf of Mexico at 2600 m depth receives about one fourth of the labile carbon through detritus as does the seafloor at 400 m depth.

9.4 Heterotrophic Fauna of Seeps and Vents

The dominant theme for general deep-sea faunal patterns and the specific manifestation of those patterns in the Gulf of Mexico can be summarized as follows: everything changes with depth. Quantitative details are difficult to develop, but the major qualitative point is that the ecology of the bottom at 1000 m depth is different than the ecology at 3000 m depth. Lacking a good depth series of seeps in the Gulf of Mexico, we are not yet ready to discuss depth gradient of seep community composition. However, available data suggest that the dominant bacteria-mytilid-vestimentiferan assemblage of seeps is relatively stable with depth, at least at the generic level.

9.4.1 Taxonomic Composition of Seeps and Vents

The study of seep and vent heterotrophs is proceeding as a series of independent taxonomic investigations. Two seminars have been held to synthesize findings. The first produced an open publication (Jones 1985b) that considered the Gulf of Mexico seeps only slightly (Hecker 1985). The second, produced proceedings abstracts (ICSEB IV 1990) which address the Gulf of Mexico in greater detail. A few important generalities can be drawn from these seminars and conversations with the participants:

(1) seep heterotrophic fauna is far more abundant than on the typical deep-sea bottom, but there are fewer species present (low species richness) and a few of those species are dominant (low diversity);

(2) seep and vent species are a mixture of taxa seemingly unique to seeps and vents as well as vagrants from the surrounding environment;

(3) only among a few taxa does there seem to be a high level of seep and vent endemism above the family level. For the most part, seep heterotrophs are in the same genera and families as typical deep-sea forms; and

(4) seep and vent heterotrophs do not appear to be biologically unique. They have a variety of reproductive and feeding modes. For the most part, the degree of specialization of heterotrophs is far less than for the chemoautotrophs.

Of these four crude generalizations, some need more discussion and debate than others. The high standing-stock and low-diversity characteristics of seep and vent communities (statement 1) seem well-established. On the other hand, statements 2, 3, and 4 depend upon the species sampled at seeps and are very much subject to change based upon differing perspective. Statement 2 needs little justification and is certainly correct. Endemism (statement 3) depends greatly upon the taxa being considered. If you consider limpet gastropods at vents (virtually absent at the Gulf of Mexico seeps), there is great endemism, However, galatheid crabs (common at both seeps and vents), are a wide spread deep-sea taxon. At this time it appears that chemoautotrophic hosts show pronounced endemism at both seeps and vents while the associated heterotrophs show less endemism. Similarly, the relative

lack of specialization by seep heterotrophs (statement 4), depends entirely on the animal being considered.

The whole matter of relative seep diversity can be made quite complex for a variety of practical and theoretical reasons (Tunnicliffe 1991). Seeps and vents are mostly hard bottom systems dominated by conspicuous epi-megafauna. By contrast, the common generalities about deep-sea diversity are based almost exclusively on soft bottom epi- and in- macrofauna. So, what is the appropriate comparison? Restricted to megafauna, on a square meter by square meter basis, seeps and vents with 10 to 20 species are more species rich than the surrounding bottom with one or fewer animals. However, abundance differences complicate comparisons. Whatever the comparison, seeps and vents do show far more dominance by a few species. The following considers the patterns that have been observed among taxonomic groups.

9.4.2 Polychaeta

Polychaete worms are such a ubiquitous component of the deep-sea fauna that they hold a special place in any comparative study. An early overview of seep and vent polychaetes has been presented by Blake (1985) and subsequently updated Blake (1990). At this time, it appears as though there may be approximately 100 species of polychaetes associated with vents and seeps. This is a remarkably low number given the great diversity of this group in the deep-sea. For the most part, the taxa inhabiting the seeps are members of typical deep-sea genera and families. Two families appear to be endemic, the Alvinellidae and the Matillinidae (Blake, per. comm..). The former lives as epifauna on the tubes of vestimentiferans and the latter is an endo-commensal in bivalves. Functionally, seep and vent polychaetes seem to fill several roles, i.e. detritivore, suspension feeder, carnivore and scavenger.

A unique feature of the Louisiana slope seep systems is the presence of abundant, large (10 cm and greater) polychaetes. This animal seems to occur in masses of hundreds of individuals within mussel beds. It has been tentatively identified as a new species, with affinities to the family orbinidae (Ruff and Blake, per comm.). Associated with samples of this orbinid-like worm are a similarly sized but much less common neriid. The bivalve *Acesta*, the base of gorgonian colonies and even some larger gastropods often have several specimens of a boring polydoriid polychaete. (Blake 1990). Boring polydoriids are common, but poorly studied. Vestimentifera tubes frequently have a small serpulid worm attached.

The polychaete specimens from the Gulf of Mexico have been distributed to Dr. James Blake and Mr. Eugene Ruff for collaborative analysis. Approximately 10 species have been found, with the large orbinid-like specimens comprising greater than 90% of the specimens. These authors are preparing a comprehensive review of seep and vent polychaetes.

9.4.3 Crustacea

Decapod crustacea are a conspicuous component of both seeps and vents. Williams and Martin (1990) provided a summary of observations on the crustacea of seeps and vents. Sixteen species of decapod crustacea have been described from seeps and vents, of which six may be vagrants from the surrounding environments. Since the deep-sea fauna is noted for the relative absence of decapod crustacea, this low diversity is not surprising. With the exception of one monospecific superfamily erected for the "vent crab," *Chorocaris*, vent species seem to be related to typical deep-sea fauna at the generic or family level.

So far, the Gulf of Mexico seeps, off Louisiana and at the Florida Escarpment, are unique in the presence of a small decapod shrimp, *Alvinocaris stactophilia*, of the family Bresillidae. This animal is common both in and on mussel mats and tubeworm clumps. In addition, a new species of the genus *Munidopsis*, a galatheiid crab, is frequently found crawling over mytilids and climbing vestimentiferan tubes. Large anomuran and brachyuran crabs are common on the upper continental slope of the Gulf of Mexico and are encountered in the seep sites. They appear to be feeding upon the seep community. These include Eumunida picta (galatheiid), *Paralomis cubensis*, which is related to the king crab, and the majiid crab *Rochinia* sp. Less closely associated with the seeps, but common in the regions surveyed are the giant isopod, *Bathynomus giganteus* and deep-sea lobster *Acanthoacaris caeca.*

It can be safely assumed that the larger decapods seen in the Gulf of Mexico seeps are generalized predators, scavengers, and selective detritus feeders. As such, they fill a role similar to a large brachyuran studied by Tunnicliffe and Jensen (1987) at vent sites. These large, highly mobile crabs are excellent examples of deep-sea foragers which enter seeps and prey upon the seep fauna. As such, they are a conspicuous link to the surrounding ecosystem. Approximately ten species of decapod crustacean have been encountered in the seeps. These have been transmitted to Dr. Austin Williams of the National Marine Fisheries Service for detailed taxonomic study. Dr. Julie Ambler of Texas A&M University is studying the galatheiid crabs.

Since vents are predominantly hard bottom areas, there has been less study of the macrofaunal crustacea than of the conspicuous large decapods. What little work that has been done is by Grassle and his associates (Grassle et al. 1985). Detailed taxonomic accounts are restricted to the copepods (Humes 1987 and 1988). Analysis of this size class at the hydrocarbon seeps is also

just beginning. Suction samples collected from tubeworm clumps have numerous amphipods. Sediment samples collected in and near seeps have the typical deep-sea taxa such as harpacticoid copepods and tanaiids.

9.4.4 Mollusca

Gastropods are both a common deep-sea form and abundant at seeps and vents. Overviews of vent and seep heterotrophic mollusks have been presented by Warren (1990), Warren and Bouchet (1989), and McClean (1990). Of the many gastropods found associated with these systems, the limpets form a special group with four endemic superfamilies. Unlike many other vent and seep taxa which have close affinities to typical deep-sea fauna, the four endemics show affinities to paleozoic shallow water forms. While the hot vents of the east Pacific have an abundant limpet fauna, other gastropods are common, and more than 100 species have been found. Half of the vent and seep gastropod fauna is comprised of limpet species, while the deep-sea gastropods in general are only 10% limpets.

The hydrocarbon seep gastropods are distinct from faunas found at other vent and seep systems. First, limpets are quite rare, only one rare species has been found. The browsing nerite, *Bathynerites judithi* is so common that it is the most abundant heterotroph in many seep samples. The trochid *Catagis* sp. is predominant at a few mussel clusters, as well as a much smaller species (<1 cm length) tentatively assigned to the genus *Alvania*. While the above species all appear to be radular browsers and grazers restricted to the seeps, the neogastropod *Bartschia canatae*, is encountered on sediments remote from seeps, in clam beds, and even climbing on tubeworms. The radula is borne on a long proboscis suggesting predatory feeding. The large slit shell, *Gaza fisheri*

is sometimes encountered at deep rock reefs in the vicinity of seeps, but shows a less obvious association than the above species.

A single heterotrophic bivalve has been found associated with the hydrocarbon seeps, the genus *Acesta*. As with other of the pen shells, *Acesta* can attach itself to the substrate with byssal fibers as well as swim though the water in a scallop-like fashion. *Acesta* is enigmatic is that it occurs in two distinct forms in the seep area. An elongated, thin shelled form is found attached to exposed carbonate. The junction between the two valves closes completely when the valves close. A second form has a distinctly thicker shell, a more compressed body, and is found attached to the end of a vestimentiferan tube. The shell edges at the junction do not meet, leaving a gap through which the end of the vestimentifera tube passes into the shell. In effect, the obturaculum of the tubeworm lies within the mantle cavity of the bivalve.

9.4.5 Less Common Taxa

Both seep and vent system heterotrophic faunae are dominated by mollusca, crustacea, and polychaeta, with relatively few other groups being common. Among the macro and megafauna of vent systems many typical deep-sea taxa, such as the echinoderms, tend to be absent in vent systems (Grassle 1986). This generalization about absences does not fully apply to the seeps in the Gulf of Mexico. Echinoderms are relatively common at Gulf of Mexico seeps. Two species of asteroids and two species of the sea urchin genus *Echinus* have been collected directly in mussel beds. The former appear to be predatory and the latter grazers. At the Florida escarpment seeps, a synaptid holothuroid is very common in mussel beds (Hecker 1985). No benthic holothuroids have been found in the shallower seeps, but the benthopelagic species *Enypniastes* sp. is common in seep areas.

Since the Gulf of Mexico hydrocarbon seeps extend to as shallow as 500 m, and there is a well developed deep hard ground fauna at this depth and shallower, it is not surprising that many sessile forms can be found in the immediate vicinity of the seeps. These include sessile colonial coelenterates, solitary corals, brachiopods, sipunculids and filter-feeding asteroids of the family Brisingidae. Mussel shells are generally free from attached epifauna, but the worm tubes may be encrusted by sponges, hydroids, bryozoans and polychaetes. It remains to be seen as to whether these hard bottom epifaunal forms will decline with depth as might be expected.

Seeps and vents have a limited fish fauna (Tunnicliffe 1991). The Gulf of Mexico hydrocarbon seeps have several conspicuous species. The large red *Chaunax pictus* is commonly found adjacent to mussel beds and vestimentiferans. The hagfish *Eptatretus* sp. seems to live within mussel beds and aggregates rapidly whenever mussels are crushed by action of the submersible. Hovering over tube worm clumps, as if territorial, *Hoplostethus* sp. forms small schools. The rock fish *Helicolenus dactylopterus* and the hake *Urophycis cirratus* are sometimes found beneath vestimentiferan bushes. The hake *U. cirratus* is a visitor to seeps since it is frequently observed in burrows between seeps. *Synaphobranclus* sp., a cutthroat eel, is frequently seen swimming above the bottom in seep sites. The cutlassfish Trichiura sp. hangs vertically and drifts above seep sites. These fish are associated with seeps, but except for hagfish actively eating broken mussels, predation has not been observed.

9.5 Trophic and Functional Considerations of Seep Heterotrophs

In the following sections we will consider two sets of observations which bear directly upon the question of how hydrocarbon seeps interact with both

the seep dwelling heterotrophs and the fauna of the adjacent seafloor. First, we will consider the observation made during submersible observations that seeps are spatially restricted and do not appear to have areas of increased consumer organism densities in their proximity. Second, we will consider the more quantitative analysis of carbon flow in and around seeps based upon compiled $^{12}C/^{13}C$ ratios.

The review of species found in seeps makes it clear that seeps can be trophically complex. Chemoautotrophic bacteria, and chemoautotrophic-host metazoans must form the basis of a food web that supports surface browsers, predators, and scavengers. These heterotrophic consumers must contribute to the support of other scavengers, predators, and so on until the low efficiencies of linkages reduces the level of available energy. An interesting aspect of seeps in comparison to other reef-like systems is that the detrital pathway may be of minimal importance in the absence of feces and pseudofeces from the dominant chemoautotrophic forms.

Two key aspects of the Gulf of Mexico seeps, or of any vent and seep system, require special attention. Foremost is the trophic relationship. Is there a significant flow of carbon/energy from the seep autotrophs into the seep heterotrophs and into the adjacent heterotrophic community? Or, are seeps relatively isolated trophically?

9.5.1 Expected Patterns of Heterotrophic Densities Near Seeps

This section will consider what types of standing stocks might be expected near seeps to see whether initial observations require that we reconsider the possibility of carbon export from seeps. Seep communities present such a visually impressive assemblage of biomass against the backdrop of a depauperate deep-sea environment that it is an immediate and logical

suggestion that they are a source of labile carbon to the food-limited surroundings. Since the first chemoautotrophic community was found off the Galapagos it has been common to refer to these systems as "oases" to emphasize not only the great biomass in the systems, but also the very sharp demarcation between the communities and the relatively depauperate surrounding bottom. This sense of isolated aggregations in a barren landscape is also apparent for the Gulf of Mexico seeps. However, a dramatic increase in the population of non-seep animals on the margin of seeps is not evident in the anecdotal reports and video records collected during submarine dives on the Gulf of Mexico seep communities. The visual impression, amply reinforced by review of videotapes, is that the burrows and animal tracks that are so ubiquitous elsewhere on the Gulf of Mexico slope (Gallaway et al. 1988) are abruptly replaced by bacterial mats (**MacDonald et al. 1989**). What we seem to be seeing are discrete communities with high densities of heterotrophic fauna, but with little apparent influence on populations a few meters away.

9.5.2 Possible Carbon Flows

The export of chemosynthetically-fixed carbon from a hydrocarbon seep can take several different forms. First, the tissue of any of the chemotrophs can be consumed by far-ranging predators and scavengers and then transferred to the surrounding areas as living biomass and fecal detritus. Second, the tissue of seep heterotrophs can be consumed by the same far-ranging predators/scavengers and similarly exported. Third, fecal material from the seep heterotrophs and possibly from the seep mussels can be exported as detritus. Fourth, biogenic structures such as mussel periostricum and tubeworm tubes can be exported as detritus. Lastly, chemosynthetic and heterotrophic bacteria can be advected by currents as detritus.

It is critical to note that each of the biologically mediated fluxes has a cost associated with it that reduces the availability of carbon to the adjacent communities. Biomass export of both bacterial and metazoan tissue has a very high metabolic cost that would result in as much as a 90% reduction across a single trophic link. Since some refractory carbon has been stripped from the fecal detritus, there will be an associated 10-15% loss of carbon along that pathway, with the residual being largely refractory. The physical advection of seep generated detritus has no similar costs, but this detritus has been subject to cycling within the seep community, and may be of very low nutrient value.

9.5.3 Carbon Flow as Modeled

Carbon flux from a seep can be modeled in a variety of ways, but the most conservative is to treat it as a simple flow across a two dimensional surface radiating in a circle from a point source. More complex seep geometries can be simulated as multiple points. In spite of the fact that we established that there is a loss of carbon associated with export from a seep, the magnitude and spatial aspect of this loss term is unknown. Therefore, the flow is treated as being conservative, with carbon being neither added or lost, once the flow leaves the point source. A crude but informative approximation of the basic pattern of flow into the surrounding environment can be determined without adding a carbon loss/distance traversed term.

If carbon is flowing without loss or gain from a point source in a plane, then the availability of that carbon to organisms on the bottom will be determined by the position of every single point on the plane relative to the source. As the flow moves away from the source, it covers an increasingly larger circle. Being conservative, the total flow of carbon across any concentric circumference must be equal. Thus, if there is a flow of 1 g C day^{-1} crossing

the outer edge of a seep community of circumference=1, then the total flow across an outlying circle of circumference=10 must also equal 1 g C day^{-1}. However, every point on that larger circle experiences 1/10th the flow experienced at the edge of the seep. In terms of simple geometry, the flux of seep carbon experienced by any point on the bottom outside the seep is a function of the flux at the source times the inverse of the radial distance to the source (circumference=2 p radius). This simple simulation makes the point that while carbon may be flowing from a seep into the surrounding food web, this flow need not manifest itself as an easily detected biomass gradient leading from the background into the seep. Therefore, the apparent lack of any such biomass gradient does not disprove the hypothesis that there is carbon export.

9.5.4 Ecological Implications and Prediction of the Carbon Flow Model

An important caveat to the model of possible flux across an area is that mobile species can forage for sparse food supplies. Thus, a forager, unless preempted by a competitor, can utilize the average flux over a large area. In the simple geometry of the seeps, competitive preemption can be best avoided by feeding as close to the source as possible. For those deep-sea species that can avoid the toxic effects of seep chemistry, foraging within the seep is the optimal means of exploiting that carbon source. Again the matter of metabolic cost arises. If there is a large consumer population foraging within the seep, the carbon available for export is greatly reduced. Certainly, large foragers, such as decapod crabs, moving out of a seep must be exporting both their own biomass and fecal material. However, when moving into a seep to forage, they import biomass and fecal detritus from the surrounding region if they have foraged on the surrounding seafloor.

It is to be expected that seeps export carbon to the surrounding seafloor. This export is both caused by, and favors population increase by mobile forages in the predatory, scavenger, and surface browsing forms. In conjunction with an increase in these forms of animals, there should be a resulting impact upon prey and competing species in the area surrounding the seeps. In effect, those animals which can forage within the seep, receive a substantial carbon subsidy via the chemosynthetic pathway, yet still prey upon and compete with the rest of the typical deep-sea fauna.

9.6 Evidence of Seep Heterotrophic Links from Stable Carbon Isotope Ratios

9.6.1 Introduction

This section will examine the data on $^{13}C/^{12}C$ ratios in seep-associated heterotrophs to gain additional insight into actual trophic links. In the preceding section, a simple geometric model demonstrated that if carbon flux from a seep site moves radially outward, any given point in the surrounding environment will experience that flux as an inverse of the distance to the seep. As a result, we should expect minimal contribution from a seep to populations of small sessile organisms in the surrounding environment. However, animals which can forage over larger areas and benefit from the integrated flux should be able to exploit seep carbon. And, since there is a loss of useful carbon associated with export, it is easily appreciated that the greatest flux of carbon from seep chemotrophs to heterotrophs will take place very near and within the actual seep site.

Isotopic ratios have been used extensively to determine the carbon sources for chemosynthetic organisms (**Fisher 1990**), but have received far less use in efforts to determine the nature of trophic links to heterotrophic seep and nearby organisms. VanDover and Fry (1989) is the only study which has taken

a more comprehensive look at the relationship between seep/vent chemoautotrophs and associated heterotrophs.

9.6.2 Methods

One hundred and fifty seven heterotrophic specimens from the deep Gulf of Mexico have been analyzed for $\delta^{13}C$. Specimens far removed from seeps were collected by trawling along depth transects in the eastern, central, and western Gulf (Gallaway and Pequegnat 1988). Trawling also produced specimens in areas containing seeps. Specimens directly in and close to seeps were collected by submersible manipulator arm. Most samples were collected by the *Johnson-Sea Link*, with additional material by *Alvin*, *Pisces II*, and *NR-1*. Specimens for analysis were selected during initial sorting of faunal samples and frozen in liquid nitrogen until analyses. Prior to analysis, tissues were freeze dried. Carbon isotope analysis was by standard sealed-tube combustion (Macko et al. 1987; LeFeuvre and Jones 1988). The $\delta^{13}C$ of purified CO_2 was analyzed with a Finnigan MAT 251 isotope ratio mass spectrometer and reported relative to the PDB standard.

9.6.3 Results

Background fauna values were determined from 16 specimens of typical deep-sea fauna collected by trawling, and have a very narrow range of values from -19.6‰ to -17.0‰ (Figure 9.1A). This was fully consistent with a photosynthetically derived detritus (phytodetritus). The organisms were fish, larger crustacea, and echinoderms. The 89 heterotrophs collected by trawling in seep areas showed a much wider range of values from -30.0‰ to -15.5‰ (Figure 9.1B) with a pronounced mode at approximately -17.0‰. Especially noteworthy is the indication of a second mode at approximately -28‰. The 52

specimens collected directly by submersible at seep sites show a dramatically greater range of -48.3‰ to 15.7‰ (Figure 9.1C), including much more light carbon.

For closer examination, the species collected by submersible were divided into four simple functional groups. Category one consisted of browsing heterotrophs found directly with the seep community. This group included the common *Munidopsis* sp. crab, the browsing gastropods (primarily the most common *Bathyneretis judithii*), and large polychaetes. Group two consisted of larger, more mobile forms that probably prey upon seep fauna, but which are also seen on the adjacent sea floor. This second group included the large decapod crabs, the giant isopod *Bathynomus*, and starfish. The third group all appear to be suspension feeders including the bivalve *Acesta*, gorgonians, brisingid starfish, and sponges. These are common adjacent to seeps on exposed rock. The fourth and final group serves largely for comparison. It is a mixture of deep-reef taxa collected from a authigenic carbonate mount more than 5 kilometers from the nearest active seep.

As seen in Figure 9.2, browsing heterotrophs living intimately within the seeps are the most depleted in ^{13}C. Except for the lowest values in this category, these animals show carbon intermediate between methanotrophic mussels (-46‰ to -44‰) and phytodetritus. Their values fall within the range of seep tubeworms. The mobile predators show somewhat heavier values, and a similar pattern is found for the suspension feeders.

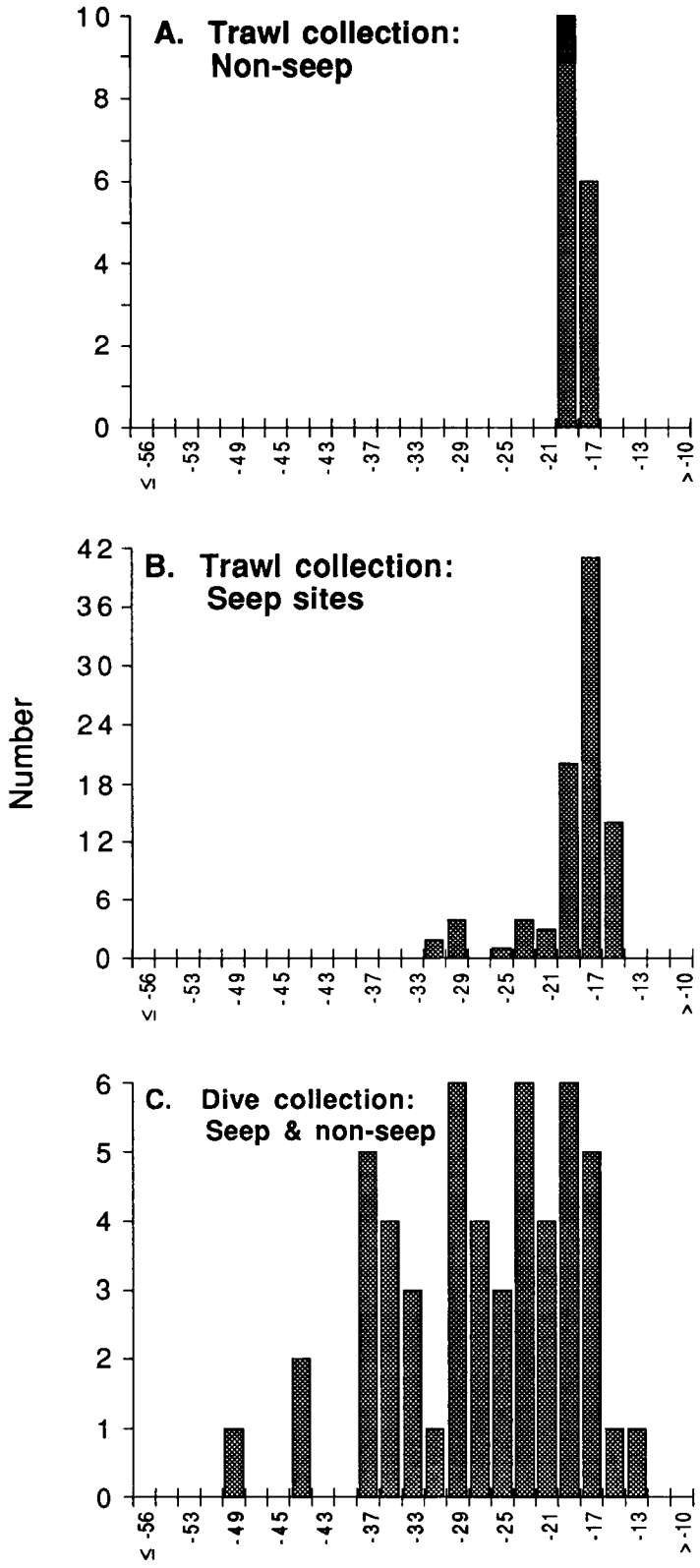

Figure 9.1 A - Deep-sea heterotrophs trawled from three transects in the eastern, central and western Gulf of Mexico (from Gallaway and Pequegnat 1988) produce a very narrow range of $\delta^{13}C$ values consistent with phytoplankton detritus origins. B - Presence of seep carbon along with the phytoplankton detritus source is evident in $\delta^{13}C$ values of heterotrophs trawled from areas containing seeps. C - The mixture of seep carbon and phytoplankton detritus is quite evident by the wide spread of $\delta^{13}C$ values in animals collected by submersible at and near seep sites.

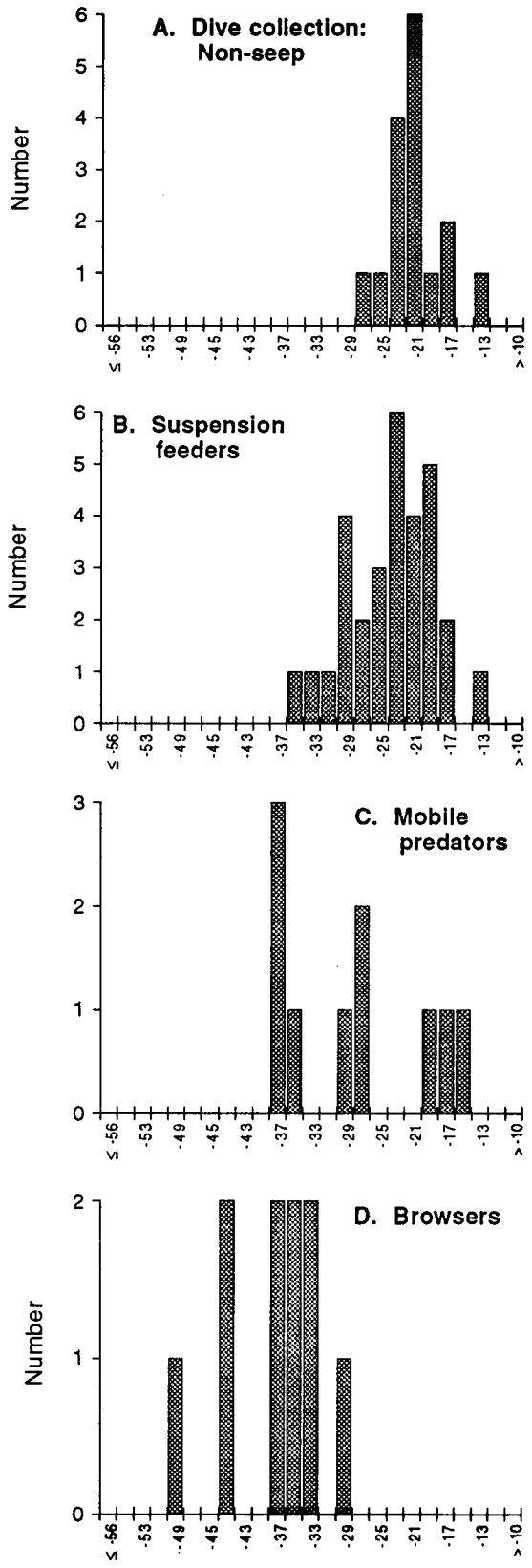

Figure 9.2 Division of submarine-collected heterotrophic fauna into (A) non-seep areas, (B) seep-suspension-feeders, (C) seep mobile predators, and (D) seep browsers shows a progressive increase in proportion of seep carbon when $\delta^{13}C$ values are compared.

9.6.4 Discussion

Our primary finding is that the seep associated heterotrophs show a range of $\delta^{13}C$ values which are progressively heavier when ordered by the degree of association with the chemosynthetic fauna. In the following discussion we will identify those carbon pools which might contribute to this isotopic shift and explore two primary alternatives. The first alternative is that this shift simply reflects a high level of incorporation of photosynthetic detritus into seep heterotroph tissues. The second alternative is that this shift can be explained without requiring a significant input of photosynthetic detritus. Resolution of these alternative is quite important with respect to understanding seep function.

Typical deep-sea organisms are exposed to two pools of carbon which can be assimilated into tissue. The most important is photosynthetically derived detrital carbon which has a $\delta^{13}C$ range of -15‰ to -22‰ (Black and Bender 1976; Gearing et al. 1984). Less important, but still problematic, is the dissolved inorganic carbon pool of seawater of 0‰ to +1‰. This latter carbon source can become fixed in tissues via anapleuortic carboxylation and magnified by the foodchain if there is exchange between the metabolic pool of CO_2 in the tissues and the surrounding DIC (Rau et al. 1986). As a result, typical deep-sea heterotrophs do show $\delta^{13}C$ values similar to their detritus food source or slightly heavier (Brooks et al. 1987, VanDover and Fry 1989). If photosynthetic detritus is extensively recycled by heterotrophs and mixed with ambient DIC through carboxylation, its isotopic content can shift through time. However, since there is a great metabolic cost, expressed as conversion of organic carbon to DIC, at each recycling, the incorporation of old carbon into tissue should be much less than the incorporation of new detritus.

The pools of carbon available for heterotrophic consumption at seep sites are more numerous and potentially complicating than in a typical deep-sea environment. In addition to photosynthetic detritus and seawater DIC, there are hydrocarbons, hydrocarbon derived tissues/detritus, multiple sources of DIC seeping from the geological structure, and tissues derived from the DIC complex. In spite of the complexity of pools, a few groups of carbon available to seep heterotrophs and adjacent fauna should be quite distinct. The tissue of chemosynthetic metazoans and detritus derived from those tissues should be the primary food source. Methanotrophic hydrocarbon seep mussel tissue $\delta^{13}C$ reflects the available methane source, -60‰ for biogenic methane and -50‰ for thermogenic methane (Kennicutt et al. in press). The source methane at the Gulf of Mexico hydrocarbon seeps has a value of -67.1‰ to -39.3‰ and the methanotrophic mussels -67.1‰ to -37.5‰ (Kennicutt et al. in press). Vestimentiferan worm tissue has a highly variable $\delta^{13}C$ composition which makes it impossible to identify this pool strictly on the basis of $\delta^{13}C$. Due to some combination of size-habitat variation in isotopic fractionation (Fisher 1990) and exposure to multiple dissolved inorganic carbon (DIC) sources (Kennicutt et al. in press), the seep tubeworms had $\delta^{13}C$ values ranging from -58‰ (indistinguishable from seep mussel tissue) to -18‰ (indistinguishable from photosynthetic detritus).

The data suggests that heterotrophic animals collected directly within seep communities have isotopic values which suggest a significant consumption of carbon from a source that is heavier than the average values found in chemotrophs. If we seek to explain this progressive inclusion of heavy carbon in terms of diet, there are three relatively simple explanations.

(1) We have failed to analyze the actual food source. Seep heterotrophs might feed predominantly on a chemosynthetically derived biomass, possibly bacteria which we have not measured, and not the conspicuous large metazoans.

(2) There is selective feeding. Seep heterotrophs might feed preferentially upon chemotrophic metazoans that are isotopically heavy relative to the mean of the local population.

(3) There is significant consumption and assimilation of photosynthetic detritus even by animals in the seep

Of these three major possibilities, the first, that we have not found the actual food source, is impossible to refute totally. Based on all evidence to date, it seems unlikely that seeps contain a reservoir of chemosynthetically derived carbon or carbon heterotrophically derived from hydrocarbons which mimics the isotopically heavier photosynthetic detritus. Similarly, the possibility of selective feeding is difficult to eliminate. **Fisher** (1990) has shown that smaller seep tubeworms are isotopically heavier than the larger. While a similar phenomena has not been found in the mussels, the possibility exists that a preferred prey or preferred microhabitat could produce prey tissues heavier than the population means of the submersible sampled specimens.

The attractiveness of the third possibility, that there is a significant consumption of photosynthetic detritus even within a seep community, lies in its simplicity and its agreement with predictions about the effect of seep carbon flux upon nearby heterotrophic populations. As seen in our results for all three sites, there is an apparent increase in heavy carbon as we look at animals found on the edge of a seep as opposed to those living directly upon mussels to tubeworms. The increase in heavy carbon is so great that animals within a few

meters of a seep may be indistinguishable from photosynthetic detritus. This is in complete agreement with the spatial model simulation which predicts little seep carbon flux beyond the edge of a seep community.

The most intriguing aspect of the apparent inclusion of photosynthetic detritus into the tissues of seep dwellers such as the dominant gastropod *Bathyneretes* is the matter of how this photosynthetic carbon came to be there. If it simply entered the seep as vertical flux, then seep carbon production may be on the same order of magnitude as the rate of detrital carbon influx. Alternately, the photosynthetic carbon eaten by seep heterotrophs may have been foraged from or advected from an area, much larger than the seep, thereby magnifying the influx of photosynthetic carbon to the seep many times over its simple vertical flux rate to the seafloor.

The complexity of carbon sources available to a heterotroph within a seep site makes it impossible to identify a primary food source based solely upon carbon isotopes, because there are multiple endpoints. However, photosynthetic detritus is at the heavier end, and most hydrocarbons or chemosynthetic carbons are at the lighter end. The troublesome exception is found in the vent tube worms, which span a great range and encompass the values of detrital carbon. There was, however, a bias in our sampling against obtaining animals associated with tube worms, due to the fact that submersible fauna samples have been primarily drawn from mussel beds.

When our own results from the hydrocarbon seeps are compared to the results of Van Dover and Fry (1989), a striking difference is found. When 27 $\delta^{13}C$ determinations for seep-associated heterotrophs from a site in the east and a site in the west Pacific were examined, the tissues were found to be appreciably heavier in ^{13}C (-22‰ to -11‰) than the tissues of the dominant molluscan chemoautotroph (-37‰ to -28‰). Unlike the case in the

hydrocarbon seep where the heterotrophs fell between the range of mussel tissue and background photosynthetic detritus, in the two vent systems of VanDover and Fry, the heterotrophs were even heavier than photodetritus and typical detritus-based organisms (-17‰ to -21‰)!

Since the vent-associated heterotrophs lay beyond the range of photosynthetic detritus, Van Dover and Fry (1989) were forced to explain their observations by calling for a significant undetected carbon pool with a $\delta^{13}C$ of approximately -11 ‰. At one of their sites, Hanging Gardens, vestimentiferan worms did have tissue values as low as -10‰ and could have provided the missing pool. However, since tubeworms were absent at the other site, and since some of the species analyzed would have no means of preying on tubeworms, this possibility was rejected. Chemoautotrophic bacteria were invoked as the possible source of the heavy carbon pool, although it was admitted that there was no additional evidence pointing to the existence of such a bacterial population.

The major question which emerges from a comparison of the vent heterotrophs and the hydrocarbon seep is what is the underlying cause of the higher $\delta^{13}C$ values in the heterotrophs? If the vent species are feeding from a chemosynthetic pool that is even heavier than photosynthetic detritus, is such a pool possible in the hydrocarbon seeps? On first examination the answer might be no, since the hydrocarbon seep forms are never lighter than normal detritus. However, a comparison of the vestimentiferan values at seeps and vents leaves the missing pool question open. At vents, vestimentiferans span a great range of values which can be heavier than normal detritus. At hydrocarbon seeps, this same taxon also shows a range of $\delta^{13}C$ values, but even the heaviest values fall within detritus range. Therefore, if there is a free-living sulfur-based bacterial population which experiences isotope fractionation

similar to that found in the vestimentiferans, its $\delta^{13}C$ at a hydrocarbon seep might be -10‰ lighter than at vent sites. If this mysterious carbon pool at -20‰ exists, it may be confused with the normal detritus pool, and will render carbon alone unsuitable for trophic investigation at the hydrocarbon seeps.

An interesting bit of speculation about the relative heavy shift in heterotrophs from the vents versus the hydrocarbon seeps concerns the relative importance of the normal detrital pool. The seeps reported in this study differ in many regards from the vents of VanDover and Fry, especially in depth. The two vent sites lay at approximately 2600 m, while the three seep sites are all nearly 2000 m shallower. While we do not have carbon influx information for any of these areas, for the sake of argument, we can assume that Suess' (1980) exponential decrease in influx as a function of depth holds true for both areas. Therefore, the flux of normal detritus experienced by the hydrocarbon seeps may be at least one order of magnitude greater than that experienced by the vents. If an unmeasured, chemosynthetic, isotopically heavy carbon pool exists, then it will manifest itself far greater at depths where normal carbon influx is less.

10.0 Conceptual Models for Seep Communities

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10.1. A Management-Relevant Model of Seep Ecosystem Function

Hydrocarbon seeps are both scientifically challenging and fascinating. However, beyond their basic scientific value, we are faced with the question of environmental impact upon a fauna that is uniquely associated with exploitable hydrocarbon reserves. For the most part, contemporary deep-sea ecology provides us with little guidance on how to proceed. Therefore, as we design studies of this system, we must employ a conceptual framework that is scientifically valid while focusing on the key applied questions.

The basic scientific model is based upon a complex geochemical process which brings reduced substrates to the seafloor. Methane, hydrogen sulfide, brine and liquid hydrocarbons migrate upward through a network of deep and shallow faults created by salt tectonics. This network serves as a separating device in the sense that the chemistry of seepage can vary in a complex manner over the region of seepage. The mechanism of separation remains unknown, but it may involve mass differences for brines and liquid hydrocarbons, pressure dependent phase shifts for methane, and chemical reaction along the migration path for methane and hydrogen sulfide. The connectivity of the network of faults may also be dynamic. Slumping, erosion, salt movement and dissolution, and authigenic carbonate precipitation all must act as agents opening and closing the paths of migration and shifting the balances of the separating process.

According to our view of seepage given above, the seafloor in a seep region can be envisioned as a complex chemical field over which conditions vary between ambient sea water and localized diffusion/advection gradients

of seeping chemicals. In those places where the chemical gradients are right and other environmental requirements are met, and there has been enough time, chemosynthetic organisms have colonized the bottom. These colonists provide both habitat and food for additional fauna, so heterotrophic fauna soon colonize the chemosynthetic aggregates and a functional community takes shape.

There are actually very few different types of chemosynthetic animals (tube worms, mussels, clams and bacteria). This low diversity suggests that it takes considerable specialization to exploit seeps and vents. Similarly, the diversity of the associated heterotrophs may be considered low in comparison to the normal deep-sea fauna. Again, considerable specialization may be required by the heterotrophic component.

At this level of understanding, our model becomes incomplete and consists of alternatives. The proposed project is designed to allow an informed choice of alternatives as the model is refined and applied to management questions.

Question 1. Are Seep Communities Robust or Fragile?

Robust Community- Since these communities are specialized to colonize and utilize changing seeps associated with petroleum, then they may be uniquely immune from impact by hydrocarbons and production activity. We predict that a robust community should rapidly recolonize disturbed area. We also predict that space and time differences in community structure and composition should be reflective of a well defined succession in a robust community.

Fragile Community- Alternately, it can be argued that these communities occupy a very narrow niche associated with different phases of

petroleum degradation and seepage. Being so very highly specialized, the narrow range of environmental conditions which support these communities might be very easily altered by drilling and production activities. Indeed, production may result in a loss of the very energy source required by these communities. We predict that a fragile community may not easily re-establish after disturbance. We also predict that space and time differences in fragile community structure and composition will reflect stochastic events, and no succession can be identified.

Question 2. **Are Seep Communities Isolated from or Connected to the Surrounding Ecosystems?**

The deep sea is a low-standing stock ecosystem due to its remoteness from surface productivity. In a region of extensive seeps, seep energy and carbon may be a significant contribution to the overall seafloor fauna. Alternately, seeps may be a relatively closed system with virtually all seep carbon degradation taking place within the community with negligible flow into the adjacent areas.

Question 3. **What is the Functional Size of a Seep Area from the Management Perspective?**

This is something of an extension in scale of the robust versus fragile question. Should seep regions be managed as large preserves with rules and regulations applied across large areas? Or, is it sufficient to restrict use of the seafloor in very limited sections?

To answer these three questions, our final model must describe the sequence and time progression of community development and change (Robust or Fragile?). Our model must describe the links to the surrounding systems (Isolated or Connected). And, our model must describe the extent

to which patterns over large areas appear to be interrelated (Management Size). The propose study shall produce this model.

10.2. Element Cycling Due to Hydrocarbon Seepage

Figure 10.1 summarizes various chemical transformations thought to be important to chemosynthetic communities. Most of the methane utilized by methanotrophic mussels probably seeps upwards from large subsurface deposits. Methane in the subsurface is formed from the decomposition of more complex organic molecules, mediated either by a complex bacterial food web or by the combined effects of time, temperature, and pressure. Near-surface gas hydrates may temporarily store large quantities of methane that can be used by the mussel communities as the hydrates decompose. Some methane resulting from bacterial processes in the upper sediment layers may also be available for chemosynthesis. Alternate fates for upwards-migrating methane include seepage to the overlying water column and bacterial consumption in the sediments followed by authigenic carbonate formation.

Similarly, the H_2S required for the sulfur-based symbioses may have both subsurface and near-surface (i.e., bacterial sulfate reduction) sources. The carbon source may be either overlying seawater or the pore water. Pore water DIC is composed of that buried at the time of sediment deposition, that added from bacterial decomposition of sedimentary organic matter, oil, or gas and any DIC seeping up from the subsurface. The processes of authigenic carbonate formation and/or dissolution may also influence the DIC pool available to the sulfur-based symbioses.

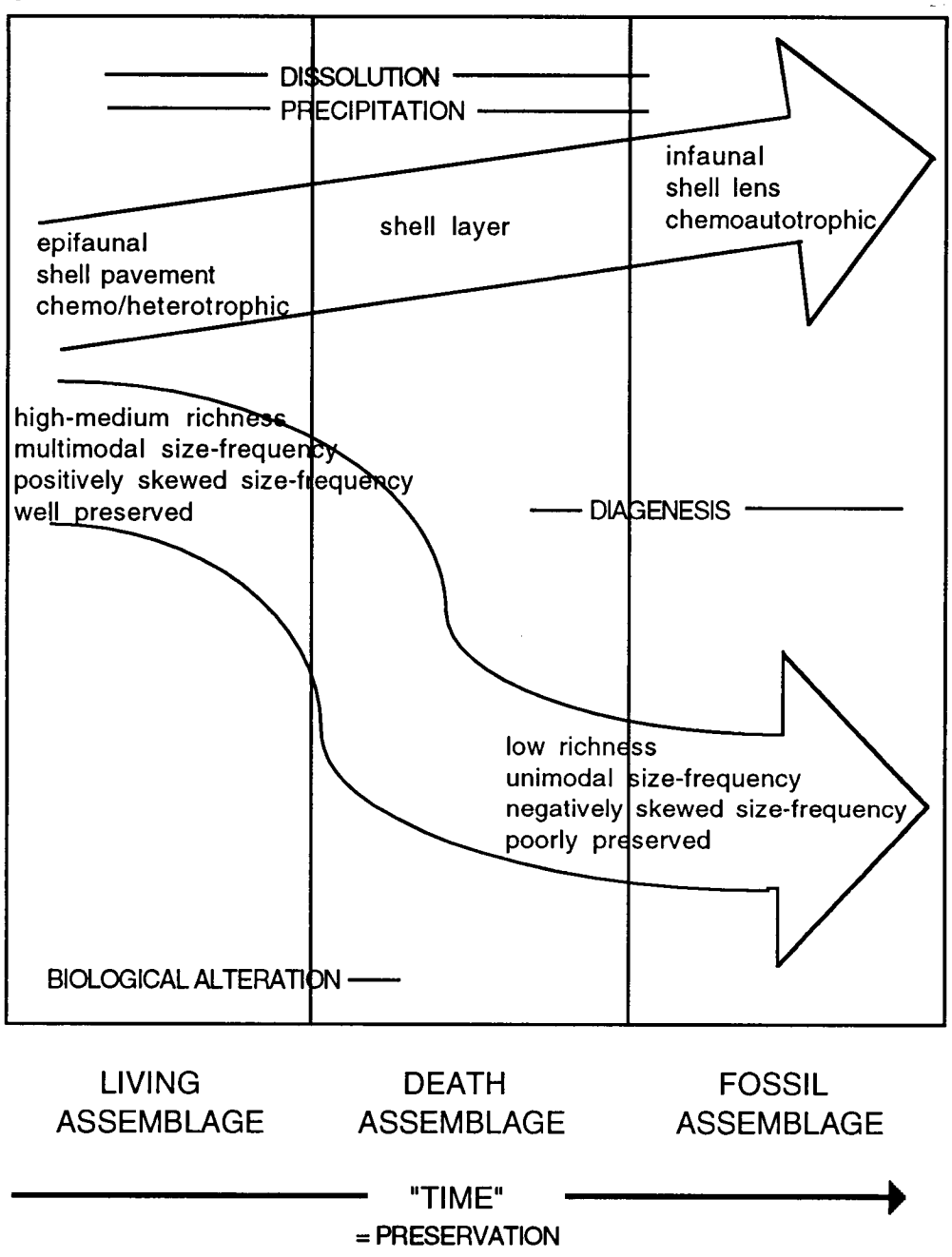

Figure 10.1 Conceptual representation of the ecological/paleoecological transformation of a cold seep assemblage. The Living Assemblage and Death Assemblage information is based on Louisiana slop assemblages. The Fossil Assemblage information is based on Campanian (Upper Cretaceous) assemblages in the Pierre Shale of central Colorado. Large arrows indicate the information shift between assemblage types. "Time," shown at the base of the figure, is a rough proxy for preservation and is not truly linear. For example, the time between a living assemblage and a death assemblage may be as short as a few years but the time between a death assemblage and a fossil assemblage may be on the order of thousands of years.

As for carbon and sulfur, multiple nitrogen sources are potentially available to chemosynthetic communities. N_2 gas for possible fixation is available from seawater and, in some cases, from subsurface gas reservoirs. Nitrate is available from the water column in fairly high concentrations (~25 mM). Millimolar concentrations of ammonia in near-surface (upper 20 cm) pore water in some locations impacted by brine seepage.

10.3. Stable Isotopes as Tracers of Food Chains and Community Structure

The partitioning of stable isotopes between organic (living and detrital) and inorganic matter was critical to recognizing and understanding the chemosynthetic nature of seep and vent communities. The utility and limitations of stable isotopes as tracers of biologically active elements in ecosystems have been reviewed elsewhere (Galimov, 1985; Fry and Sherr, 1984 and other references cited therein). The stable isotopic composition of tissues derived from chemosynthetic fixation is the product of a complex series of chemical and biological processes. The stable carbon isotopic compositions of thiotrophic bivalves tend to be location-dependent and not species-dependent. The range and value of the stable isotopic compositions of thiotrophic bivalves suggest that seawater DIC is the primary source of carbon for chemosynthesis and that these bivalves possess a similar sulfide oxidation metabolism. The variability in tissue $\delta^{13}C$ values is most likely due to subtle variations in the source of DIC. Methanotrophic mussels exhibit $\delta^{13}C$ values primarily controlled by the source of the methane, with little or no kinetic fractionation associated with methanotrophy. Vestimentiferan carbon isotopic compositions reflect an interplay between carbon limitation and source. Vent vestimentiferan utilize seawater (or vent) DIC but $\delta^{13}C$ values appear to be most influenced by carbon limitation due to anatomy and

size. Seep vestimentiferan $\delta^{13}C$ values are reflective of the variable isotopic composition of pore-water DIC, a major source of carbon.

How the nitrogen requirements of vent and seep organisms are met is not clear. Nitrogen (N_2) fixation is consistent with observed isotopic compositions, but the presence of the extant biochemical systems has not been demonstrated. Circumstantial evidence suggests that a variety of nitrogen sources (N_2, NH_4^+ PON, and NO_3^-) are utilized by vent and seep organisms and that nitrogen requirements are not linked to the type of symbiont. The role of sulfur is key to vent and seep environment since thiotrophy is a major chemosynthetic activity. However, as with nitrogen, the sources of sulfur appear to be highly variable though intimately linked with free living and/or symbiont bacterial activity. Mixotrophy appears to be prevalent with sulfide being a major sulfur source, but variable dependence on sulfate, thiosulfate, and organic sulfur also occurs. The ^{34}S depleted values associated with vestimentiferans suggests an obligatory dependence on endosymbionts that derive their energy from hydrogen sulfide.

The cycling of elements within vent and seep communities can be complex owing to the multiplicity of available substrates that exhibit variable isotopic compositions. The primary fractionation of isotopes occurs during the assimilatory reduction of inorganic substrates and this fractionation is characteristic of a given enzymatic system. However, fractionation can be affected by the rate of metabolism, the temperature, the carbon source, and the degree of substrate depletion. The wide range of chemical environments at seeps can provide the nutrients necessary to support a variety of metabolic strategies. By themselves, stable isotopic compositions do not definitively demonstrate the sources of these substrates, but they do

provide useful insight into the diverse metabolic strategies represented by chemosynthetic seep and vent communities.

10.4. Creation of Chemosynthetic Habitats

Exploration to date has revealed thriving biological communities on the continental slope south of Texas, Louisiana, and Alabama in a bathymetric range of 350 to 2200 m at sites where seepage of oil and gas produces seismic wipe-out zones. Utilization of reduced compounds associated with seeping hydrocarbons has been observed directly (in the case of methane-based chemosynthesis) or has been inferred from the stable carbon isotope ratios of animal tissue. Four types of communities can be recognized based on the predominant species of chemosynthetic fauna: 1) tube worms clusters or "bushes," with isolated seep mussel beds, 2) linear mussel beds at brine seeps, 3) beds of two species of surface-living vesicomyid clams, and 4) extensive areas having a scatter of dead lucinid clam shells on the surface sediments and a living population burrowed beneath the surface. Community development appears to be determined by whether seepage provides methane or sulfide compounds to the benthos and by the geological characteristics of the surface sediments. Seep mussels occur in discrete beds defined by the flowage patterns of methane-saturated brine at the sediment/seawater interface. Results from Brine Pool *NR-1* suggest that a re-examination of high-resolution seismic data from the slope would reveal additional brine pools and that these may support seep mussel communities. Tube worm clusters are most commonly associated with hummocky topography in the crests of grabens or half grabens. Clam communities tend to be dispersed over larger areas than tube worm or

mussel communities and may be either infaunal (Lucinidae and Thyasiraidae) or epibenthic (Vesicomyidae).

These examples, based on the work of the PIs, demonstrate that hydrocarbon seep communities differ sharply from hydrothermal vent communities in that the chemosynthetic species at seeps form distinctive community types. We hypothesize that the process of community formation is due generally to greater spatial and temporal homogeneity in hydrocarbon seepage than in hydrothermal venting. Community formation might occur via two different route within this context.

Hypothesis 1. Community types form due to distinctly different seepage processes (e.g., gas seepage versus oil seepage), which are spatially separated to a greater or lesser degree at different sites.

Hypothesis 2. Community types form successionally due to a uniform seepage process that changes gradually over time at different sites.

Testing these hypotheses will be carried out by examining the spatial correlation of community types with geological formations and by examining the geological record of seepage preserved in seep biofacies.

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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.