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Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico hydrocarbon vents

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Abstract The analogy between desert oasis and deep-sea chemosynthetic community arose from the biomass contrast between vents and the relatively depauperate background benthic fauna. Fully developed, the analogy helps pose questions about interactions with the background fauna with respect to resources, colonization, and persistence. The chemosynthetic sites of the Gulf of Mexico provide an opportunity to consider possible interactions between vent and nonvent fauna over a 3000-m depth range. It is postulated that deep chemosynthetic communities require the operation of geochemical transporting and concentrating processes to overcome low levels of in situ methane and sulfide production. Clathrate reservoirs may serve these functions. A few chemosynthetic species at the Gulf of Mexico upper slope sites are related to shallow-water sulfide species, but it can be speculated that the dominant chemosynthetic fauna may have originated in a wide spread deep sulfide biome of the Cretaceous. Generic endemism of consumers is low in Gulf of Mexico sites, suggesting a high level of colonization from the surrounding benthos. Chemosynthetic communities may avoid excessive colonization by predators in spite of the apparent food limitation of the surrounding benthos due to toxicity or an evolutionary mechanism selecting against specialized predators. The abundance of large predators is related to the composition of the surrounding benthos and is high at the Gulf of Mexico upper slope sites. Exclusion of chemosyntheic communities from shallower depths may be due to excessive predation by generalists.

Introduction

All assemblages of chemosynthetic organisms clustered within and supported by sulfide and methane venting from the cold or hydrothermally active sea floor are characterized by biomass so much greater than that of the surrounding deep-sea benthos that they are commonly called oases (Laubier 1993). This desert oasis analogy can be more than a convenient literary device when it is used to stress that oasis community structure and function are dependent upon the surrounding deserts. Fully developed, the analogy provides a starting point from which to ask about the interactions between spatially restricted vent communities supported by great in situ chemosynthesis and the vast surrounding benthic community supported by an influx of photosynthetic detritus. The deep sea is not an ecologically monotonous desert, but is characterized by bathymetric and latitudinal gradients of biomass, species diversity, and species composition (Carney et al. 1983; Gage and Tyler 1991; Grassle and Maciolek 1991; Rex et al. 1993). From the hot vent communities of the Pacific ocean ridges to the upper slope hydrocarbon vents of the Gulf of Mexico, vent communities experience a considerable range of background conditions in terms of type, variety, and abundance of species encountered. Since the background fauna shows distinct bathymetric and geographic patterns, parallel bathymetric and geographic patterns of chemosynthetic community structure should exist if the background fauna exerts an influence. It is the purpose of this study to compare the community structure of the Gulf of Mexico vent communities found over a 3000-m depth range and to employ the oasis analogy to answer or refine questions about vent–background interactions.

Three aspects of oasis ecology are especially pertinent when developing questions about deep-sea vent communities: (1) resource—there is a localized abundance of an otherwise rare resource; (2) colonists—there is a fauna dependent upon that resource capable of colonizing the site, and (3) persistence—there is some form of protective isolation preventing excessive exploitation of the oasis residents by consumers. Desert oases exist because local subsurface hydrology, rather than regional climate, produces the necessary concentrations of the resource water. Most resident oasis producers are colonists from wetter regions capable of broad dispersion. These oasis producers accu-

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mulate a high biomass standing stock because the surrounding desert lacks a sufficiently large or appropriately adapted herbivore fauna to overly exploit production.

When the oasis properties of resource, colonization, and persistence are considered, chemosynthetic communities are oasislike with respect to a localized resource. Methane and sulfide can be shown to be as out of place in the deep sea as water in the desert. The situation with colonization and persistence are much less well defined. Resident chemosynthetic species patterns at vents are not oasislike since few vent species can be considered colonists from larger remote regions of sulfide and methane abundance. Colonization by heterotrophic species from the surrounding benthos does take place, but only a small fraction of background species is involved. Persistence of high levels of chemosynthetic biomass is superficially oasislike, but this cannot be due to simple oasislike isolation from consumers. The normal deep-sea environment is food poor, and the bounty of chemosynthetic communities should be aggressively exploited.

Gulf of Mexico hydrocarbon vent systems

The Gulf of Mexico is a marginal basin of the Atlantic Ocean with a maximum depth of approximately 3600 m. The deep fauna of the gulf is closely related to that of the Atlantic, but some degree of uniqueness is to be expected due to geographic isolation by sills at approximately 1650 m in the straights of Yucatan and 800 m at the straights of Florida. The sources of methane and hydrogen sulfide for chemosynthesis reflect a complex geological history. Methane and sulfide advection on the continental slope are primarily related to methane discharge from thermogenic petroleum reservoirs perforated by salt domes with secondary venting of biogenic compounds in sediment pore water (Brooks et al. 1987). Venting at the base of the West Florida escarpment has been attributed to brine discharge from the Florida carbonate platform (Paull et al. 1985). Gulf of Mexico chemosynthetic communities have been documented in three general regions: (1) the upper continental slope (400–1000 m off Louisiana); (2) the Alaminos Canyon site on the lower continental slope (2200 m off Louisiana), and (3) the West Florida Escarpment site (3500 m). More exploration of the lower bathyal and abyssal regions may add to the list of documented sites.

The continental slope off Louisiana has been most extensively studied since 1985 using the Johnson Sea-Links I and II. General descriptions of the fauna have been given by MacDonald et al. (1990). Hard substrate chemosynthetic fauna consists of mussel mats and tube worm clumps. Typical of the group, the mussel mats are formed by attachment to carbonate rock or other mussel shells by byssal fibers. Worm tubes tend to be anchored to rock with the small distal ends interwined with the open framework of carbonate. As many as three new and separate species of chemosynthetic mussel have been reported, but a single *Bathymodiolus*-like species predominates. Two species of tube worm have been collected, *Lamellibranchia* sp. and *Escarpia* sp. All of these species are currently undergoing systematic study. Soft sediments adjacent to and interspersed among exposed vent carbonates are either devoid of obvious chemosynthetic fauna or populated by infauna. These infauna include metazoans harboring chemosynthetic symbionts: a pogonophora *Galathealinum* sp. and bivalve mollusks: the vesicomyid clams *Calyptogena ponderosa* and *Vesicomya cordata* and lucinids *Lucinoma atlantis*, *Lucinoma* sp., and *Thyasira oleophila* (Calender et al. 1990).

There is an abundant heterotrophic fauna exploiting both the food source and habitat of the upper slope vents. This fauna is numerically dominated by gastropod Mollusca (summarized in Warén and Bouchet 1993). In approximate sequence of dominance the most common species present are *Bathynerita naticoidea*, *Provana sculpta*, *Cataegis meroglypta* and, *Buccinum canetae*. Less common gastropods include *Cancellaria rosewateri*, *Cantrainia macleani*, *Gymnobela extensa*, *Hyalorisia galea*, *Gaza fisheri*, a chiton *Ischnochiton* sp., and a rarely collected limpet. All except *G. fisheri* have been collected directly from mussel mats. A limid bivalve, *Acesta bullisi* is found attached by byssal fibers to the rocks or enclosing the anterior opening of tube worms.

Crustacea living in close association with mussel mat and tube worm bushes are a common galathetiid, *Munidopisis* sp., a much rarer galatheiid *Eumunida picta*, and the shrimp *Alvinocaris stactophila*. An atelecylidiid crab and a magid crab, *Nibilia antilocarpa*, are found in mussel mats. Larger mobile crustacea are conspicuous in vent areas but less commonly in direct contact with vent communities. These include the decapods *Paralomis cubensis*, *Rochina crassa*, *Chaceon quinquedens*, *Chaceon fenneri*, and the giant isopod *Bathynomus giganteus*. Echinoderms are represented by a common predatory starfish, *Sclerasterias tanneri*, which feeds on mussels and forms less directly linked to the vent community, a filter feeding starfish of the family Brisingidae and two urchins *Echinus contorta* and *E. affinis*. More than 10 species of fish have been sighted during dives, but only four seem to have a close affinity for the vent communities: *Eptatretus* sp. (hagfish), *Synaphobranchus* (cutthroat eels), *Urophycis cirratus* (hake), *Hoplostethus* sp., and *Chaunax suttkusi*.

Alaminos Canyon lies near the base of the Sigsbee Escarpment in the northwestern Gulf of Mexico at a water depth of 2200 m. The canyon is associated with lateral movement of salt. The tubeworms of the Alaminos canyon site appear to be conspecific with those of the shallower Louisiana slope sites, *Lamellibrachia barhami* and *Escarpia laminata*, although size and tube morphology differences necessitate additional taxonomic investigation. Two species of chemosynthetic mussels were collected. One appears to be the same found at the shallower sites, while the other appears to be a unique species. The gastropod fauna is markedly reduced. Archaeogastropod limpets predominate to the virtual exclusion of all other forms. A single crushed specimen of a buccinid, differing slightly from *Buccinum canetae*, was collected. Bresiliid shrimp of the same genus but different species than at the upper slope sites, *Alvinocaris muricola* (Williams 1988), are common. Large (1 cm) amphipods are abundant. Galatheiid crabs were observed, but only a single specimen recovered. It was not the *Munidoposis* sp. found shallower. Large decapod crustaceans appear to be absent, and only a single fish was collected, an eel pout. Authigenic carbonate rocks in the vents had scattered specimens of a verrusamorph barnacle and small ophiuroids.

The principal description of the fauna of the West Florida Escarpment has been given by Hecker (1985). Comparison with other Gulf of Mexico sites is limited by a lack of detailed taxonomic information. However, it appears that the gastropod fauna is distinct from the upper slope and the Alaminos canyon site. Chemosynthetic fauna consists of a *Bathymodiolus*-like mussel and tubeworms attributed to *Escarpia laminata.* In soft sediments, a species of *Calyptogena* is present. The associated heterotrophs are dominated by gastropods. An undescribed trochid is very abundant, and a neogastropod and limpet reported. Crustacea collected consist of a species of *Munidopsis* and the shrimp *Alvinocaris muricola.* Unidentified ophiuroids and a vermiform holothuroid identified from photographs as *Chiridota* sp. were common.

Oasislike aspects of vent communities

Factor 1—availability of resources

One of the most peculiar aspects of the faunally distinct vent communities is that they are restricted to depths greater than 400 m, while the required methane and sulfide are more characteristic of shallow depths on the continental shelf. If a strictly chemical cause for this peculiar mismatch between resource and faunal distribution exists, then the supply of methane and sulfide below 400 m must be distinct in some way. This chemical/geological possibility can be explored by examining the marine methane and sulfide system in general and then considering two aspects of that system that are distinctive at greater depths. The first of these deep characteristics, extremely low levels of in situ methane and sulfide generation, would seem to make the existence of the chemosynthetic communities unlikely. However, the second, existence of stable solid gas hydrates, may provide a mechanism which compensates for low in situ generation via transport and concentration.

Biogenically produced methane and sulfide are common chemical constituents of marine sediments. Their biological generation and consumption are linked processes in the complex system of carbon diagenesis by bacteria in sediments (Fig. 1). The overall types and sequences of reactions are considered to be ubiquitous throughout the ocean, but geographic and bathymetric variation, primarily in carbon influx to the bottom, produces regionally different rates, gradients, and distinctive biogeochemical environments (Berner 1980; Janhke et al. 1982). Photosynthetic carbon biomass sinks as detritus to the sea floor and is constantly under attack by consumer organisms. The biological demand is so great that oxidizing agents are totally depleted when input is high relative to burial. If carbon influx and burial are great enough to exhaust the supply of oxygen, then the resident biota must be capable of anaerobic metabolism. In the anaerobic zone, seawater-derived sulfate serves as an electron acceptor and produces sulfides. Deeper in the sediment where sulfate has been exhausted, methane is produced by several pathways collectively termed methanogenesis. The production of sulfides and methane is characteristic of shallow marine sediments where detritus input is high enough to assure anoxic conditions, and inshore sea water nitrate levels are low enough to limit competition from denitrifying bacteria. There sulfide production can account for approximately half of the carbon oxidized, and as much as 30% of the carbon fluxing out of the system can be in the form of methane (Martens and Val Klump 1984). By comparison, sulfide production in the deep ocean sediments is meager. Out on the abyssal plain with meager detritus input through thousands of meters of water, 95% of carbon is oxidized aerobically, and only a small fraction of that buried in the sediments is converted to methane (Bender and Heggie 1984).

Methane and sulfide can be present in sediments below the level of biogenic production due to burial of biogenic material by sediment accretion or by thermogenic production. Thermogenic production of methane and sulfide is restricted to depths on the geothermal gradient where temperatures range from 144° to 220°C (Hunt 1979). This point may be reached more than 1–2 km into the sediment column or very near the sea floor in the high heat flow environment at ocean spreading centers. At continental margins, such as in the Gulf of Mexico, buried organic detritus and sulfate yield thermocatalytic sulfide, methane, and other hydrocarbons that vent to the ocean floor. Remote from the coastal productivity, the thin sediment cover at spreading centers contains little organic detritus for conversion to methane, but seawater sulfate is still abundant and available for conversion to sulfide.

The existence of chemosynthetic communities in deep water with little in situ biogenic methane and sulfide generation and no near-surface thermogenic sources is strong evidence that migration and concentration processes are active. Migration of interstitial fluids carrying methane and sulfide has been most fully modeled for the Oregon subduction zone (Henry and Wang 1991) where it is associated with chemosynthetic fauna (Kulm et al. 1986; Kulm and Suess 1990). Migration alone, however, only moves the low interstitial biogenic and thermogenic concentrations from one place within the sediment layer to the sea floor.

The existence of solid-phase gas hydrates of methane and water, which are stable at the pressure and temperature conditions below 400–500 m of water depth in the Gulf of Mexico, may be that unique aspect of deep ocean methane and sulfide chemistry that allows for chemosynthetic community development. The equilibrium model for clathrate formation at continental margins proposed by Hyndman and Davis (1992) is especially appealing because it allows clathrates to be formed by low concentrations of

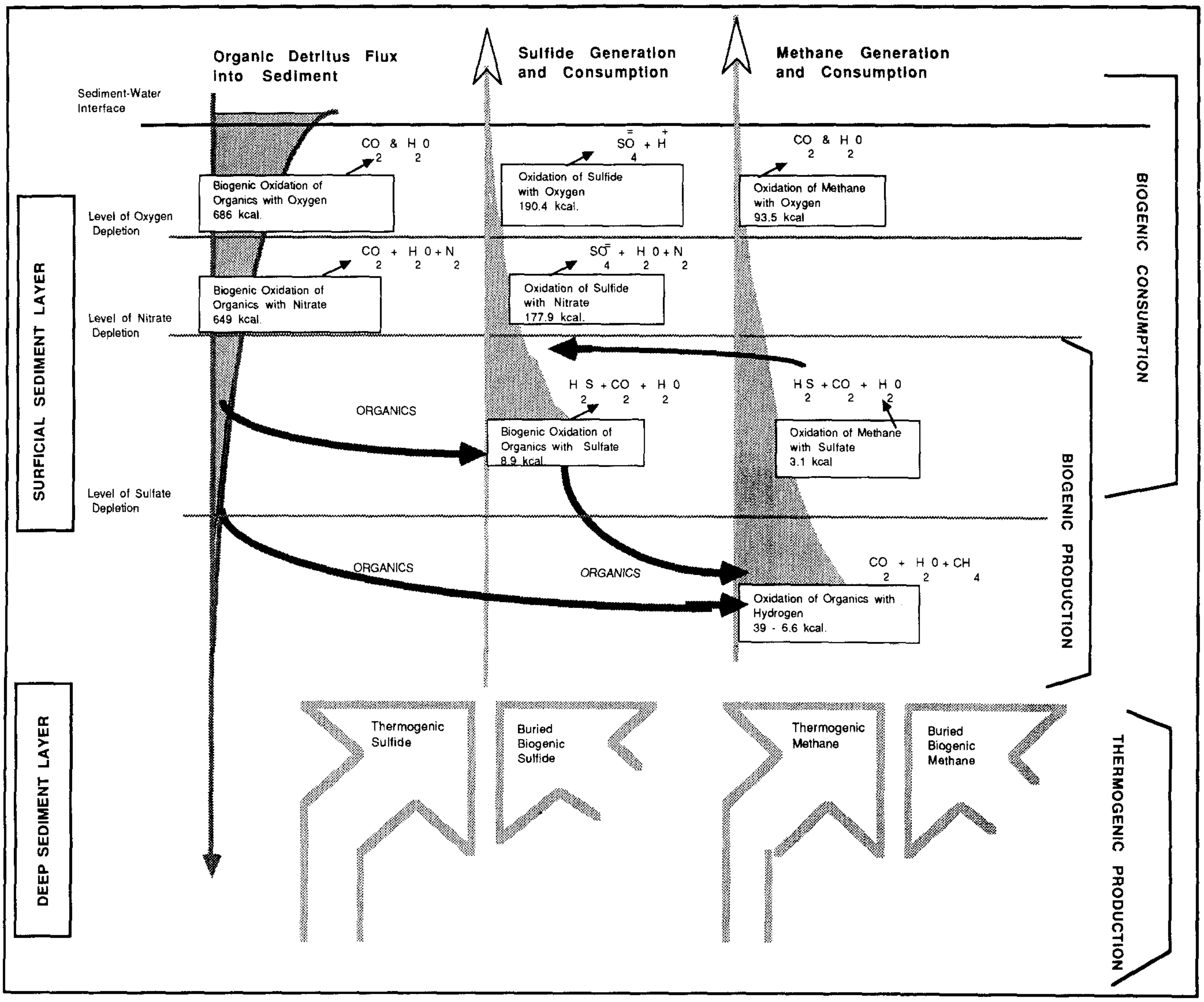

Fig. 1 Sea-floor methane and sulfide production and consumption system. Biogenic oxidation of methane (methanotrophy) and sulfide (thiotrophy) depends upon biogenic or thermogenic generation of these energy-rich compounds. Biogenic formation takes place during oxidation of organics buried below the depletion level of more efficient electron acceptors diffusing from seawater. Methane and sulfide generation are linked. Sulfide production depletes sulfate and allows for methanogenesis to proceed. Methane, from any source, can be oxidized by sulfate causing cogeneration of sulfide. This representation omits fermentation and metal electron acceptors for simplicity. Calorimetric values are based upon Fenchel and Blackburn (1979)

dissolved methane rather than from supersaturated solutions. Thus, the meager deep-sea biogenic methane in upward migrating pore fluids "freezes" into concentrated clathrates at the lower boundary of a pressure/temperature stability zone for the solid phase. Methane dissolving from the layer of clathrate at local points of instability could vent through the sea floor at high concentrations. Once in contact with seawater sulfate and a bacterial flora, sulfide would be generated by methane oxidation-sulfate reduction and added to the concentrated upward flow.

The postulation that clathrate formation and dissolution may be the concentrating mechanism necessary for vent community existence can be tested in part by compareing the distribution of vent communities in presentday space and over geological time with the observed and theoretical distribution of venting clathrates. The dependence of clathrate stability upon temperature and pressure provides the means of testing, since temperature at depth varies both geographically and temporally. We know that there are exposed clathrates that are near the upper temperature/pressure level of stability at the Bush Hill chemosynthetic community site at a depth of 400 m. Except for possible sighting of dead tubeworms and mussel shells in inaccessible cervaces at 290 m depth (Roberts et al. 1990), no communities have been found shallower. It is to be expected that cold vent communities dependent upon biogenic methane should not be found shallower than approximately 400 m depth in temperate seas, but may shallow with temperature to 300 m in polar regions. The most dramatic temperature fluctuation in the deep ocean, the 10–12°C temperature drop in the mid-Miocene (Shackleton 1982) should have resulted in a shallowing of the zone of clathrate stability to present depths. Previously, in the warmer ocean, clathrates would not have been stable above 1000 m and vent communities similarly restricted in distribution. The fossil Italian Miocene vent chemosynthetic communities reported by Taviani (1994) might serve as the critical test site. If a paleotemperature and paleodepth can be determined reliably and prove incompatible with clathrate formation, then the clathrate dependency hypothesis may be rejected.

Factor 2—Two types of colonists

In order to effectively consider the community structure aspects of the oasis analogy and to infer relationships between chemosynthetic communities and the surrounding benthos, it is necessary to partition the component species into a chemosynthetic (producer) and heterotrophic (consumer) group. Theoretically, this is warranted since the distributions and origins of the producer group must be linked to the geochemistry of sulfide and methane emissions, while the consumers may not. The chemosynthetic species at all Gulf of Mexico sites are vestimentiferan tube worms, bathymodiolid mussels, and vesicomyid clams (abbreviated as the VBV association) typical of all deep venting systems, along with lucinid clams and pogonophoran worms. A preliminary assessment of these VBV chemotrophs is that there is a high degree of similarity among the well-studied upper slope site and the less-known deep Alaminos Canyon and West Florida Escarpment sites. This is true at the level of genus and may prove true at the level of species. A comparison of associated heterotrophs produces contrary results; there is a much lower degree of similarity among sites at generic and specific levels.

Chemosynthetic fauna patterns

The desert oasis analogy poses two questions about chemosynthetic species that can be examined taxonomically or geochemically. First are the presentday deep-sea chemosynthetic species colonists from shallow sulfide- and methane-rich environments? Second, are presentday deep-sea chemosynthetic species relicts of a time when vast areas of the deep-sea floor were sulfide- and methane-rich? A definitive answer to both questions must await results of phylogenetic studies. However, drawing upon data from the Gulf of Mexico systems and recent reviews of ecology (Lutz and Kennish 1993; Tunnicliffe 1991) and physiology (Fisher 1990) of vent systems, it is possible to refine the questions and speculate about answers.

Is there a link to the shallow thiobios?

Having established in the discussion of methane and sulfide availability that in situ generation is greater in shallow water than in deep, it is appropriate to question whether such an anaerobic shallow environment was the point of origin for deep-water chemotrophs. More than a decade before the discovery of deep-sea chemosynthetic communities, Fenchel and Reidl (1970) proposed that a "sulfide biome" existed in anoxic muds as an extensive shallow benthic environment. Subsequently termed the "thiobios" (Boaden 1975), this system was seen as containing truly anaerobic metazoans in the meiofauna size class exploiting chemotrophic bacterial productivity. The proposal that a metabolically and evolutionarily distinct thiobios exists has met with rejection and modified acceptance. In spite of debates about the thiobios, parallels between this shallow system and the deep chemosynthetic systems obviously exist. Like the vents, the shallow anaerobic environment affords opportunities for energy exploitation. Both contain an aerobic metazoan fauna metabolically adapted to anoxia, harboring chemosynthetic bacteria, or otherwise trophically exploiting the aerobic–anoxic gradient.

The upper slope Gulf of Mexico systems do show a limited phylogenetic affinity to the shallow sulfide biome, in lucinid clams and possibly the pogonophoran worms, but not in the members of the VBV association. The Lucinacea superfamily of burrowing bivalve mollusks constitutes the most obvious link between shallow anaerobic sediments and the upper slope vents of the Gulf of Mexico. Morphologically, they are unique in that contact with oxygenated water is maintained via a burrow excavated by a specialized foot, rather than by an elongated siphon (McAllester 1966). Prior to the discovery of chemosynthetic communities, it was recognized that some Lucinacea had reduced feeding/digestive structures, and with discovery of symbionts in hot vent *Bathymodiolus* mussels and vesicomyid clams, the existence of bacterial symbionts in the *Lucina* was quickly confirmed (Reid and Brand 1986). Fisher (1990) reports 18 cases of symbiotic chemosynthesis dependent upon sulfides.

Evolutionary affinities between the VBV association and the shallow thiobios are much more problematic. There is a phylogenetic relationship between vestimentiferan tube worms and pogonophorans (Jones 1985; Southward 1988), but it has only a tenuous link to shallow water. Pogonophorans are tube-dwelling vermiform metazoans without digestive structures, possessing some chemosynthetic symbioses (Schmaljohann et al. 1990), and numbering about 100 species. Often considered a deep-sea phylum, they can be common at shelf depths (Ivanov 1991). It is conceivable that the pogonophoran–vestimentifera lineage originated from thiobiotic annelid worms. Although some burrowing mussels exist, epifaunal forms are not considered part of the thibios. Chemosynthetic mussels belong in a species complex collectively assigned to the genus *Bathymodiolus* Kenk, which has a sulfur- or methane-based symbiosis but retains a functional filtration system, feeding palps, gut, and digestive enzyme system (Page et al. 1990). One possible origin for chemosynthesis in mussels may lie in the geochemistry of fecal and pseudofecal deposits of "mussel mud" trapped under large mats. If these biogenic deposits produce sufficient sulfide to require biochemical defenses, such defenses may have produced the precursor to chemosynthetic forms. Vesycomid clams are burrowing infauna known primarily from vent and nonvent bathyal depths. They are sulfide-utilizing forms found both in soft sediments and nestled among rock fields at some hot vent sites. In the Gulf of Mexico they are restricted to the sediments. They may comprise a deep-water analog of the luncinids and show no obvious systematic link with shallow sulfide systems.

A Cretaceous deep-sea thiobios?

Due to the initial discovery of the VBV association along submarine ridges and the dependence of chemosynthetic fauna on the thermogenesis at such hydrothermal systems, it is natural to suspect that there may be some link between the history of sea-floor spreading and the evolutionary origin of the component taxa (Tunnicliffe 1992; Lutz and Kennish 1993). Yet, when cold vent systems are considered, it becomes obvious that the origins of the VBV association may just as likely have been influenced by secular changes in biogenic methane and sulfide production. The Cretaceous change in deep-sea carbon diagenesis is the most likely candidate to have had a major evolutionary impact. During the Cretaceous there were times, marked by deep-sea shale deposition (Arthur and Schlanger 1979), when methane- and sulfide-rich sediments were once as typical of the deep sea as they are of inshore waters in the contemporary ocean. Indeed, the flux rates of the carbon cycle and the associated methane and sulfide systems were so exceptionally great that 60% of the source rocks for large hydrocarbon reservoirs (Thierstein 1983) were lain down at that time. In spite of a carbon influx great enough to have produced localized sediment anoxia, the deep Cretaceous ocean may have had large areas of sea floor with sufficient oxygen in the water to support aerobic metazoan life (Pendersen and Calvert 1990). That environment would be chemically similar to modern nearshore sediments but would have the darkness and other physical conditions of the abyss. Taxa from a shallower Cretaceous thiobios may have colonized this deep methane and sulfide system. Upon the disappearance of deep anoxic sediments, only that handful of taxa forming the VBV association remained, capable of dispersing to, exploiting, and competing for relatively ephemeral areas of venting.

Origin of heterotrophic associates

Chemosynthetic communities afford both a complex biogenic habitat and a rich food source exploited by heterotrophic species. Like hydrothermal systems (Tunnicliffe 1991, 1992), it is to be expected of cold vents that the associated heterotrophic species reflect mixed sources. Therefore, a primary question is the extent to which cold vent species are vagrants, colonists, or endemics. Some may be truly endemic to chemosynthetic communities. Some may be colonists from the surrounding benthos that have established resident vent populations, while others are vagrants making temporary use of the vent site but not developing resident populations. The tremendous difficulty in actually assigning species to these classifications lies in a lack of knowledge of the species composition of the surrounding benthos. That environment can be very species rich and inhabited by such an abundance of rare species that a complete inventory is virtually impossible. Apparent vent endemics may just be colonists or vagrants whose more widely scattered kin simply have not made it into a museum collection.

Fortunately, the Gulf of Mexico has been extensively sampled and the bathymetric distribution of the larger normal (megafauna) benthos is well documented, making it possible to determine for many species which are colonists and which vagrants. Determination of endemics remains uncertain, but the bathymetric range affords an indirect method of assessment. Should apparent endemics show a bathymetric species turnover akin to the background fauna, then their endemism may be suspect.

A comparison of heterotrophic forms is presented in Table 1. The comparison is limited to larger organisms (greater than 0.5 cm) and the more common groups. The species listed were primarily collected by manipulator grabs from the Johnson SeaLink submersible and retained on a 500-µm sieve. Large crabs and fishes were recorded in video or still camers images. The faunal tables in Pequegnat (1983) were used to determine the composition of the background fauna and to establish the preliminary classifications of vent fauna. Species that have never been recorded from outside a vent are classified as endemics. Colonists have been recorded outside vents, but obtain high population levels only within vents. Vagrants are those species that are found outside vents and do not appear to achieve unusually high population levels within. An "unresolved" classification is applied to all species in which the taxonomic position is uncertain at this time. The list of dominant associated species is restricted to mollusks, crustaceans, echinoderms, and fishes. Other taxa occurred too rarely to be of use in the comparisons.

Several observations are readily apparent. First, the upper slope and Alaminos canyon heterotrophic fauna are very dissimilar. If faunal elements are shared, their relative abundance at the two sites must be so dramatically different as to have escaped detection at this level of sampling. Second, endemism is low at the species level: five endemics out of 39 species. At the level of genus, only the two coiled gastropods *Bathynerita naticoidea* and *Provanna sculpta*, possibly the Alaminos canyon limpet, and the shrimp *Alvinocaris stactophila* and *A. muricola* are endemic to chemosynthetic systems. Third, the colonists and vagrants reflect only one tenth of the surrounding species richness: 25 species in vents at the upper slope sites versus 251 species in the background fauna. Fourth, the distinction between vagrant and colonist seems to be related to size and mobility. Colonists tend to be smaller, slower, and subdominant in the background. Vagrants tend to be larger, highly mobile, and may include dominant elements from the background.

The low endemism and changing heterotrophic fauna of sites at 400–1000 m, and 2200 m are generally consistent

Table 1 Species composition of chemosynthetic system heterotrophs at Gulf of Mexico sites compared to the surrounding benthos based on Pequegnat (1983)

Upper slope seep sites	Residence type	Upper slope background 400–1000 m depth	Alaminos Canyon sites	Residence type	Lower slope background 2000–3000 m depth
Gastropods		102 reported species; dominant species include *Gemmula periscelida*, *Leucosyrinx tenoceras*, *Gymnobela ipara*	Gastropods		32 reported species; dominant species include *Leucosyrix tenoceras*, *Gymnobela bairdi*
Bathynertia naticoidea	Endemic		limpets	Endemic	
Provanna scuplta	Endemic		*Buccinum* sp.	Unresolved	
Cataegis meroglypta	Colonist				
Buccinum canetae	Colonist				
Ischnochiton sp.	Colonist				
Cantrainia macleani	Colonist				
Gymnobela extensa	Colonist				
Cancellaria rosewateri	Vagrant				
Hyalorisia galea	Vagrant				
Crustacea			Crustacea		
Galatheiid crabs		18 reported species; dominants include *Munidopsa sigsbei*, *Munida valida*, *Munida longipes*	Galatheiid crabs		6 reported species; dominants include *Munidopsis bermudezi*
Munidopsis sp.	Endemic		*Munidopsis* sp.	Unresolved	
Eumunida picta	Vagrant				
Other crabs		33 reported species; dominants include *Parapagurus* sp., *Bathyplax typhla*, *Chaceon quinquedens*	Other crabs		1 reported species; *Chaceon quinquedens*
Paralomis cubensis	Vagrant		None		
Rochina crassa	Vagrant				
Chaceon quinquedens	Vagrant				
Chaceon fenneri	Vagrant				
Nibilia antilocarpa	Vagrant				
Atelecylidae	Unresolved				
Large isopods		1 reported species: *Bathynomus giganteus*	Large isopods		1 reported species; *Bathynomus giganteus*
Bathynomus giganteus	Vagrant		None		
Shrimplike forms		35 reported species; dominants include *Systellapsis pellucida*, *Pasiphaea merriami*, *Glyphocrangon alispina*, *Glyphocrangon nobilis*, *Penaeopsis serrata*, *Parapenaeus longirostris*, *Benthesicymus bartletti*	Shrimplike forms		13 reported species; dominants include *Nematocarcinus acanthitelsonis*, *Benthesicymus cereus*, *Hemipenaues carpenteri*
Alvinocaris stactophilus	Endemic		*Alvinocaris muricola*	Endemic	
Echinoderms			Echinoderms		
Asteroidea		25 reported species; *Plutonaster intermedius*, *Nymphaster arenatus*, *Astropecten americanus*	Asteroidea		21 reported species; dominants include *Dytaster insignis*, *Ampheraster alaminos*, *Benthopecten simplex*
Sclerasterias tanneri	Colonist		None		
Ophiuroidea		26 reported species; *Ophiernus adspersum*, *Bathypectinura heros*	Ophiuroidea		13 reported species; dominants include *Ophiomusium planum*, *Bathyplectinura hero*
None			Unidentitied A	Unresolved	
			Unidentified B	Unresolved	
Fishes		111 reported species; dominants include *Gadomus longifilus*, *Dibranchus atlanticus*, *Nezumia aequalis*, *Dicrolene intronigra*, *Synaphobranchus* sp.	Fishes		21 reported species; dominants include *Dicrolene intronigra*, *Coryphaenoides macrocephalus*
Eptatretus sp.	Vagrant		Liparid	Unresolved	
Synaphobranchus sp.	Vagrant				
Urophycis cirratus	Vagrant				
Hoplostethus sp.	Vagrant				
Chaunax suttkusi	Vagrant				

with colonization from a vertically changing deep-sea fauna. However, the factors that limit successful colonization to such a small percent of the background species remain obscure. Purely random colonization can be ruled out, since all of the more than 10 locations sampled at the upper slope site had the same suite of colonizing species (Carney unpublished data). Perhaps the species of this suite are the only ones of all the background fauna capable of persisting in the unique chemical environment of the vent sites. Alternatively, they may predominate locally due to contagious colonization in which the very high population densities of initial successful colonists assure colonization of nearby sites.

The observed distribution of apparent endemics is puzzling. The possible absence of the gastropods *Bathynerites* and *Provanna* from the deeper Alaminos Canyon site could suggest that these abundant forms are actually colonist from the vertically zoned background fauna. However, other evidence points to true endemism. A nerite similar to *Bathynerites* appears to have had a long association with vents, being found in Miocene deposits in Italy (Taviani 1994), and has been reported from no other sites. Other species of the genus *Provanna* are associated with vent sites in the Pacific (Warén and Bouchet 1993).

Since the high species richness of the deep sea provides many potential colonists, it seems likely that colonization must influence the species composition of vent assemblage to some degree. The extent of this influence should be apparent in zoogeographic patterns of species composition. If the heterotrophic component of vent communities is dominated by colonists, then such fauna should parallel deep-sea community changes bathymetrically, geographically, and in the fossil record. If, however, endemism is predominant, then the heterotrophic component should not parallel the surrounding benthos and may share with the taxa of the VBV chemosynthetic assemblage common origins and convergent adaptations for colonization and persistence. It is even tempting to suggest that heterotrophic and chemotrophic endemics may have linked life histories. A possible example of this has been found in the upper slope sites. Juvenile *Bathymodiolus* are common on shells of *Bathynerities* and *Provanna* and the cuticles of *Munidopsis* sp. Tube worms have been found growing from the shells of *Bathynerities*. Such epizootic associations provide the sessile members of the VCV a postsettlement means of dispersion that may be important in maintaining viable populations as the chemical gradients of vents undergo local shifts.

The low endemism of the Gulf of Mexico sites, especially the upper slope, and the degree of colonization by fauna from the surrounding sea floor are markedly different from those found for hydrothermal systems. As noted by Tunnicliffe (1991, 1992), as much as 95% of hydrothermal vent fauna is endemic, with little taxonomic similarity to continental margin systems except the members of the VBV assemblage. On the basis of the results presented herein, it can be suggested that the hydrothermal versus cold vent faunal distinction may be due to the geographic and bathymetric gradients of the surrounding benthos. Vent systems associated with continental margin geology exist within the biodiversity framework of the continental slope. High overall species richness at the base of the slope and increasing large predator diversity on the upper slope afford many opportunities for colonization and exploitation of vent systems. Displacement by colonists and extermination by predators may eliminate many hydrothermal vent endemics from continental slope communities. Hydrothermal systems, due to their association with spreading centers, tend to be remote from continental margins. While overall surrounding species richness may be high, low overall abundance and substrate dissimilarity may limit opportunities for colonization. Large predators, especially decapod crustaceans are absent, thus reducing predation.

Factor 3—persistence: surviving heterotrophic exploitation

Persistence in geological and ecological time of any spatially restricted producer requires some type of protection from overexploitation by predators. As a potential rich food source in the food-limited, species-rich, deep-sea environment, it is expected that vent chemosynthetic producers have been subjected to considerable predation pressure through time. Thus, a major question is what protects all vent communities from being driven to local and global extinction by predators from the surrounding sea floor? Oddly, rather than the anticipated high predation, there is some very preliminary suggestion that few large predators are associated with chemosynthetic systems. Only a few examples of obvious predation have been noted for hydrothermal systems (Tunnicliffe and Jensen 1987; Tunnicliffe 1991, 1992) and deeper continental margin cold vent systems (Juniper and Sibuet 1987; Jollivet et al. 1990).

In the Gulf of Mexico, the presence of large predators at vent sites may be bathymetrically determined, reflecting the overall decrease in these forms with depth (Table 1). The upper slope sites are populated by large predatory colonists and vagrants. These include the gastropod *Buccinum canetae*, the starfish *Sclerasterias* sp., and all the large crabs and fishes. The deeper Alaminos Canyon site and the West Florida Escarpment (Hecker 1985) are relatively free from large predators, consistent with low numbers of such species in the surrounding benthos.

The Gulf of Mexico sites provide trials of two broad categories of answers to the question of why vent communities survive what should be intense predatory pressure. The first, proposed as an explanation for hydrothermal vent fauna persistence (Tunnicliffe 1991, 1992), is environmental toxicity or defensive biological toxicity. The second, proposed herein, is that few specific predators have evolved, since the isolation and limited foraging options of the deeper sites make specialized predation upon vent communities evolutionarily disadvantageous.

Avoidance of predation by environmental or defensive toxicity is an attractive suggestion for three reasons. First, it is chemically feasible; hydrogen sulfide and brine, often associated with venting, are toxic and may kill some invading species or cause general avoidance of vent areas by all but a few species. Second, it is consistent with faunal observations; only a small percent of background species are found associated with vent communities. Third, it is amenable to testing by surveying consumer fauna for detoxification mechanisms and tolerance levels and by surveying the prey fauna for toxicity.

It is in the deeper environment that the lack of predation is most puzzling. Even if toxic, these systems are a rich food source and are successfully exploited by some background fauna and endemic grazers. Background predators may be rare, but why are endemic predators seemingly lacking? It is proposed that the answer lies in some combination of a relative lack of candidates for evolutionary specialization and a selective disadvantage to such a specialization. The deep sea has relatively few species suitable to become predators on shelled fauna living on hard substrate. There is little shelled background epifauna prey in the abyss, and thus no predators adapted to exploit them. Specialized predation is disadvantageous due to the very low background biomass. Being small and widely dispersed, individual sites are at great risk of local extinction if colonized by efficient predators. Once local extinction of the prey had occurred, a specialized predator's own survival would hinge upon its ability to locate another unexploited site prior to starvation. The low background biomass of deep areas greatly limits the option for prey switching between chemosynthetic sites. Obviously, as background biomass increases with depth, predators can survive by switching to background prey species while moving between vents. This is only possible high up on the continental slope, where detritus input maintains a relatively high background biomass. If the biomass of deep vents is an evolutionarily risky predatory food option, successful strategies for colonists and endemics may be limited to scavenging, consumption of by-products from the producers (tubes, mucus, etc.), and other nonlethal cropping of biomass.

The observation that vagrant predators are more common at shallower vent sites in the Gulf of Mexico and the speculation that deeper predators are absent due to limited opportunity for prey switching lead to a question of upper distribution limits. It has been proposed above that the distribution of vent fauna is related to the zone of clathrate stability in ocean regions of limited in situ methane and sulfide generation. However, this does not explain their apparent absence in shallower regions, where ample reduced substrates also exist. A biological explanation can be proposed based upon the points previously made. Above the shelf break, detritus input to the bottom is high, in situ photosynthesis becomes increasingly prevalent, and shelled epifauna are common. At this depth and shallower, predators are both abundant and amply supplied with alternate prey items. Quite simply, members of the VBV association do not survive exploitation at these depths. Slightly deeper, production exceeds predatory loss, and deeper yet, predation is minimal.

Conclusions

This exploration of the oasis analogy has provided no definite answers to questions about why chemosynthetic communities are so distinctive in the deep sea when methane and sulfide genesis is more typical of shallow water, about the evolutionary origins of the vent producers and consumers, or about how physical and biological processes may shape chemosynthetic communities and restrict their distribution. Rather, explanations have been put forward that allow development of testable hypotheses. Central to the success of testing the ideas put forward is recognition that chemosynthetic communities must interact with the surrounding benthic fauna. The composition of hydrothermal communities and possibly their local survival may be determined by where on the faunal gradients of potential exploiters geological processes make methane and sulfide available.

Existence of chemosynthetic communities in the deep sea requires high methane and/or sulfide production. At spreading centers, thermogenic production in close proximity to the sea floor from precursors in seawater may be sufficient. Elsewhere, low in situ biogenic rates and deep burial of thermogenic conversion of sediment precursors require concentration and migration to the sufficient. If clathrate formation is a primary mechanism for concentration, then community distribution must coincide with the zone of clathrate stability through time and over space. Polar basin communities (if they exist) and Miocene fossil sites afford a test of this hypothesis.

The higher taxa of the vesicomyid–*Bathymodiolus–Vestimentifera* assemblage are ubiquitous to all deep chemosynthetic systems—spreading center and continental margin. Therefore, their evolutionary history may have been influenced both by changing biogenic and thermogenic oceanic processes. Although evolutionary reconstruction is a problematic approach, examination of suites of traits might lead to a conclusion as to whether the continental margin species or the spreading center species are more likely to be ancestral. Determining the origins of the associated heterotrophs is very much hindered by a sampling asymmetry. On the continental margins, the background fauna may be relatively well studied, while at the more remote and deeper spreading centers, it is the chemosynthetic fauna that is better known. This bias assures lower apparent endemism in the former case and higher in the latter. Greatly increased deep-ocean sampling with an emphasis on seeking background specimens of nominal endemics is the only means of improving this situation.

The persistence of high levels of chemosynthetic biomass in an environment often considered food limited and populated by a fauna thought to be foraging specialists is especially puzzling. Toxicity may afford some protection but be insufficient under the extreme predatory pressure of upper slope decapod crabs, shell crushing fishes, and predatory starfishes. Conceivably this could be tested by toxicity screening, predator exclusion, and transplanting.

However, the need for comparable geochemistry among experimental treatments may make all but screening impractical. The prevalence of nonpredatory grazers and nonlethal predators at the deepest sites may reflect an evolutionary disadvantage to specialized lethal predation, but such an evolutionary explanation is probably not testable.

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