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VOLCANOES, FLUIDS, AND LIFE AT MID-OCEAN RIDGE SPREADING CENTERS

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■ **Abstract** The recent recognition of a potentially vast, unexplored hot microbial biosphere associated with active volcanism along the global mid-ocean ridge network has fundamentally shifted concepts of how planets and life coevolve. Many processes intrinsic to the dynamics of the spreading center volcanic system provide partial or complete nutritional fluxes that support diverse microbial communities that thrive under extreme conditions on and beneath the seafloor. Mantle melting, volcanism, and fluid-rock reactions transport volatiles from the asthenosphere to the hydrosphere. Volcanic heat and exothermic reactions drive circulation of nutrient-rich fluids from which chemosynthetic organisms gain metabolic energy. In turn, many of these organisms symbiotically support macrofaunal communities that populate the vents. Long-term seafloor observatories will allow exploration of linkages between volcanism and this newly discovered biosphere. Such approaches may provide essential new information about our own planet while providing critically needed insights into how we can explore other planets for life.

INTRODUCTION

The past decade has seen a fundamental change in our ideas concerning the linkages among geological, chemical, and biological processes at mid-ocean ridge spreading centers. This change has been brought about in part by the growing realization that many processes intrinsic to the dynamics of the Earth (e.g., volcanism, earthquakes, fluid flow, sediment maturation) provide partial or complete energy/nutrient fluxes necessary to support substantial, diverse microbial communities. Evidence that microorganisms inhabit both terrestrial and oceanic subsurface environments is rapidly increasing. From deep aquifers, oil wells, and boreholes have come reports of high incidence and diversity of microorganisms (Grassia et al. 1996, L'Haridon et al. 1995). Dense colonies of microbes are found to thrive in the warm pools of Yellowstone (Barns et al. 1994, Huber et al. 1998, Reysenbach et al. 2000), and deep marine sediment cores continue to yield microscopic evidence for

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the ubiquity of microorganisms to the greatest depths sampled (Cragg et al. 1990, Parkes et al. 1994, Summit 2000, Summit et al. 2001). There is evidence for active microbial communities in deep basaltic rocks from oceanic environments and from large igneous provinces (Fisk et al. 1998, Stevens & McKinley 1995), and microbes have been found within deep boreholes in granitic intrusions (Pedersen 1997, 2000).

The connection between volcanism and life perhaps is nowhere more evident than at mid-ocean ridge spreading centers. From investigation of active hydrothermal vents comes documentation of oases of vibrantly colored tubeworm communities and of arrays of clams, crabs, and gastropods that surround the volcanically driven warm vents. These macrofauna are supported by colonies of heat-loving microorganisms that thrive in the absence of sunlight (Baross & Hoffman 1985, Gold 1992, Deming & Baross 1993, Karl 1995, Takai et al. 2001, Wirsen et al. 1993). These organisms are sustained by mantle-derived volatiles released from below the seafloor either through direct volcanic degassing or through leaching by hot, circulating fluids. Some of these organisms in culture optimally grow at temperatures of 113°C (Blöchl et al. 1997), and intact microorganisms have been detected in smoker fluids, black smoker sulfides, and sediments that are at temperatures considerably higher than 113°C (Deming & Baross 1993, Baross & Deming 1995, Schrenk et al. 1999a, Takai & Soko 1999, Summit 2000, Summit et al. 2001). In addition, membrane lipids from archaea have been detected in the hottest sections of sulfide flanges and chimneys where temperatures are believed to be 200°C–300°C (Hedrick et al. 1992, Schrenk et al. 1999a). Such findings raise questions concerning the survival mechanisms of these organisms and what the upper temperature of life is within the subseafloor environment.

Even more spectacular are dramatic observations of massive microbial biomass emissions from the crust following recent seafloor diking-eruptive events (Huber et al. 1990, Haymon et al. 1993, Holden et al. 1998, Delaney et al. 1998, Summit & Baross 1998). The emissions may reflect extensive microbial blooms that last for several months following these eruptions. It is believed that the microbes are fed by released gases associated with the injection and expulsion of basaltic material (Holden et al. 1998, Delaney et al. 1998). Many of these microorganisms are archeae, thought to be the most ancient of extant hyperthermophilic organisms (organisms that optimally grow at temperatures $>80°C$, with a maximum growth temperature of 90°C or higher) (Baross & Hoffman 1985, Woese et al. 1990, Pace 1997, Summit & Baross 1998). High numbers of different thermal groups of microorganisms are discharged in diffuse-flow fluids associated with these eruptions, and in more stably venting systems that are too cold or tepid to support their growth (Holden et al. 1998, Summit & Baross 2001, Huber et al. 2002). These last two findings have been instrumental in forming the hypothesis that a potentially vast, but unexplored, microbial biosphere exists in the crust in close proximity with volcanoes and active submarine hydrothermal systems (Gold 1992, Baross et al. 1997, Holden et al. 1998, Delaney et al. 1998, Summit & Baross 1998).

Partly because the overlying ocean provides a pressure medium, mid-ocean ridges and other active seafloor volcanoes may represent the best natural environment currently known in which humans can study the linkages between magma-hydrothermal systems and the microbial communities they support. We have only begun to explore and instrument these environments in detail, and there is much left to be discovered. Major new insights will be gained by the use of long-term, in situ observatories on and beneath the seafloor. Investment in understanding as much as possible about linked processes here on Earth may provide important guides in the search for volcanic ecosystems elsewhere in the Solar System.

This paper provides a broad overview of processes associated with seafloor volcanism, hydrothermal systems, and the life that they support. We start with a brief summary of processes operative in the mantle and plutonic section of the oceanic crust, for it is from the mantle and shallow-crustal magma chambers ultimately that much of the heat and nutrients are supplied that feed chemosynthetic organisms (microbes that utilize inorganic compounds as their energy source) within the vent environments. We then discuss recent results from submarine diking-eruptive events, which provide unequivocal evidence for the presence of a subseafloor biosphere and new insights concerning the initial colonization of nascent venting systems by macrofaunal communities. This section is followed by a discussion of relatively long-lived hydrothermal systems. We use the Mid-Atlantic Ridge (MAR) TAG site, the East Pacific Rise 9°N site, the Juan de Fuca Endeavour site, and the newly discovered MAR site known as the Lost City as case studies. We then present an overview of energy requirements and microbial habitats within submarine environments, followed by development of what is known about microbes within these systems and a description of how these organisms are connected to macrofaunal communities that thrive in nutrient-rich, diffusely flowing vent fluids. Finally, we pose basic questions that must be addressed, and we discuss potential developments in technology that may accelerate model evolution in the exploration of the interface between microbiology and the physical-chemical environment of the subseafloor.

FROM THE MANTLE TO THE BIOSPHERE

The scientific community was astounded by the discovery in 1977 (Corliss et al. 1979) of rich and unusual fauna that owed their existence to chemosynthetic microorganisms fueled by the products of magmatic degassing and water-rock reactions associated with hydrothermal convection on the Galapagos Rift. These hydrothermal vent communities were initially viewed as isolated, widely spaced oases on an otherwise barren seafloor. However, in the past 15 years the discovery rate of vent sites has been high in response to maturation of search strategies and improved detection techniques, and at least 50 of these sites have now been documented along the mid-ocean ridge spreading center with hints of many more (Figure 1) (Rona et al. 1986, 1992; Tivey & Delaney 1986; Haymon et al. 1991; Charlou et al. 1992; Fouquet et al. 1993; Robigou et al. 1993; Fornari & Embley 1995; Auzende et al. 1996; Barriga 1998; Kelley et al. 2001a, Klinkhammer et al. 2001; Van Dover et al. 2001). The linkages between these systems and deeper Earth processes are the focus of this section.

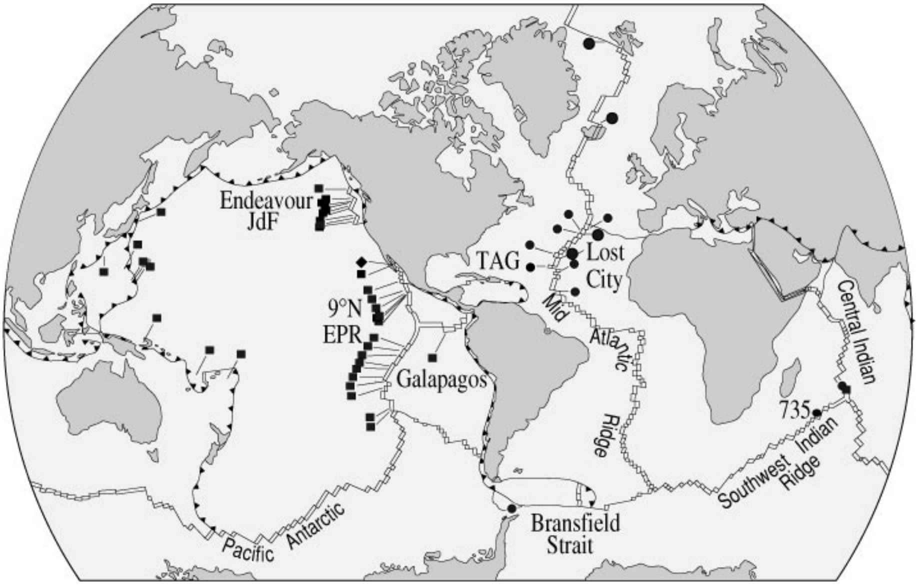

Figure 1 Location map showing vents in a variety of seafloor-spreading and margin environments and the location of Ocean Drilling Program Site 735B (modified from T. Shanks, Woods Hole Oceanographic Institution).

Melt and Volatile Source Regions

One of the initial and perhaps most crucial links in the development of submarine environments involves the process by which melt generation occurs beneath mid-ocean ridge spreading centers. It is within the mantle that basaltic melts obtain their initial composition and volatile content, and this in turn influences the composition of shallow crustal magma chambers, their deformational and eruptive behavior, the partitioning of trace elements both within the rocks and between the rocks and fluids, the volatile contents of venting systems, and a portion of the energy sources available for life on and beneath the seafloor.

Partial melting of peridotitic material occurs during adiabatic decompression associated with upwelling beneath the spreading ridges (Green & Ringwood 1967, McKenzie & Bickle 1988, Kelemen et al. 1997, see Kushiro 2001 for a review). Portions of the released melt, through a series of complex and not well-understood processes, rise through the mantle to form the plutonic foundation of the oceanic crust, the overlying dike sequence, and the basaltic extrusive layer (Figure 2). Inferences based on experimentally determined stability fields for minerals in mantle peridotites and compositional studies of residual mantle material (lherzolite & harzburgite) recovered from the ocean basins indicate that melting may occur over a depth interval from 90 km to <10 km beneath the seafloor (Green & Rindwood 1967, Presnal et al. 1978, Fallon & Green 1987, Elthon 1989, Niu

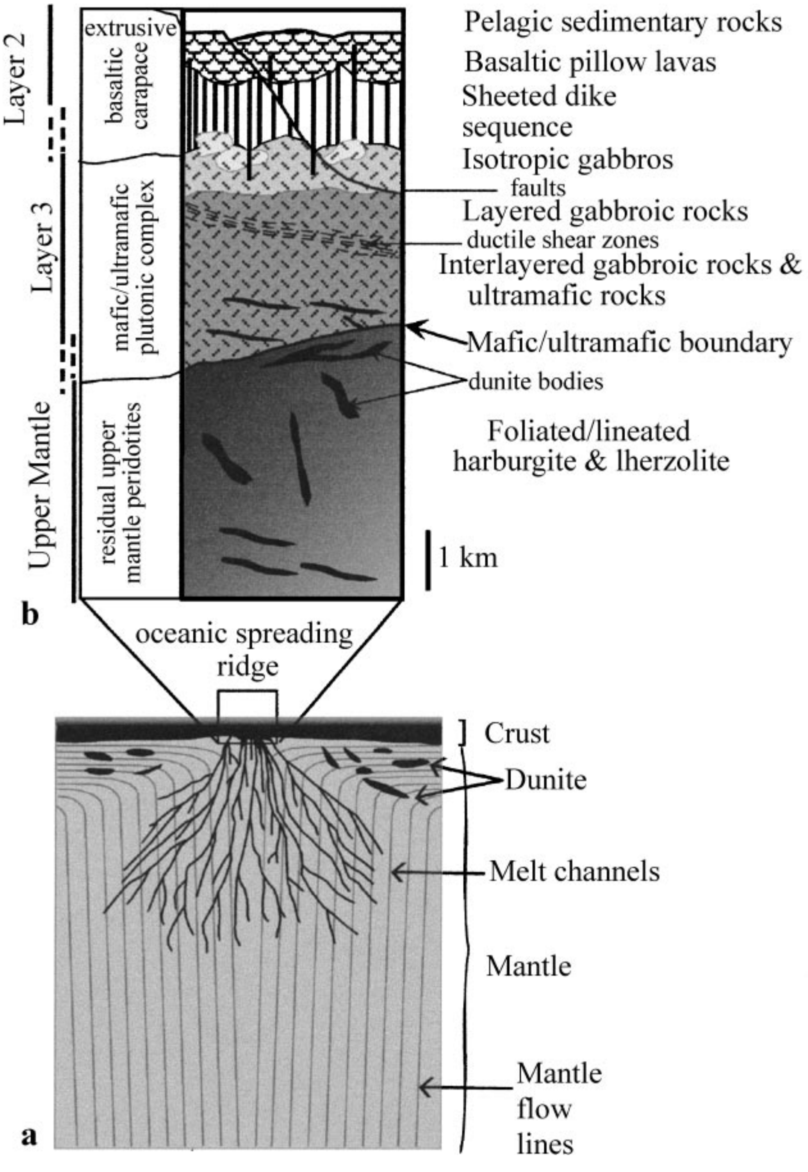

Figure 2 Schematic showing focusing of mantle-hosted conduits for melt to the plutonic foundation of submarine spreading centers (*a*) (after Kelemen et al. 1995) and a composite cross-section of the upper mantle and oceanic crust (*b*) (after Karson 1998).[1]

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[1] Melts formed beneath the ridge during adiabatic upwelling of the mantle coalesce into conduits marked by dunitic veins. Melts may eventually pond in crustal magma chambers ~1–4 km beneath the ridge axis to form the plutonic foundation.

1997, Niu et al. 2001). The depth at which the onset of melting occurs governs the amount of melt produced and to some extent its volatile content. There are still questions concerning how much melt is generated to produce appropriate basalt compositions, but values of 10%–20% are typically cited (Falloon & Green 1987, Johnson et al. 1990, Dick & Natlund 1996, Casey 1997).

During initial melting, which may occur at temperatures as high as 1400°C, incompatible volatile species such as H_2O and CO_2 are preferentially incorporated into the primitive melts; their concentrations are determined by the depth of melting, the oxidation state of the rocks, and the initial volatile content of the mantle. Significant effort has been devoted to determine the composition and speciation of mantle fluids because of their importance to mantle rheology and viscosity, melt generation and migration, the development of hydrous mineral phases, and the transport of trace and rare earth elements (Schneider & Eggler 1986, Green et al. 1987, Taylor & Green 1988, Bell & Rossman 1992, Hirth & Kohlstedt 1996). As with the depth of melting, however, the concentration and distribution of volatiles such as CO_2, H_2O, and CH_4 remains enigmatic. In a study of nominally anhydrous minerals, Bell & Rossman (1992) calculated H_2O contents of 25 to 175 ppm in spinel and garnet lherzolites, respectively. Other estimates for water range from 80 to 950 ppm (Michael 1988, Sobolev & Chaussidon 1996). Estimates for the concentration of CO_2 in primitive mantle range from 230 to 550 ppm (Zhang & Zindler 1993, Jambon 1994). The low volatile contents indicate that these species are likely incorporated into the structure of minerals, but with decompressional melting a free volatile phase may be formed. There is compelling evidence that virtually all mid-ocean ridge basalts (MORBs) are saturated with respect to CO_2 (Dixon & Stolper 1995), and some studies suggest that trace amounts of CH_4 may be present in addition to CO_2 and H_2O (Taylor & Green 1987, Ballhaus & Frost 1994, Wyllie & Ryabchikov 2000).

The Mantle-Crust Connection

During the past decade significant progress has been made in understanding the flow mechanisms and compositional changes that take place as basaltic melts rise through the upper mantle (asthenosphere) to the overlying crust. Many of these new insights have come about through detailed examination of extensive exposures of mantle material in ophiolites, of in situ sections of core recovered by the Oceanic Drilling Program, and through seismic imaging (Karson 2002; Kelemen et al. 1992, 1995, 2000; Dick & Natland 1996; Cannat et al. 1997; Casey 1997; Karson & Lawrence 1997; Niida 1997; Magde et al. 2000; Dunn et al. 2001). Theoretical and seismic investigations of ridge crest systems, coupled with field studies of upper mantle outcrops in ophiolites, indicate partial melting may occur over an $\sim$100-km wide region, with focusing at near crustal depths to a zone <5 km wide (Figure 2*a*). (Langseth et al. 1966; Kelemen et al. 1995, 2000; Forsyth et al. 1998). The exact pathway that these melts take is not well known, but field observations and modeling support the idea of a network of channels (Kelemen et al. 2000) that coalesce into a narrow region beneath the spreading ridges where continuous flow of melts occurs.

During their ascent, melts interact with the residual mantle through which they are rising. At mid-ocean ridges, the eventual product, MORBs, reflects mixtures of melts equilibrated at a variety of depths (Yoder & Tilley 1962, Yoder 1979, Kelemen et al. 1992, Sparks & Parmentier 1994, Dick & Natland 1996, Cannat et al. 1997, Kelemen et al. 2000, Kushiro 2001). It has now been well documented that during their ascent melts interact with mantle peridotites, stripping them of one of their main mineral phases, orthopyroxene, while at the same time depositing olivine (see Kelemen et al. 2000 for a review). Examination of lenses, pods, and veins of replacement olivine shows that they are in equilibrium with MORBs, suggesting that these features may represent upflow conduits for the melt. In contrast, the compositions of MORBs are out of chemical equilibrium with the residual mantle material through which they migrated. In Oman, dunitic veins composed of the minerals olivine and spinel mark conduits for melt transport through at least the uppermost 30 km of the mantle (Kelemen et al. 2000) (Figure 2). Whether this flow occurs as porous flow or highly focused flow is still being debated (Nicolas & Rabinowicz 1984; Buck & Su 1989; Aharonov et al. 1995; Kelemen 1995, 2000; Kelemen & Dick 1995; Jousselin et al. 1998), but eventually a portion of the melts breaches the mantle-crust boundary to form mid-ocean ridge magma chambers. It is through this process that volatiles such as CO_2, H_2O, H_2, and SO_2 eventually reach the lower and upper crust (Carroll & Holloway 1994).

From the Magma Chamber to the Seafloor

The exact morphology of any spreading system is governed by the interplay among melt supply rate, spreading rate, and the effectiveness of hydrothermal cooling so that, along a given spreading center, slow-, intermediate-, and fast-spread morphologies may develop. Characterizing the linkages among these processes and the spatial and temporal scales over which they interact is fundamental because it is through these processes that volatiles are released to the overlying ocean and microbial habitats are formed.

The rate of melt supply to a given ridge system has a profound affect on the structure of the lower and upper oceanic crust (Figure 3) (Karson 2002). In fast-spreading systems (full spreading rate = 80–160 mm/year), where magma supply is large, a steady state magma chamber is believed to exist along major lengths of the ridge axis (Sinton & Detrick 1992). In this model, diking events and volcanic eruptions surpass the effects of tectonism and the ridge forms a topographic high (Figure 3). For example, at 9°N on the East Pacific Rise the ridge gradually rises 100 m above the surrounding seafloor (Macdonald 1998). The shoalest portion of the ridge directly overlies the partially molten region in this area, and it is characterized by a 50–80-m wide, 5–8-m deep collapsed zone that marks the most

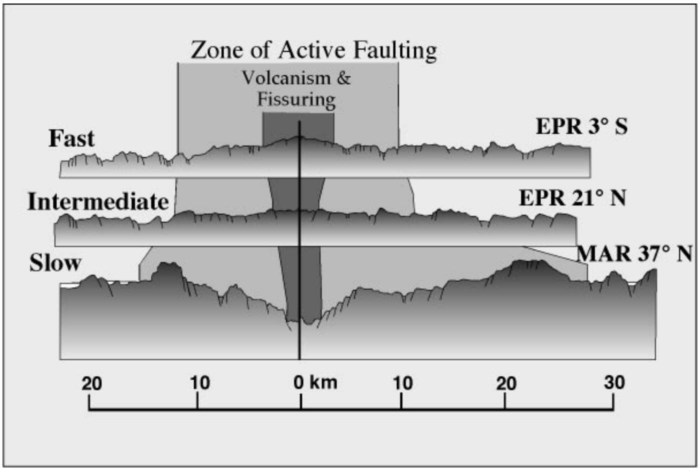


Figure 3 Cross-axis profiles of spreading centers. Topography, magma chamber depth, frequency of eruptive events, size of hydrothermal deposits, and vent fauna diversity and composition all show strong correlations with spreading rate (after MacDonald 1992). EPR = East Pacific Rise; MAR = Mid-Atlantic Ridge.

volcanically and hydrothermally active part of the ridge (Macdonald & Fox 1988, Haymon et al. 1991, Fornari et al. 1998, Lagabrielle & Cormier 1999).

By contrast, in slow-spreading environments (full spreading rate = 10–40 mm/year full rate) such as the Mid-Atlantic Ridge (e.g., 37°N), melt supply is intermittent and the crust is believed to be built by a series of small intrusions. In this case, tectonic processes dominate, and the ridge is commonly characterized by a deep, up to 15-km across, fault-bounded axial valley populated with sporadic volcanic edifices (Ballard & van Andel 1977; Smith & Cann 1990, 1992; Perfit & Chadwick 1998; Smith et al. 1999) (Figure 3). Coupled magma-tectonic processes result in a variety of discontinuities in the ridge structure (Karson 2002). These range, at the small scale, to local deviations of <1 km in the linearity of the spreading axis to, at the large scale, transform faults where the ridge axis may be offset by >30 km (see Macdonald 1998). Near large offset transform faults, relief can be especially dramatic. It is not uncommon for the seafloor to rise from a water depth of 5000–6000 m to 1000–700 m over distances of 10 to 15 km.

Insights on how melts migrate through the upper mantle and lower crust to form the plutonic foundation of submarine volcanoes have been obtained by examining gabbroic rocks that represent the crystallized portions of mid-ocean magma chambers (Figure 4). These rocks commonly preserve "fossilized" melt channels of gabbroic and more compositionally evolved crystalline material (Figure 5). The compositions and textures of minerals (i.e., olivine, clinopyroxene, orthopyroxene, and plagioclase) that make up this crustal section commonly show extensive

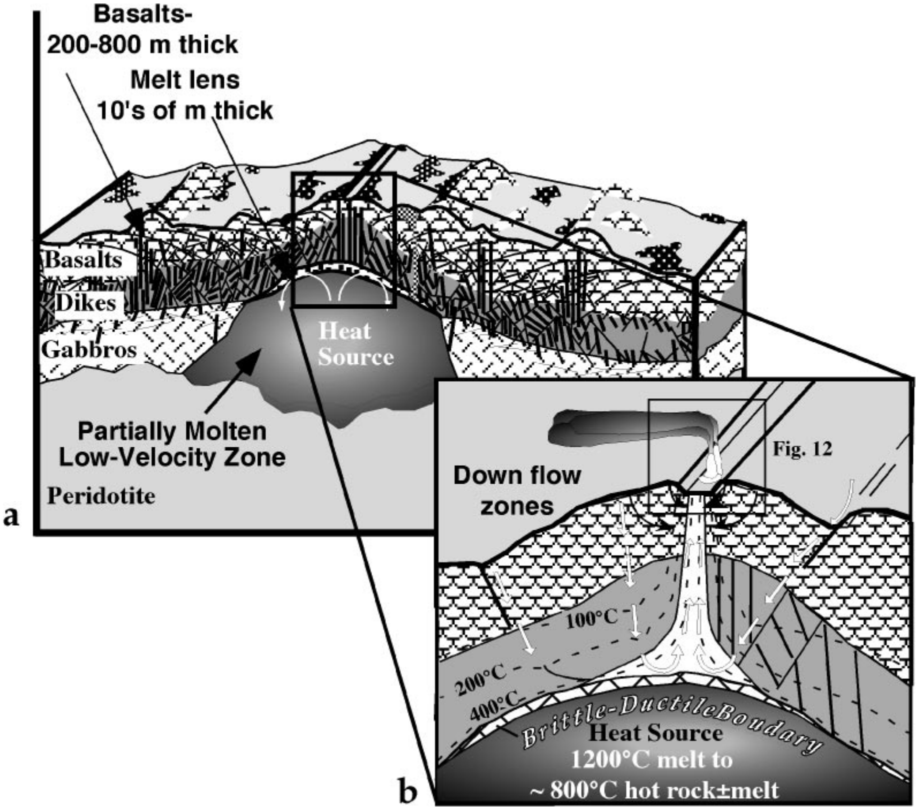


Figure 4 Schematic drawing showing mantle-crust relationships beneath ridge crests. (*a*) Crustal magma chambers, fed from melt percolating through the underlying mantle section, typically form at depths of 1–4 km below the seafloor (after Karson 2002). (*b*) Steep thermal gradients resulting from intrusion of 1200°C basaltic melt into cool, water-saturated and porous crustal rocks drive hydrothermal circulation beneath the spreading centers. High-temperature limbs of the resultant hydrothermal cells focus metal-rich, acidic fluids onto the seafloor, which form sulfide deposits upon mixing with cold, oxygenated seawater.

melt-mineral reaction (Dick et al. 1991, 2000; Meyer & Sapp 1994; Kelley & Malpas 1996; Gillis & Meyer 2001). In concert, these observations have been interpreted to indicate that both channeling and porous flow of melts are important processes in the crust and the mantle. Recent models call for layered gabbros at the base of the crust to form an impermeable barrier to melt migration. Overpressuring in the lower crust may ensue due to the continual rise of melts from the mantle and ponding of the melts in the lower crust (Kelemen & Aharonov 1997). Resulting excess pressures are relieved during hydraulic fracturing events, allowing focused melt flow in the ensuing channel network.

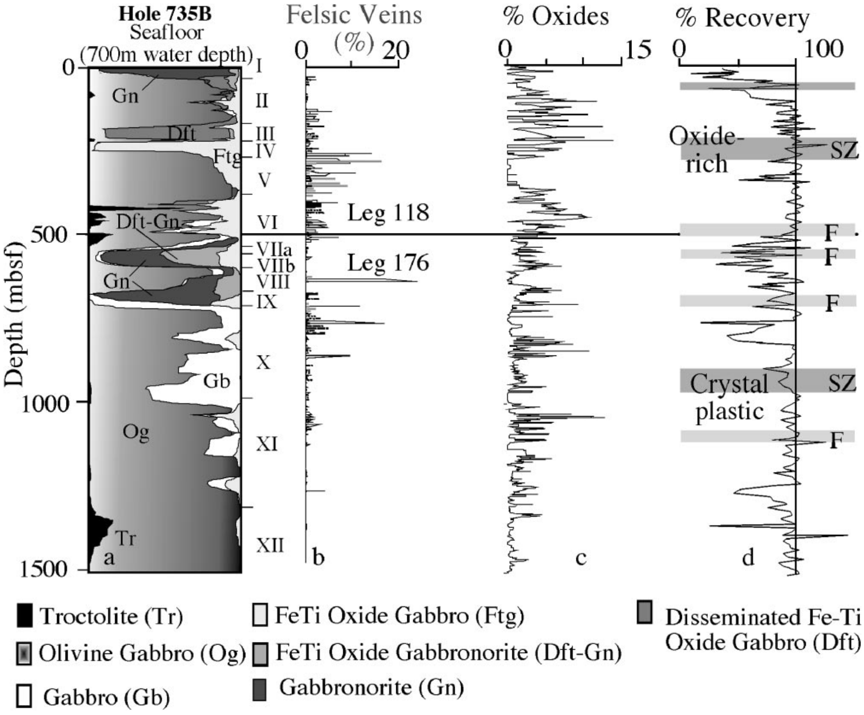


Figure 5 Lithostratigraphy of a 1500-m section of plutonic rocks recovered from Hole 735B during Ocean Drilling Program Legs 118 and 176 (see Figure 1 for location). The suite of rocks that include gabbros to compositionally evolved iron-titanium (Fe-Ti) oxide gabbros are cut by abundant felsic veins. These veins mark fossilized flow of volatile-rich late-stage melts through the plutonic sequence. Roman numerals indicate different lithologic units based on mineralogy and grain size. Also shown is the percent of oxide minerals down section (*c*) and the percent of recovery as a function of deformation zones logged in the hole. F = fault zones, SZ = high temperature shear zones (after Dick et al. 2000). Deformation is strongly correlated to oxide abundance.

Accumulation of melt in the shallow crust occurs as melts reach a zone of neutral buoyancy, which is determined by the density of the melts and the enclosing host rocks (Ryan 1987, Sparks et al. 1980, Ryan 1994, MacLeod & Yaouancq 2000). Multichannel seismic, tomographic, and near-bottom-source seismic studies allow comparison of the depth to the inferred magma chamber at different spreading environments. Seismic data indicate a zone of high-velocity material that generally occurs over a depth interval of 1–4 km below the seafloor, with faster-spreading systems in general having shallower magma chambers (Mutter et al. 1988; Toomey et al. 1990, 1994; Christenson et al. 1994; Sinton & Detrick 1992; Phipps Morgan & Chen 1993a; Perfit & Chadwick 1998).

Theoretical modeling, seismic studies, and field observations indicate that, in fast-spreading systems, melt may accumulate in a steady state magma chamber as a small lense at the top of a crystal-mush zone (Figure 4). This 1200°C lense, which may extend for several kilometers along the spreading axis, is on average a kilometer wide and perhaps 40 m to <100 m thick (Sinton & Detrick 1992, Fornari & Embley 1995, MacLeod & Yaouancq 2000). Intense thermal gradients imposed by colder cap rock likely promote convection within this lense. A crystal-mush halo composed of crystalline material and trace amounts of melt that persist down to temperatures of 700°C is believed to surround the lense (Sinton & Detrick 1992). Below this temperature the material is believed to be entirely crystalline (Sinton & Detrick 1992, Phipps Morgan & Chen 1993b, Perfit et al. 1994, Perfit & Chadwick 1998, Hirth et al. 1998, Gillis & Roberts 1999). The caprock and lense are bounded by a brittle-ductile region in which material nearest to the lense deforms plastically; transitional to this is a region in which the cooler rocks are strong enough to sustain significant stresses, which allows brittle failure (Figure 4) (Lister 1974, 1983; Hirth et al. 1998). This transition zone is of particular importance in governing the cooling of melt and hot rock, as the brittle-ductile transition controls the depth to which seawater-derived fluids can migrate into the crust (Lister 1983, Kelley & Delaney 1987, Phipps Morgan & Chen 1993b, Gillis 1995, Wright 1995, Gillis & Roberts 1999, Kelley & Früh-Green 2000, Dunn & Toomey 2001).

In contrast to fast-spreading environments, a few seismic studies show evidence for melt accumulation in slow-spreading systems (Calvert 1995, Sinha et al. 1997, Magde et al. 2000), and field studies suggest that magma chamber development may be more complex than in fast-spreading environments (Karson 2002). Intrusion events may be separated by tens of thousands of years (Pockalny et al. 1988, Perfit & Chadwick 1998), and crosscutting relationships among intrusions are common (Dick et al. 1991, 2000).

Many of our concepts regarding accretion and aging of the crust in non–steady state systems have been profoundly changed by examination of a plutonic suite of rocks recovered by the Ocean Drilling Program from the Southwest Indian Ridge (SWIR) at Hole 735B (Figure 5). [Although this site has become a true section for studying linked magmatic-tectonic-hydrothermal processes, many of the features observed in the core are common in rocks recovered from other slow-spreading environments (e.g., Gillis et al. 1993, Kelley 1997, Cannat et al. 1997, Casey 1997).] This site is located on a fault-bounded, wave cut plutonic terrace ~93 km south of the present-day axis of the SWIR and ~18 km inboard of the Atlantis II Fracture Zone (Dick et al. 2000). The plutonic rocks at 735B are considered to represent crust formed beneath the median valley of the ultra slow-spreading (1.6 cm/year total rate) SWIR ~10 Ma ago. In total 1.5 km of gabbroic material was drilled at this site, with ~1300 m of core being recovered.

The lithostratigraphy and chemistry of the 735B plutonic sequence show that the crust was built by at least two principal intrusive episodes and several smaller intrusive events (Figure 5*a*) (Dick et al. 2000). Gabbroic rocks constitute >99% of the igneous lithologies, with the remaining material comprising felsic veins, hydrothermal breccias, and small evolved pockets and veins that span trondhjemitic, quartz dioritic, and granitic compositions (Figure 5*b*). The complex igneous stratigraphy is interpreted as representing a series of small, 100- to 500-m thick intrusions, the chemistry of which becomes slightly more evolved with depth (Dick et al. 2000). Olivine gabbros are the most common rock type recovered, although gabbros, gabbronorites, and oxide gabbronorites are also present (Figure 5*a*). Oxide gabbros occur sporadically throughout the section, but they are concentrated in a zone between 500 and 700 mbsf (Figure 5). Chemistry, grain size, and modal mineralogy change over centimeter distances along the core, reflecting the interplay among melt migration, cooling, and mineral-melt-fluid reactions. One of the most important insights to come out of this study concerns the linkages among the compositions of melt, melt and volatile migration, and initiation of high-temperature deformation. The variably altered and deformed plutonic rocks record a remarkably complex magma-hydrothermal history. Magmatic fluids within this suite followed two chemically distinct paths during cooling through the subsolidus regime: The first path included formation of $CO_2 + CH_4 + H_2O + C$ fluids with up to 43 mol% CH_4; the second path produced hypersaline brines that contain up to 50% NaCl equivalent salinities (Kelley & Früh-Green 2001). These fluids may be incorporated into subsequent shallow hydrothermal systems during leaching attendant with seawater penetration.

The development of extensive, long-lived fault systems within the oceanic crust is a fundamental component of ridge crest formation, especially in slow-spreading environments (Dick et al. 1991, Escartin et al. 1997, Lagabrielle et al. 1998, Karson 1998). The recovery of long, nearly continuous sections of core from the SWIR has been critical to examination of this problem. Deformation within the 735B plutonic suite is highly variable and complex, but there is strong correlation in the occurrence of late stage, oxide-rich gabbros with zones of moderate to intense crystal-plastic deformation (Figure 5). In areas rich in oxides, there is evidence for injection of oxide-rich melts into shear zones and contemporaneous crystal-plastic deformation, overprinting of crystal-plastic fabrics by iron-titanium oxides, and overprinting of some oxide-rich zones by brittle deformation (Dick et al. 1991, 2000). Mineral-fabric analyses of the 735B samples show that deformation in some of the rocks initiated in the presence of water- and CO_2-saturated melts at temperatures >800°C–1000°C (Stakes et al. 1991, Kelley & Früh-Green 2001). Similar zones are observed in rocks recovered from the MARK and Atlantis areas of the Mid-Atlantic Ridge and the Mid-Cayman Rise. In contrast, deformed, oxide-rich rocks do not appear to be a common feature of fast-spreading systems.

VOLATILE FORMATION IN THE OCEANIC CRUST

Volatiles play a profound role in the evolution of any tectonically active planet. For example, degassing of volatiles is responsible for formation of the early oceans and atmosphere, and the deformation and eruptive behavior of mid-ocean ridge magma chambers is governed in part by their volatile content. Yet, until recently, few data have been available concerning the composition and evolution of C—O—H volatiles in mid-ocean ridge magma chambers. New insights into these high-temperature plutonic systems have been gained through (*a*) the successful recovery by ODP of in situ submarine plutonic rocks and (*b*) by examining tectonically exposed sections of oceanic crust (Karson & Dick 1983, Kelley & Delaney 1987, Vanko & Stakes 1991, Mével et al. 1991, Vanko et al. 1992, Gillis et al. 1993, Kelley et al. 1993, Gillis 1995, Früh-Green et al. 1996, Manning et al. 1996). Based on examination of fluid inclusions in multiple suites of plutonic samples recovered during these programs (Kelley & Delaney 1987, Vanko 1988, Nehlig & Juteau 1988, Nehlig 1991, Vanko et al. 1992, Kelley et al. 1993, Kelley 1996, Kelley & Früh-Green 2001), comparison with data on fluids in igneous complexes (Mathez et al. 1989), and by analogy to similar systems within porphyry copper environments (Gustafson & Hunt 1975, Bodnar & Beane 1980, Reynolds & Beane 1985, Fournier 1999), two general compositional trends for evolving magmatic fluids are suggested for submarine plutonic systems:

$$1200^\circ\text{C} \rightarrow \text{decreasing temperature} \rightarrow 500^\circ\text{C}$$

$$\text{Path 1: } CO_2 + (H_2O + CO + S) \rightarrow CO_2 + CH_4 + H_2O + C \rightarrow CH_4 + H_2O + C$$

and

$$\begin{aligned}\text{Path 2: } & CO_2 + (H_2O + CO + S)\\ & \rightarrow H_2O \pm CO_2[\text{V}] \rightarrow H_2O \pm CO_2 + \text{Brine [L]} \rightarrow \text{Brine.}\end{aligned}$$

These two trends are obviously generalized, and the exact fluid compositional paths are likely to vary significantly depending on the T-fO_2 path and whether minerals such as graphite precipitate (Gerlach & Nordlie 1975, Mathez et al. 1989). Characterization of the fO_2s of mafic magmas shows that some primitive basalts may reflect relatively reduced conditions near the iron-wustite (IW) buffer [IW to MW (magnetite-wustite)] (Christie et al. 1986). Under these conditions, modeling suggests that the plutonic-hosted fluids are dominated by CO_2, H_2O, and CO; and reduced species such as H_2S, H_2, and CH_4 may be stable (Mathez 1984). In highly evolved systems, CH_4 may be of particular importance in systems in which graphite precipitation occurs (Holloway 1984, Mathez et al. 1989, Kelley 1996, Kelley & Früh-Green 2001). Progressive degassing of fluids in a shallow crustal environment will drive the system to more oxidizing conditions near or above the quartz-fayalite-magnetite buffer (QFM) where CO_2, H_2O, and SO_2 dominate (Gerlach & Nordlie 1975, Mathez 1984).

Analyses of gabbroic rocks and submarine basaltic glasses, in concert with experimental data on CO_2 and H_2O in mafic systems, indicate that, due to the low solubility of CO_2 in basaltic melts, mid-ocean ridge melts are saturated or oversaturated with respect to CO_2, with typical concentrations of <600 ppm (Delaney et al. 1978, Pineau & Javoy 1983, Fine & Stolper 1986, Stolper & Holloway 1988, Dixon & Stolper 1995). In contrast, the incompatible nature of H_2O, coupled with its low concentration, means that basalts are generally undersaturated with respect to H_2O, with concentrations in glasses of typically <5000 ppm (Moore 1977; Delaney et al. 1978; Dixon et al. 1988, 1995). Methane within plutonic rocks may reach values of 40–50 mol%, with concentrations up to 35 ppm (Kelley & Früh-Green 2001). For many mid-ocean ridge systems, water saturation is only achieved in compositionally evolved, residual melts that remain after more than approximately 95% crystallization (Burnham 1979, Holloway & Blank 1994). These fluids exhibit extremely heterogeneous isotopic compositions that reflect multiple degassing events, mineral-fluid reactions, and incorporation of fluids from different sources.

Volatiles as Agents for Deformation

Although it is unclear how large, long-lived high-temperature fault systems develop within and adjacent to magma chambers, it may be that feedback loops involving volatile phases serve to focus deformation. As effective lower pressures are developed within fault zones, there is a tendency to draw in volatiles (and melt) from the surrounding wall rocks, further weakening material in a shear zone. Such a process appears to be recorded by fluids trapped within the 735B rocks (Kelley & Früh-Green 2001). Analyses of these samples show that the melts within the shear zones were saturated with H_2O and CO_2. In addition, many of the deformed oxide gabbros are very depleted in ^{13}C, and they contain higher CO_2 concentrations than would be predicted by degassing models. Within localized low pressure shear zones, volatile infiltration from the surrounding wall rocks results in higher than predicted CO_2 concentrations. Such late-stage fluids are likely very evolved in composition and have extremely light $\delta^{13}C$ values ($\delta^{13}CCO_2 = -28.6‰ \pm$). In addition, it is probable that within such environments significant reworking of carbon may occur as fluid and melts infiltrate and migrate in the brittle-ductile regime so that carbon becomes progressively oxidized; this will also result in higher than predicted CO_2 concentrations with very negative $\delta^{13}C(CO_2)$ values and will contribute to the carbon heterogeneity in the lower oceanic crust (Kelley & Früh-Green 2001).

The buildup and eventual release of volatiles profoundly affects mineral formation, the viscosity of melts, and the nature of the brittle-ductile transition (Knapp & Knight 1977, Sparks et al. 1994). With progressive melt fractionation, magmatic fluids evolve from CO_2-rich fluids to immiscible CO_2-H_2O-rich vapors and metal-rich, CO_2-H_2O-NaCl brines that are exsolved at temperatures in excess of 700°C (Kelley & Delaney 1987, Kelley & Früh-Green 2000). This phase separation process must occur during the life history of all mid-ocean ridge magma chambers (Figure 6). Condensation of brines is important because choride-complexing largely governs the transport of metals in the volatile phase. However, at the margins of a crystallizing magma chamber, phase separation can have far-reaching effects on fracture development (Kelley & Delaney 1987, Fournier 1999). At some depth-temperature within the seafloor, rocks will begin to behave in a ductile manner so that near the magma chamber–gabbro interface there is a progressive shallowing of the region where phase separation occurs for a fluid of a given salinity.

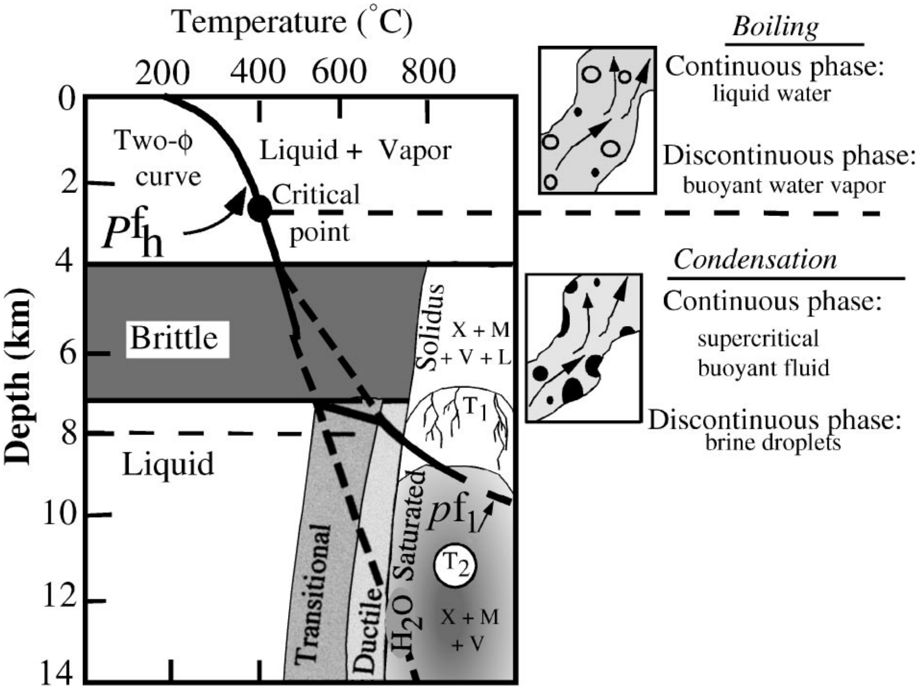


Figure 6 Schematic temperature-pressure relationship for the two-phase curve of seawater under lithostatic ($p\text{f}_\text{l}$) and hydrostatic ($p\text{f}_\text{h}$) conditions. The upper part of the crust is well fractured; the lower part is represented as being partially molten or too ductile to sustain significant stress. The solidus marks the boundary of a magma chamber, separating high-temperature partially molten zones, which contain crystals (X) + melt (M) + volatiles (V + L), from plutonic material that is entirely crystalline. At shallow crustal conditions, high-temperature fluids will be exsolved from the melts as vapors (V) and brines (L). This must occur during the lifetime of all mid-ocean ridge magma chambers. As the carapace cools (T1) over time (T2) the melt region will migrate to deeper crustal levels allowing penetration of hydrothermal fluids into progressively deeper crustal rocks (after Kelley & Delaney 1987).

This change from hydrostatic to lithostatic conditions will occur over a depth interval corresponding to the brittle-ductile transition (Figure 6). In any evolving magma-hydrothermal system, this boundary is not static but will fluctuate with migration of the crystallization front, with changes in volatile exsolution, and with changes in rock-melt lithology (Kelley & Delaney 1987, Fournier 1999, Kelley & Früh-Green 2001). Calculations by Hirth et al. (1998) predict temperatures of 700°C–800°C for the brittle-plastic transition in moderately shallow gabbroic rocks, and these temperatures agree well with results of fluid inclusion and mineral analyses (Kelley & Delaney 1987, Vanko 1988, Gillis & Roberts 1999, Kelley & Früh-Green 2000).

A downward shift in the brittle region due to fracturing events either within the carapace or with faulting of the host rock may result in substantial decompression of fluids within the chamber and surrounding pore fluids, which may induce two-phase separation (Figure 6) (Kelley & Delaney 1987, Kelley 1997). Because of the large positive volume change of fluids attendant on condensation and exsolution of a gas phase, this process may lead to a cascading sequence of fracturing, volatile exsolution, and volcanic eruption (Burnham 1979, Kelley & Delaney 1987, Kelley et al. 1992, Fournier 1999). Magmatic breccias and pervasively fractured wall rocks above intrusions in recovered core and in ophiolites attest to the importance of this process in melt migration and faulting (Stakes et al. 1991, Kelley et al. 1992, Gillis & Roberts 1999, Dick et al. 2000, Kelley & Früh-Green 2001). Phase separation and concomitant fracturing may occur many times over the lifetime of a magma chamber as periodic intrusions of melt promote new degassing episodes and phase-separation events.

SEAFLOOR DIKING ERUPTIVE EVENTS

A significant fraction of magma solidifies slowly in submarine chambers to form coarse-grained gabbros, but where melt and volatile accumulation near the carapace produce pressures in excess of lithostatic, magma episodically breaks through the crystalline roof of the chamber and rises through planar, ridge-parallel conduits called dikes (Figure 7). If these dikes breach the surface, a submarine eruption of basaltic lava flows is produced. Observations of eroded oceanic crust on land and tectonically exposed crust on the seafloor confirm that at depths of approximately 1 to 4 km, the entire oceanic crust comprises a dense complex of dikes that are commonly, but not always, ridge parallel. The dikes are typically about 1 m in width, up to 1–4 km in vertical extent, and tens of kilometers long (Kidd 1977, Francheteau et al. 1992, Gillis 1995, van Everdingen 1995, Hooft et al. 1997, Lawerence et al. 1998, Karson 2002). They represent a virtually endless series of impulsive magma transfer episodes from the chamber toward the seafloor as the ocean basins open along the spreading center. In spite of the fundamental role submarine diking plays in the evolution of our planet, until recently because it had not been observed in progress, it was not possible to investigate the active processes involved in this component of crustal accretion.

Dike injection is accompanied by intense earthquake activity that records the "unzippering" or brittle failure of the crust as melt is intruded parallel or subparallel to the spreading axis. Seismic monitoring of these T-phase events or swarms (acoustic signals from small earthquakes recorded by underwater hydrophones) records several tens to several hundred small earthquakes a day associated with breaking of the crust along axis (Fox et al. 1995, Dziak et al. 1995, Fox & Dziak 1998; see http://www.pmel.noaa.gov/vents/acoustics/seismicity/seismicity.html). Discrete swarms recorded over short time periods are believed to represent the arrival of new magma pulses and the shoaling and eventual eruption of dikes as they migrate along an axis (Fox et al. 1995, Dziak et al. 1995, Schreiner et al. 1995, Fox & Dziak 1998). This activity may last for several weeks and is associated with dike intrusion and eruption of material onto the seafloor. Dike propagation at mid-ocean ridges has been documented by observing the migration of earthquakes at velocities of several kilometers per day using the Navy's Sound Surveillance System (SOSUS) submarine hydrophone array in the Northeast Pacific (Fox et al. 1995). These data have shown that dikes can propagate 60 km along a ridge over a 2-day period (Fox et al. 1995, Dziak et al. 1995). Similar migration patterns have been documented on the volcanically active islands of Hawaii and Iceland (Klein et al. 1987, Einarsson & Brandsdottir 1980). Recent detailed mapping of the seafloor shows that dike intrusion may be expressed as distinct grabens, which on the Juan de Fuca Ridge are 10–100-m wide and 5–15-m deep (Chadwick & Embley 1994, 1998, Embley et al. 2000). Similar features have been documented on the fast-spreading East Pacific Rise that are 5–40-m deep and 40–250-m wide (Auzende et al. 1996, Perfit & Chadwick 1998). Modeling of these systems indicates that graben width may reflect the depth to the dike, with wider, deeper grabens associated with deep-seated dikes and narrower grabens associated with shallow dike systems (Chadwick & Embley 1998).

The processes that drive dike propagation are complex, but factors such as excess magma pressure in the chamber and in the dike and volatile accumulation at the advancing dike tip likely provide part of the driving force necessary for migration (Shaw 1980, Rubin & Pollard 1988, Rubin 1995, Curewitz & Karson 1998). Rapid heating and vaporization of aqueous fluids in the crack tip and surrounding wall rock may promote hydraulic fracturing of the rocks in advance of the dike, allowing melt to move more easily through the crust. In areas where there has been a long interval between dike injections, ambient tensional stresses may be near critical failure, and only small stresses induced by dike intrusion may be required to promote dike propagation (Perfit & Chadwick 1998). If there is sufficient melt in the source region, and the driving forces for propagation are great enough, the dikes will breach the seafloor, and a submarine eruption ensues. Particularly in fast-spreading systems, the eruption and drainout of significant volumes of melt from a shallow magma chamber may form large summit troughs >500 m in width. These features have been interpreted to represent calderas formed during collapse of the overlying brittle, shallow crust subsequent to eruptive episodes (Lagbrielle & Cormier 1999, Fox et al. 2001).

ERUPTIONS AND LIFE

The profound impacts that diking-eruptive events have on submarine hydrothermal activity and on the chemical and biological fluxes from below the seafloor to the overlying ocean is one of the most important discoveries to be made in the past decade. Although real-time observations of seafloor eruptions are still exceedingly rare along the mid-ocean ridge spreading network, fortuitous exploration and access to the SOSUS array have fundamentally changed our view of submarine volcanoes and our ability to respond to these events (Fox et al. 1995, Fox & Dziak

1998, Fox et al. 2001). Through rapid response cruises, which have allowed onsite investigation of eruptions within days to weeks following the detection of earthquake swarms, it has been possible to examine the transient events associated with active submarine volcanoes and to study the covariation of processes that are key interactions endemic to oceanic crustal formation (Embley et al. 1995, Delaney et al. 1998). These studies have begun to influence perceptions of the role that volcanically supported microbial habitats can play in planetary systems in general. The interlinked geochemical and microbial activities triggered by diking-eruptive events are likely to have been an integral component of oceanic crustal formation throughout much of Earth's history. Since 1986, 12 submarine diking-eruptive events have been inferred or directly observed. Many of these events have shown a commonality in the hydrothermal and biological activity triggered by the eruptions. In the following discussion, we discuss the general characteristics of these events and present a model of the mechanisms and consequences of submarine diking-eruptive episodes.

Even though eruptive events are a fundamental component of oceanic crust formation, surprisingly, relatively few quantitative analyses of submarine eruptive flows have been made. This is due in part to the fact that, until recently, few side-scan sonar or bathymetric systems had the capacity to generate the high-resolution maps necessary to characterize these environments. However, recent imaging studies have begun to shed light on the style, location, size, and periodicity of eruptions. The Cleft segment of the Juan de Fuca Ridge was the first location where recent submarine eruptive events were documented (Baker et al. 1987, Baker & Lupton 1990, Chadwick et al. 1991, Butterfield & Massoth 1994, Embley & Chadwick 1994). This segment is an intermediate spreading ridge but has the general morphology of a fast-spreading system in that it exhibits a smooth, shallow relief and hosts a nearly continuous central cleft that is 10 km in length, 30–50 m in width, and 20-m deep (Kappel & Ryan 1986, Embley & Chadwick 1994). Comparison mapping using Seabeam bathymetric data in different years and follow-on side-scan surveys of this segment show that an eruption of pillow mounds reaching a thickness of up to 45 m and having a total volume of 55×10^6 m^3 occurred between 1983 and 1987 (Chadwick et al. 1991, Fox et al. 1992, Chadwick & Embley 1994). The mounds are bounded by young sheet flows, which exhibit a range of lava morphologies that include lobate, ropy, and jumbled flows. These flows are thought to have erupted along an ~020° trending fissure system at least seven months before the pillow eruptions. The most intense hydrothermal activity and low-temperature diffuse flow sites are also located along this trend. In 1986 and 1987, extensive, transient, hydrothermal plumes were found in the upper water column associated with this site (these are discussed in more detail in the follow-on section) that are believed to have formed in response to the eruptions (Baker et al. 1987, 1989). These "megaplumes", or "event plumes" as they came to be called, contained a thermal discharge of 10^{16}–10^{17} J (Figure 7) (Baker et al. 1987, 1989).

Subsequent to Cleft, a fortuitous dive program in 1991 at 9°N on the East Pacific Rise resulted in exploration of a lava flow just a few weeks after its eruption.

Surveys using the submersible Alvin showed that effusion of lava occurred from an eruptive fissure, which was nearly continuous over an ~8.5-km distance within the axial summit caldera (Haymon et al. 1991, Haymon et al. 1993, Wright et al. 1995, Gregg et al. 1996). Lava pillars and flows that spilled over the caldera walls indicate that the flow must have been 8-m thick. Modeling suggests that the entire 3.6–5.8 × 10^6 m^3 volume of basaltic melt was emplaced over a 1–2-h period at an average rate of 10^3 to 10^6 m^3/s. These rates are comparable to magma eruption rates at the East Rift Zone of Kilauea in Hawaii (Gregg et al. 1996, Gregg & Fornari 1998). The summit trough along many sections of the East Pacific Rise is characterized by lava pillars formed during collapse of lava lakes, lava tube orifices, partially collapsed lava lake roofs, and low-relief volcanic edifices much like those observed at Cleft. Such features are consistent with the rapid expulsion of melt, whereas pillow flows are believed to form at lower eruption rates (Gregg et al. 2000, White et al. 2000). Lava pillars, marked by drainback features reminiscent of bath tub rings formed during the 1991 eruption, reached 1–20 m in height and 0.25–20 m in diameter. They are believed to have formed during a 2–5-hr period during single eruptive phases as the lava ponds drained (Gregg et al. 2000). Volcanic-hydrothermal cycles for this area have been proposed that include an episode of dike intrusion and volcanic eruptions along a fissure network that is accompanied by or immediately followed by hydrothermal activity. Magma drainage leads to collapse of the axial caldera summit. This cycle is repeated many times over a full cycle that may last 10^2–10^3 years (Haymon et al. 1991, 1993).

The first rapid response to an eruptive event involved water column mapping and submersible studies of the CoAxial segment of the Juan de Fuca Ridge (Embley et al. 1995, Delaney et al. 1998). On June 26, 1993, intense seismic activity beginning on the northern flanks of the large volcano called Axial Seamount migrated laterally approximately 40 km along the trend of the ridge axis from a latitude of approximately 46°11.5′N to a latitude of about 46°31′N (Embley et al. 1995, 2000). Follow-on diving operations with the remotely operated vehicle ROPOS (Remotely Operated Platform for Ocean Science) showed that this activity terminated near a fissure eruption that formed a flow ~2.5-km long and up to 300-m wide (Chadwick et al. 1995, Embley et al. 1995). The flow, which has an estimated volume of 5.4 × 10^6 m^3, occurred from a 20-m wide fissure and resulted in a pillow ridge at least 30-m thick, 3.8-km long, and up to 500-m wide. A zone of grabens and fissures that extends for at least 1-km north of the main flow site hosts several smaller flows, indicating a total length of 4.5 km for the eruptive event. A nearly continuous 50-m wide zone centered on the crest of this flow was venting fluids at up to 51°C (Embley et al. 1995). Comparison of Seabeam bathymetric data and calculations of changes in relief delineate a second pillow eruption 800-m east of the 1993 flow that occurred sometime during the period 1982–1991 (Chadwick et al. 1995). A third flow was imaged, using the Seabeam differencing technique, which is located 24-km south of the 1993 eruptive site. This southern eruption had occurred between 1981–1991; it is characterized by glassy flows that extend for 7 km in length and which reach up to 25 m in thickness (Chadwick et al. 1995, Embley et al. 2000). It has been suggested that this rifting episode, which covered a 12-year period, may be broadly analogous to those on Iceland where long-term records have indicated that accumulated stress may be released by a series of major rifting/eruptive events every 100–150 years (Bjornsson et al. 1979, Embley et al. 2000).

Recent magmatic eruptions have not been mapped at slow-spreading ridges, and data on flow dimensions and volumes are sparse. In contrast to intermediate- to fast-spreading systems, eruptive centers seem to be dominated by pillow flows that form small hummocks, hummocky ridges, or seamounts that range in size from <50 m in height and 500 m in diameter, to hundreds of meters tall, widths of several kilometers, and lengths of tens of kilometers (Bryan & Moore 1976, Stakes et al. 1984, Karson et al. 1987, Smith & Cann 1990, Bryan et al. 1994, Perfit & Chadwick 1998, Smith et al. 1999). Dike penetration and eruptions at these sites must be operative for long periods of time to allow for construction of extensive volcanic edifices. It is estimated that eruptions on slow-spreading systems may occur perhaps every 5000 years and that flow volumes range from 50–1000 $\times$ 10^6 m^3 (Perfit & Chadwick 1998).

Megaplume/Event Plume Formation

A key feature of submarine diking-eruptive events appears to be the catastrophic and voluminous release of volatile-enriched, warm buoyant hydrothermal plumes that rise up to 800 m or more above the seafloor, extend for up to 20 km along the axis, and achieve thickness of several hundred meters (Baker et al. 1987, 1989, 1999, 2000; Lupton et al. 1989; Nojiri et al. 1989; Lupton 1995; Baker et al. 1995a, 1995b; Delaney et al. 1998; Baker 1998). In addition to their spectacular size, the heat content of these ephemeral plumes is formidable; estimates indicate that each plume contains heat equivalent to that produced annually by a typical black smoker field (Lupton 1995). These event plumes, or "megaplumes," are a common manifestation of diking-eruptive events as indicated by their detection from water column studies in 1986–1987, 1993, and 1996 on the Cleft and CoAxial Segments and on the Axial Volcano Rift Zone of the Juan de Fuca Ridge; on the Gorda Ridge in 1996 (Baker et al. 1987, 1989; Lupton et al. 1989; Lupton 1995; Baker et al. 1995a, 1995b; Delaney et al. 1998, Baker 1998); and in the North Fiji basin in 1987 (Nojiri et al. 1989). Their importance lies not only in their thermal and chemical properties, but also in the insights they may provide to the subseafloor biosphere.

The specific mechanism by which event plumes are generated is unclear, but various models have been proposed. These include (*a*) the cataclysmic emptying of a hydrothermal reservoir that resides within the porous and fractured shallow portions of the oceanic crust and (*b*) rapid heating of crustal and/or seawater-derived fluids by heat transfer from the dike or by heating due to cooling of an emplaced lava flow (Baker et al. 1987; Cann & Strens 1989; Cathles 1993; Lowell & Germanovich 1995; Wilcock 1997; Palmer & Ernst 1998; Lupton et al. 1999, 2000; Lowell & Xu 2000; Palmer & Ernst 2000). Constraints on these two hypotheses may be obtained from various chemical data [e.g., the fraction of Fe(II) and helium concentrations in the plume; Massoth et al. 1995, 1998; Kelley et al. 1998) and modeling (Lavelle 1995), which show that plume formation must occur over a few days. These results may favor a model involving the rapid expulsion of a hydrothermal reservoir from the crust as pore fluids come into contact with 1200°C melt or very hot rock associated with the dike injection; additional data are required before the specific mechanism can be unequivocally determined.

Evidence for the seafloor expression of an event plume may have been documented during the 1991 eruption on the East Pacific Rise where there is strong evidence for an impressive explosive event associated with the eruption (Haymon et al. 1993). This includes large amounts of fragmental glass, pieces of tube worms displaced at least 60 m outside the axial summit caldera, voluminous amounts of shimmering water emerging from freshly generated pits, and a several centimeter thick layer of ash-like metal sulfide material that extended over an area ~60 m along strike and ~30 m cross strike which reached heights 10–13 m above the seafloor (Haymon et al. 1993).

Not only is significant heat released during these eruptions, but over short periods of time significant concentrations of volatiles may be both generated and released during submarine diking-eruptive events (Sansone et al. 1991, 1996; Kelley et al. 1998b; Halloway & O'Day 2000). In studies of both the Cleft and CoAxial event plumes, real-time characterization of volatiles such as H_2 and CH_4 were not possible because of the lag in response times, the transient nature of the plumes, and the extremely labile nature of many of the volatile species (de Angelis et al. 1993, Lilley et al. 1995, McLaughlin et al. 1996, McLaughlin 1998, Cowen et al. 1998). However, in 1996, the rapid response to an intense period of seismicity detected by SOSUS on the northernmost segment of the Gorda Ridge (Chadwick et al. 1998, Fox & Dziak 1998) allowed examination of the event plume within days following the eruption. The eruption resulted in the formation of an extremely thick pillow flow reaching nearly 80 m in height and extending for nearly 2.5 km, with an estimated volume of 18×10^6 m^3 (Chadwick et al. 1998). The rapid response to this eruption allowed the first comeasurement of ^3He, H_2, and CH_4 in the associated event plumes, examination of the chemical transformation of these volatile species during aging of the plumes (Kelley et al. 1998b), and the characterization of entrained microbial communities.

The diking-eruptive event at the Gorda Ridge generated an extensive event plume that was roughly 1-km thick. It extended 15 km along axis and at least 8 km across axis, with temperature anomalies ($\Delta\theta$) up to ~0.12°C above background ocean water values (Figure 8) (Baker 1998). Typical of other event plumes, the Gorda plume had a low ^3He/heat ratio of 0.4×10^{-12} cm^3 STP $gm^{-1}{}^\circ C^{-1}$ (Kelley et al. 1998b). A similar megaplume was discovered during the 1987 Cleft event that rose up to 800 m above the seafloor, which extended 17 km along the axis of the rift valley and 20 km across axis. It had a maximum temperature anomaly of nearly 0.20°C and a ^3He/heat ratio of $\sim 0.3 \times 10^{-12}$ cm^3 STP cal^{-1} (Baker et al. 1987, Lupton et al. 1989, Baker et al. 1995, Lupton 1995). The Cleft plume exhibited

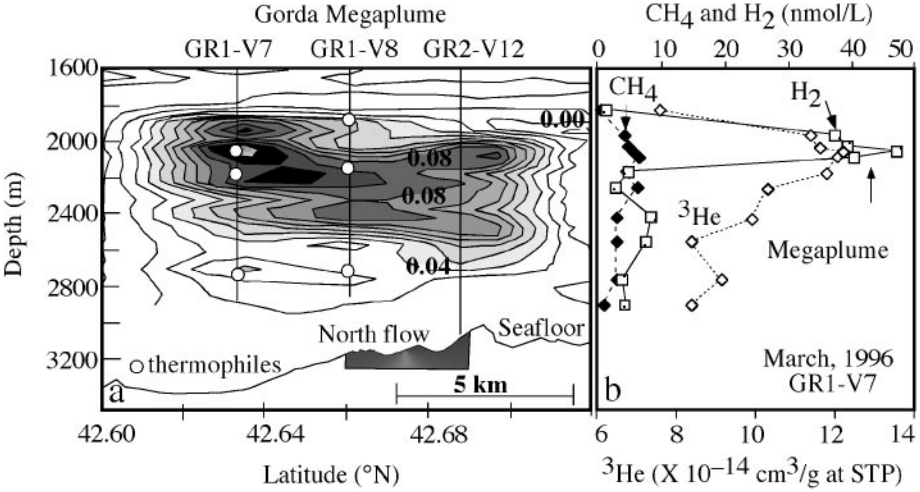


Figure 8 Event plume or megaplume (*a*) as defined by along-axis temperature anomalies ($\Delta\theta$ values in bold) mapped during the first rapid response cruise in March, 1996, just a few weeks after the eruption of the Gorda Ridge (after Baker 1998). Contour intervals are 0.01°C. Vertical water casts (V) were completed to measure temperature, particulates, chemistry, and microbial character of the plume and background ocean water. A subset of these is shown for March (GR1-V7 and V8) and for a follow-on cruise in April (GR2). Thermophiles were only cultured from plume samples, indicating they likely came from a subsurface source (Summit & Baross 1998). (*b*) Corresponding profiles of CH_4, H_2, and ^3He for discrete fluid samples from vertical casts through the megaplume during cast V7. Note elevated concentrations of these volatile species in the plume fluids (after Kelley et al. 1998b).

a distinct layered structure inferred to form from multiple injections of buoyant hydrothermal fluid and was associated with a deeper plume characteristic of steady-state venting. Particles of anhydrite in the megaplume, which dissolve in seawater at temperatures below 150°C, show that the Cleft plume was formed only days before it was sampled (Lupton 1995). The event plumes were ephemeral and were no longer observed two months after the initial surveys, although the deeper chronic plumes were still present.

Tracing the evolution of helium and excess heat in these environments is useful because variations in these two parameters may allow distinctions to be made between plumes emanating from stable hydrothermal sources and highly ephemeral plumes released during magmatic events (Baker 1998; Baker et al. 1987, 1995a,b; Lupton 1995). Studies of these plumes indicate that $^3He/\Delta\theta$ ratios in lower steady-state plumes are 5–15 times higher than event plume fluids in the same localities (Lupton 1995, 1989). For example, stable venting systems that have been perturbed by magmatic events typically exhibit $^3He/\Delta\theta$ ratios of 1.9 to 4.4 cm^3 STP $g^{-1}{}^\circ C^{-1}$

in contrast to event plumes that have $^3He/\Delta\theta$ ratios of 0.3 to 0.4 cm^3 STP $g^{-1}{}^\circ C^1$. Time series monitoring of near-bottom, steady-state plumes following volcanic eruptions shows that in a few years $^3He/\Delta\theta$ ratios decay to values typical of venting environments such as the Galapagos or 21°N on the East Pacific Rise (Baker et al. 1995, Lupton 1995). The monotonic decrease is interpreted to reflect large magmatic inputs to the ridge system in helium and heat during the eruption (in addition to other volatile species), which then decay over a period of a few years or less to values typical of venting systems. Modeling of a two-year time series of temperature and light attenuation measurements from the CoAxial event suggests that simple convective cooling of a dike can produce the observed temporal changes in heat fluxes assuming permeabilities in the range 10^{-11}–10^{-12} and a 3- to 5-m wide dike (Cherkaoui et al. 1997).

Because ^3He and heat are conservative hydrothermal tracers, corresponding measurements of $^3He/\Delta\theta$ and nonconservative tracers that exhibit varying residence times (e.g., H_2, CH_4, and Mn) allow assessment of the source fluids, chemical evolution of the event plume fluids, and possible effects of microbial activity on gas concentrations (Lupton 1995, Lilley et al. 1995, Massoth et al. 1998, McLaughlin 1998). For example, hydrogen concentrations in the initial event plume at Gorda reached a maximum value of 47 nM, 235 times that of ocean background concentration (0.2 nM) (Figure 8) (Kelley et al. 1998b). In contrast, roughly one month later H_2 concentrations, although still elevated, had dropped drastically to 40 times ocean water background values. The highly elevated and variable H_2 concentrations in the Gorda plume, which correlate with well-defined maxima in ^3He and temperature (Figure 8) are interpreted to reflect the intense and rapid interaction of seawater with the basaltic flows and very high-temperature seawater-rock interactions in newly developed subseafloor fractures generated during the diking events (Kelley et al. 1998). Hydrothermal experiments involving the interaction of fluids and olivine show that significant H_2 is generated during oxidation of ferrous iron to magnetite (Berndt et al. 1996, Allen et al. 1998). This interpretation is consistent with field data from sea-surface plume fluids generated during direct interaction of Kilauea lava with seawater where H_2 concentrations of up to 2 μM were measured (Sansone et al. 1991). Calculations by Holloway & O'Day (2000) show that intrusion of a 2-km high dike may release 6.2×10^5 mol H_2/m^2 surface area of dike.

The 1991 eruption on the East Pacific Rise also triggered significant perturbations in volatile concentrations. Hydrogen in "A" vent increased from 25 to 45 mmol/kg, and CH_4 concentrations increased from 0.13 to 0.19 mmol/kg (Lilley & Olson 2001). Plume fluids with H_2 concentrations of 20 nM were also measured following an eruption at Loihi Seamount in 1996 (Sansone et al. 1996), and hydrogen values two to three times normal were measured in the Main Endeavour Field of the Juan de Fuca Ridge following a magnitude 5.0 earthquake in 1999 (Lilley et al. 2000, Lilley & Olson 2001). This burst of hydrogen associated with intense water-rock reactions is likely short lived due to the rapid cooling of the lava flows and cessation of crack propagation. For example, low H_2 concentrations were measured in a weakly developed plume associated with the northern Gorda eruption 2 months after the eruption, and at 9°N, H_2 values had declined to 1 mM in a perturbed hydrothermal vent 11 months following the eruption (Lilley et al. 1992, Kelley et al. 1998b). Similarly, in the Main Endeavour Field, H_2 had returned to its pre-event levels approximately one year following the earthquake (Lilley et al. 2000, Lilley & Olson 2001).

Methane concentrations in the Gorda event plume fluids reached concentrations 16 times background values and are similar to those from stable venting systems in unsedimented ridge environments, where concentrations typically range from ~2 nM to 100 nM (Figure 8) (Lilley et al. 1995). The source for much of this CH_4 may be biogenic as $\delta^{13}C$ is depleted with values of -28 to $-33‰$ (Lupton et al. 2000). Hyperthermophilic organisms called methanogens that utilize CO_2 to produce CH_4 have been isolated from diffuse vents at 9°N on the East Pacific Rise and from the Endeavour Segment of the Juan de Fuca Ridge (Lilley, unpublished data). As discussed previously, CO_2 forms a significant component of gases released during eruptive events, and it is likely that organisms utilize these gases as an energy source (McCollom & Shock 1997, Delaney et al. 1998, McCollum 2000). The elevated concentration of CH_4 in the event plume fluids, its isotopically light nature, and field data from Kilauea (Sansone et al. 1991) that indicates CH_4 is not produced during transient high-temperature alteration episodes associated with new surface eruptions, all suggest that much of the source fluid for event plumes comes from within the deeper crust and not from the lava flows themselves (Kelley et al. 1998b, Lupton et al. 2000).

Major element fluid chemistry of the vents is also affected by seafloor eruptions (Butterfield et al. 1997). The Cleft and 9°N events showed that, immediately after the eruptions, pore water in and beneath the vents was generally heated to boiling. Phase separation produced fluids with low Cl^- concentrations and high concentrations of volatiles and metals in fluids with low pH and low oxygen fugacity (Von Damm 1995, Von Damm et al. 1997). An excellent example of this behavior was the "A" vent at 9°N. This vent was visited three times (at weekly intervals) in April 1991. Water efflux temperatures increased from 390° to 396° to 403°C, H_2S increased from 34 to 66 to 71 mmol/kg, and Cl^- decreased from 80 to 32.6 to 45.2 mmol/kg. Eleven months later, this vent had cooled to 332°C, and Cl^- and H_2S concentrations were 286 and 30 mmol/kg, respectively. By 1994, the Cl^- concentration had reached 453 mmol/kg (Von Damm 1995). This vent appears to have been influenced by hydrothermal circulation along a shallow dike (Haymon et al. 1993). It is suggested that, as the dike rapidly cooled, circulation moved progressively deeper in the crust, promoting venting of chlorine-rich fluids that were sequestered at depth. Increasing Cl concentrations with maturation of perturbed hydrothermal systems is commonly observed. At F-Vent at 9°N, the Cl^- concentration increased from 46 to 846 mmol/kg (0.1 to 1.5 times seawater) between 1991 and 1994 (Von Damm et al. 1997). Similar patterns were observed at both the Cleft and CoAxial sites (Butterfield & Massoth 1994, Butterfield et al. 1997).

Evidence for a Subseafloor Biosphere

Of all the impressive natural phenomena that researchers have witnessed on the seafloor, the massive effusions of biogenic particles emitted from fissures, cracks, and pits following an eruptive event must be one of the most remarkable and important of the past decade (Figure 9) (Haymon et al. 1993, Embley et al. 1995, Delaney et al. 1998). Studies of submarine eruptions reveal unequivocal evidence that beneath the seafloor, to some depth, live diverse populations of single-celled, heat-loving organisms that thrive in the absence of sunlight and oxygen (Holden et al. 1998; Summit & Baross 1998, 2000) (Figure 8). Much is yet to be learned about this biotope and about biological responses to submarine eruptions, but it is clear that microbes are intimately linked to the mantle as a nutrient source.

The first hint of a connection between eruptive events and microbial output came in 1988 on the Cleft Segment of the Juan de Fuca Ridge (Embley et al. 1994). Although there was no explicit study of bacterial activity following the detection of the 1986 megaplume, white biogenic deposits were observed on glassy basalts during Alvin dives to the area. Evidence as to the origin of this material was provided by an eruption in 1989 of MacDonald Seamount (Huber et al. 1990) and by the 1991 study of the East Pacific Rise at 9°N (Haymon et al. 1993). During the eruption of Macdonald Seamount and immediately following it, a sea-surface slick that contained viable hyperthermophiles was sampled 1 km away from the caldera. Cell counts measured $>10^9$ cells/liter of water, and a variety of H_2-oxidizing, sulfur- and sulfate-reducing hyperthermophilic microorganisms were identified (Huber et al. 1990). Alvin observations of 9°N indicated that associated with this eruption was the massive, widespread, and chaotic output of high-temperature, diffusely flowing fluids emanating from a network of cracks, deep pits, and 1–5-m wide fissures in the seafloor between $9°49.6'$N and $9°50.4'$N (Haymon et al. 1993, Shank et al. 1998). Contemporaneous with these changes was the rapid and substantial effusion of microbial-generated particles called “floc” that were entrained in the diffusely venting fluids emanating from the seafloor. This intense, particle-laden hydrothermal flow created “snowstorms” that reached 50 m above the seafloor (Figure 9). In addition, mats of filamentous bacteria, 1–10-m thick, covered 50 m^2 areas of fresh lava flows, and floc accumulated as deep drifts (Haymon et al. 1993, Shank et al. 1998). Follow-on studies of the flocculant material showed that it was composed primarily of inorganic, sulfur-rich filaments with a low organic carbon content (Nelson et al. 1991). Subsequent laboratory work indicated that this material may be rapidly produced by microscopic ($0.3 \times 0.6\ \mu$m) vibrioid organisms that grow at the interface between sulfide and oxygen (Taylor & Wirsen 1997).

In 1993, similar observations were made following the diking-eruptive event on the CoAxial Segment (Embley et al. 1995, Holden et al. 1998). Shortly after the eruption, water began flowing through the interstices of pillow and lobate lava flows at temperatures up to 51°C in a 50-m wide zone centered over the crest of the flow. Extensive venting was documented for at least 4 km south of the flow along the southern part of the fissure. Temperatures of fluids venting from the flow decreased from 50 to 36°C between July and October, 1993. By July of 1994, venting at the Flow Site had virtually stopped except in one area that was venting 9°C water (Butterfield et al. 1997, Embley et al. 2000). Hydrogen sulfide was undetectable in these waters; CH_4 concentrations were low in October, and Fe and Mn concentrations were elevated (Massoth et al. 1995, Butterfield et al. 1997). No hyperthermophilic bacteria were isolated from samples collected at the lava flow sites, but extensive surfaces of the fresh pillow ridge were coated with yellow-orange bacterial mat (up to 10-cm thick) composed predominantly of iron-oxidizing bacteria (Figure 9) (Holden et al. 1998). ROPOS observations over the new lava and the active fracture system revealed no evidence of pre-existing vent animal communities (Tunnicliffe et al. 1997).

Roughly 20 km to the south of the Flow Site, widespread evidence of massive ejection of flocculated microbial material was encountered in July and October of 1993 at a site called Floc (Embley et al. 1995, Delaney et al. 1998, Holden et al. 1998). This site lacked any previous signs of venting (the closest known area of hydrothermal venting previously known was 15 km to the south). In this area, a blizzard-like "storm" of flocculated mat fragments rose buoyantly 200 m into the water-column for hundreds of meters on either side of the axial valley. Extensive bacterial mats covered the local seafloor. Observations with Alvin showed that flocculate-laden fluids were issuing from openings tens of centimeters across within the fissure network. In some locations, intense effusions of flocculent exhibited a very high buoyancy flux, which was most likely caused by the massive low-temperature venting. All venting temperatures observed at the Floc site in 1993 were below 23°C. Scanning electron microscopy and microscopic examination of flocculant material collected from both the Flow site and Floc site show that it was composed of filamentous, coccoid, and rod-shaped microbial forms coated by iron and silica (Juniper et al. 1995).

Continued diffuse, low-temperature venting at the Floc site of water containing culturable hyperthermophiles showed that a microbial community had developed in this area. Several physiological types of thermophilic (organisms that grow at temperatures >50°C) and hyperthermophilic microorganisms were isolated from the fluids (Holden et al. 1998). Microbes cultured at temperatures in excess of 90°C include sulfur-reducers and methanogens (Holden et al. 1998). Temperatures of the fluids sampled were more than 50°C lower than the minimum growth temperature of some of the hyperthermophiles cultured, suggesting that there was a previously stable, high-temperature, anoxic biotope below the seafloor and that the microbial organisms were entrained into the cooler vent fluid. This interpretation is also supported by the chemistry of the venting fluids at Floc, which had CH_4 concentrations of >120 μmol/kg (Kelley et al. 1998b). This level is significantly higher than the value of 2–4 μmol/kg expected if the CH_4 in these diffuse vents was produced exclusively by seawater dilution of typical high-temperature vent fluids (Kelley et al. 1998b).

In 1996, water column and microbial data collected from Gorda allowed testing of the hypothesis that seafloor microbial communities inhabit the seafloor in areas where no previous venting had been observed. Microbiological sampling of the event plumes and background ocean water on three occasions investigated a total of 21 plume samples and 12 background ocean water samples (Summit & Baross 1998, Summit 2000). Thermophiles were isolated from 17 of the event plume samples, but none from the background water (Figure 8). Most of the isolates grew over a broad temperature range (45–90°C), with optimal growth temperatures between 80 and 90°C and doubling times of one hour. The abundance of organisms in the plume exceeded 200 organisms/liter, and DNA analyses indicate that all of the organisms are in the order *Thermococcales* (Summit 2000). These organisms appear to be nutritionally and phylogenetically distinct from previously described marine species in that they can grow on lower concentrations of organic carbon than any heterotrophic thermophillic archaeon sampled to date (Summit 2000, Summit & Baross 2001). The detection of thermophiles and hyperthermophiles only in plume water and not in ocean background water from the Gorda event shows that their occurrence could not have been due to simple entrainment from seawater. In addition, their inability to grow below temperatures of 45°C requires that they could not have populated the plume after its formation. These data, coupled with the chemistry of the plume fluids, lead to the conclusion that the novel microorganisms were entrained in the plume from a warm, anoxic, subseafloor environment that was tapped during the eruptive event (Summit & Baross 1998, Summit 2000).

Although investigation of these systems is relatively young, data collected during rapid-response studies support a model in which subseafloor biotopes are episodically perturbed by diking-eruption events that temporarily destroy or enrich thermophilic zones within the subsurface (Delaney et al. 1998) (Figure 10). The correspondence between the massive effusion of microbial material from the seafloor, the apparent bloom of microorganisms for several weeks following an eruption, and the enriched volatile concentrations in megaplume fluids and in hydrothermal vents perturbed by eruptions (Lilley et al. 1992, Haymon et al. 1993, Embley et al. 1995, Holden et al. 1998, Delaney et al. 1998, Kelley et al. 1998b). Delaney et al. (1998) and Summit & Baross (1998) suggest that some of the supporting energy for these microbes comes from the degassing of volatiles associated with the eruption and from volatiles released during high-temperature interaction of seawater and dike-extrusive material (Figures 7 and 8). Viewed in this context, a major new insight has arisen—submarine volcanoes support life in the absence of sunlight.

The strong thermal, chemical, and porosity-permeability gradients in submarine environments directly influence the habitat locations and types of microorganisms living on or below the seafloor (Figure 10). Within young shallow crust, porosities can be as high as 12%–36% (Pruis & Johnson 1996, 1998; Fisher 1998). These systems are water dominated with ample void space for microbial habitats (Figure 10). In the uppermost extrusive layers, away from high-temperature upflow zones, fluid temperatures are likely to be low (<20°C), and fluid chemistry is similar to that of seawater. With increasing depth, fluid temperatures generally increase, and the system may be either aerobic or anaerobic, depending on the conditions of fluid circulation (McCollom & Shock 1997, Delaney et al. 1998). In deeper, higher temperature environments, anaerobic conditions are likely to dominate, bulk permeabilities are generally lower, and hyperthermophilic habitats are stable. In this setting, reductive reactions involving methanogenesis and sulfate and sulfur reduction are likely sources of energy for the microorganisms. In the absence of an intrusive event, these environments may remain stable for extended periods of time (Figure 10).

During a volcanic event, the subseafloor biotope may be strongly disrupted (Figure 10). Organisms along with interstitial fluids entrapped in the void spaces of the basalts and older dikes are released into the water column within hours to days following intrusion of the dike and ensuing eruption (Baker et al. 1987, Butterfield 1997, Delaney et al. 1998) (Figure 10). The diking events may either temporarily destroy or enrich the thermophilic biotope within some subsurface areas affected by the dike, resulting in the flushing of thermophiles into the event plume followed by decreasing concentrations in the plume over time (Figure 10). Diffuse flow at the CoAxial sites harbored high numbers of thermophiles within weeks to months following the eruption; however, when these same sites were sampled a year or more after the eruption, no hyperthermophiles were cultured or their numbers were greatly reduced (Holden et al. 1998).

Within days to weeks of the diking event, carbon and energy sources from magmatic volatiles and hydrothermal fluid are mixed in the high porosity layer with oxygen, sulfate, and nitrate from seawater (Butterfield et al. 1997, Delaney et al. 1998). This results in the enrichment of a metabolically diverse group of mesophilic microorganisms (growth between 5 and 45°C) including sulfur, iron, and methane oxidizers (Holden et al. 1998). This is manifested as massive amounts of white floc material resembling "snow" that has been observed at four of the new eruption sites (Embley et al. 1995, Haymon et al. 1993, Juniper et al. 1995, Holden et al. 1998). Similar material from the CoAxial vent on the Juan de Fuca Ridge contained iron-encrusted sheaths (Juniper et al. 1995, Holden et al. 1998). Filamentous sulfur that is morphologically similar to the floc material collected at 9°N can also be produced by mesophilic, aerobic, hydrogen sulfide–oxidizing microorganisms (Taylor & Wirsen 1997). These oxidative microbes are responsible for the mats that extended for hundreds of meters, which coated the surface and interstices of the new pillow flows. Within a year, macrofaunal communities (tubeworms, polychaetes, crabs) colonize sites of diffuse flow, thriving off the chemical energy and diverse microbial populations that now inhabit the area (Tunnicliffe et al. 1997). Macrofaunal assemblages and microorganisms die off or become dormant with loss of a heat and nutrient source.

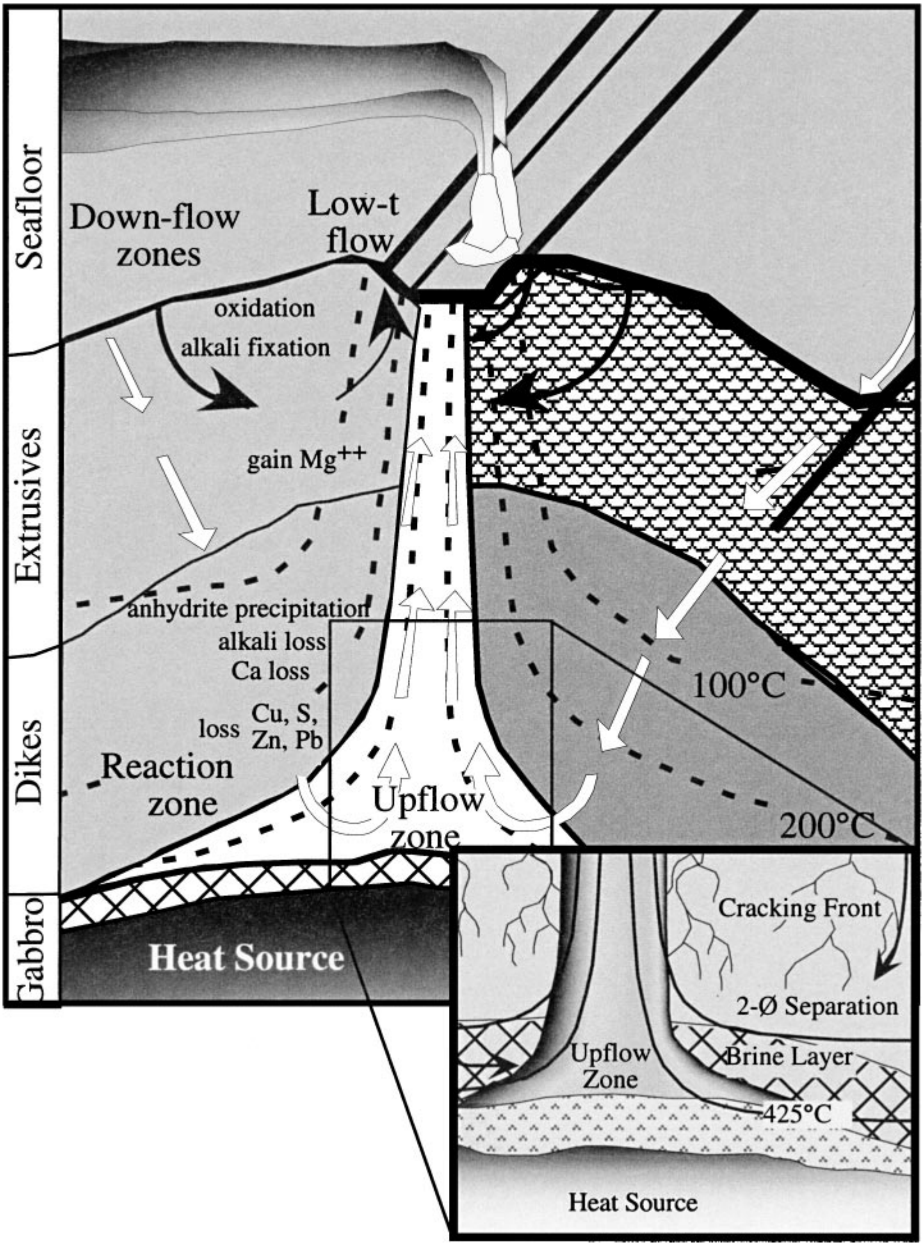
The source of organic carbon necessary to support the thermophilic heterotrophs is unknown, although we hypothesize that microbial carbon from dike-stimulated microbial oxidative metabolisms could settle into high-temperature biotopes as the dike cools and oxidative microbial productivity and venting decrease (Figure 10). Again, this model predicts that there exists an active thermophilic biotope in the subsurface. The methanogens are supported by hydrogen and CO_2, and the heterotrophs could be supported by downward migration of carbon supplied from mesophilic organisms from the extrusive layer or from carbon produced by methanogens. Low levels of these oxidative mesophilic organisms remain in the extrusive layer between diking events and are the source organisms for the massive microbial blooms following the eruption. They would be either in a dormant stage or growing slowly depending on whether or not some hydrothermal fluids are reaching the surface layers.

An implication of this model is that the area in the crust occupied by thermophiles may be extensive. Diking events, which occur on timescales of years to decades in magmatically active fast- to intermediate-spreading environments, may provide the mechanisms for replenishing thermophilic biotopes with organic carbon and nitrogen. Tests of this model could include drilling through the extrusive layer of the crust at a site not known to have had a recent eruption event and determining if the zone between 50 and 150°C harbors high numbers of thermophiles.

STABLE HYDROTHERMAL-MICROBIAL HABITATS

In addition to transient hydrothermal systems induced by diking-eruptive events, the heat from cooling of deep oceanic crust and mantle supports hydrothermal circulation systems that may be operative episodically for tens of thousands of years and that supply a significant, but as yet poorly quantified, amount of volatiles to the overlying ocean (Figure 4). In these more-stable environments, circulation of seawater through the crust is the major pathway of geochemical exchange between the oceanic lithosphere and the hydrosphere (Figure 11). Long-lived hydrothermal circulation systems occur in young crust on axis, in old crust several kilometers away from spreading centers, and also in the cooler ridge flanks in crust up to ~65 Ma (Fisher et al. 1990; Davis et al. 1992, 1996; Alt 1986, 1996; Wheat & Mottl 1994, 2000; Lalou et al. 1995; Gracia et al. 2000; Kelley et al. 2001a,b; Buatier et al. 2001; Butterfield et al. 2001).

Vigorously venting black smokers on the ocean floor that reach temperatures of >400°C are fueled by circulation and heating of seawater at depths of 2–8 km within the oceanic crust (Figure 4). The same process also supports more subdued, lower-temperature venting systems that typically emit fluids at 5°C–50°C. There is a growing body of evidence that the lower-temperature, diffuse systems may also carry a significant amount of heat out of the crust within spreading environments (Rona & Trivet 1992, Schultz et al. 1992, Schultz & Elderfield 1997). In volcanically active areas such as the East Pacific Rise, convection of heated seawater, or hydrothermal fluid, is driven by heating from magma chambers at depths of ~2 km below the seafloor. Shallow circulation is believed to occur through large axial faults and through the highly porous and fractured extrusive layer where permeabilites may exceed 10^{-10} m^2 (Fisher 1998). At deeper crustal levels, the exact fluid pathways are unclear, but many models support a fine fracture network called a cracking front (Figure 11) (Lister 1974, 1983). In this model, the magma


Seafloor
Extrusives
Dikes
Gabbro
Down-flow zones
Low-t flow
oxidation
alkali fixation
gain Mg++
anhydrite precipitation
alkali loss
Ca loss
loss Cu, S, Zn, Pb
Reaction zone
Upflow zone
100°C
200°C
Heat Source
Cracking Front
2-Ø Separation
Upflow Zone
Brine Layer
425°C
Heat Source

chamber-hydrothermal transition is bounded by a very narrow conductive boundary layer, below which the hot rocks are too ductile to sustain significant stress (Figures 4 and 6). A thin conductive boundary layer, perhaps only tens of meters in thickness, is required to maintain a high heat flux for extensive periods of time (Lister 1983, Lowell et al. 1995, Wilcock & Delaney 1996).

It is at the leading edge of the cracking front where down-welling, hydrothermal fluids are believed to obtain their final compositions before rising buoyantly to the seafloor (Seyfried 1987, Alt 1995, Seyfried & Ding 1995, Alt & Teagle 2000). This "reaction zone," which occurs at the highest temperature and deepest portion of the hydrothermal cell, is poorly understood. Field studies (Kelley & Delaney 1987, Kelley et al. 1993, Gillis et al. 1993) suggest that it may be characterized by a downward propagating set of fluid-filled fractures that are eventually filled in with high-temperature minerals such as amphibole ± epidote, and quartz (Nehlig et al. 1994, Gillis et al. 2001). Geothermometric and isotopic analyses of deep-seated plutonic rocks indicate that penetration of fluids may occur at temperatures of 500°C to as high at 750°C (Stakes et al. 1991; Gillis & Roberts 1999; Manning et al. 1996, 2000). These temperatures agree well with those obtained at the basal section of sheeted dikes based on amphibole geothermometry (Gillis et al. 2001). During fluid circulation within the narrow crack network, heat is mined from the surrounding wall rock, setting up a series of complex feedback loops. Because heat is withdrawn, the host rocks contract and fracture, which allows additional deepening of the crack network and removal of more heat (Lister 1974, 1983). Crack propagation rate is limited by the efficiency of fluids within the cracks to carry heat upward. Modeling of this process suggests that the sheeted dike-gabbro transition may be breached by the cracking front within ~1 km of the ridge and to the mantle within 6 km of the axis (Manning et al. 2000). As discussed previously, the brittle-ductile transition that controls the depth of fluid penetration is not stable but is affected by processes such as the input of new melt into a magma chamber, dike injection, and failure of the cap rock by melt-volatile overpressuring. In systems that are not in a magmatic phase, such as the Endeavour Segment of the Juan de Fuca Ridge and large portions of slow to ultra-slow spreading ridges, on-axis circulation is believed to be driven by cracking of hot crystalline rocks at temperatures of

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Figure 11 Schematic showing chemical reactions and mineral precipitation associated with down-welling recharge systems, low-temperature shallow circulation, and deep penetration by hydrothermal fluids into the reaction zone. At the base of many mid-ocean ridge hot springs, the seawater-derived fluids undergo either boiling or condensation (2–0 separation). If condensation occurs for prolonged time periods, a brine layer may develop deep within the crust. These fluids may be expelled during waning of high-temperature hydrothermal flow. Fluid penetration is believed to occur during downward migration of small fracture networks and cooling of the crust along a cracking front, which allows fluids to have continual access to hot, fresh rock.

500°C–700°C to depths of 8 km or by lower-temperature exothermic serpentinization reactions (Rona et al. 1987, Wilcock & Delaney 1996, Kelley et al. 2001a).

Along the downward journey from the ocean floor to depths of 2–8 km beneath it, seawater-derived fluids undergo significant changes in temperature, composition, and volatile concentration as the heat source is approached (Figure 11). The chemistry of the resultant hydrothermal fluid is determined by three factors: the temperature of the rocks through which the fluids circulate, how much water has previously passed through that same crack network, and the composition of the host rock. As cool, dense seawater migrates deep within the crust along large- and fine-scale networks of cracks, the fluids interact and exchange elements with the surrounding host rock. In the shallow, cooler parts of the fluid pathways away from hydrothermal discharge sites, low-temperature oxidation and alkali fixation dominate (Figure 11) (Alt et al. 1986, 1996; Alt 1995; Gillis & Robinson 1990; Gillis & Banerjee 2000). In down-welling zones, extensive replacement of the glassy rinds of pillow basalts and sheet flows occurs by minerals such as Fe-oxyhydroxides, zeolites, and clays, which are common at temperatures below ~100°C (Gillis & Robinson 1985; Alt et al. 1986, 1996; Alt 1995; Gillis and Robinson 1990; Gillis & Banerjee 2000). These minerals are also common as veins that fill radial fractures in the basalts. Alkalis such as K, Rb, and Cs are fixed within the replacement minerals as are rare earth elements and water. Uptake of these elements is balanced in the rocks by loss of Mg, Si, S, and in some cases Ca (Muehlenbachs & Clayton 1972; Thompson 1983; Mottl 1983; Seyfried 1987; Alt et al. 1986; Gillis & Robinson 1985, 1990; Alt 1995; Gillis & Banerjee 2000).

As fluids migrate deeper into the crustal section, elements such as Cu, Zn, Fe, Pb, S, and SiO_2 are leached out of the rocks at temperatures of 350°C–550°C and are incorporated in the hydrothermal fluid (Figure 11) (Mottl 1983, Seyfried 1987, Seyfried et al. 1988, Von Damm 1995). In addition, at temperatures above ~150°C, the uptake of Mg in the rocks is accompanied by loss of alkalis (K, Rb, Li) from the basaltic material (Humphris & Thompson 1978, Thompson 1983, Seyfried 1987, Gillis & Robinson 1990). Elements such as Na, Mg, and Ca are added to the rock to form greeschist facies mineral assemblages that include minerals such as chlorite, amphibole, and albitic plagioclase (Thompson 1983, Mottl 1983, Gillis et al. 1993, Alt 1995). These minerals commonly form along grain boundary margins and fill microfractures that crosscut mineral phases (Kelley & Delaney 1987, Gillis et al. 1993, Kelley et al. 1993). The base of the reaction zone, where hydrothermal fluids reach their end-member composition, is believed to occur either near the sheeted dike-gabbro interface or within the underlying gabbroic rocks. In most basaltic environments, fluids that eventually reach the seafloor at temperatures of 350°C–400°C are reduced, acidic (pH 2–6), and highly enriched with respect to seawater in Li, K, Rb, Cs, SiO_2, Cu, Fe, H_2S, CO_2, He, H_2, and CH_4 (Von Damm 1995). Transient thermal and chemical perturbations may occur in the gabbros and sheeted dikes during intrusion of melt into the country rock. Such events may manifest themselves by overprinting of high-temperature mineral assemblages on lower-temperature assemblages (Gillis et al. 2001).

Condensation and Boiling

In addition to water-rock reactions within high-temperature reaction zones, there are many different processes that can affect the composition of vent effluent during ascent to the seafloor. Two of the most important of these processes are condensation and boiling. These processes govern the volatile concentration of the vent fluid and are of particular importance in partitioning of chloride and metals. The development of low-salinity vapors and brines by condensation and/or boiling has been inferred to be an active process in high-temperature systems operative beneath hydrothermal vents at 9°N on the East Pacific Rise (Von Damm et al. 1991, 1997; Lilley et al. 1992; Haymon et al. 1993; Von Damm 1995, 2000; Fornari et al. 1998) and on the Juan de Fuca Ridge within Axial Seamount, and at the Endeavor Segment (Delaney et al. 1992, 1997; Butterfield et al. 1990, 1994; Fox 1990; Lilley et al. 1993).

In an evolving magma-hydrothermal system, as seawater-derived fluids penetrate into the oceanic crust and approach the heat source, they must traverse a series of compositionally dependent condensation curves (Kelley & Delaney 1987; Fournier 1987, 1999). As hydrothermal fluids migrate into the high-temperature reaction zone and obtain their end-member fluid compositions (Seyfried et al. 1987, Berndt et al. 1989, Seyfried & Ding 1995, Alt 1995), the fluid properties undergo dramatic changes: Viscosity and density decrease, heat capacity increases, the coefficient of thermal expansion increases, and near the two-phase curve there is a maximum in quartz solubility (Norton 1984, Lowell et al. 1995, Fournier 1999). These changes translate into a zone of maximum transport efficiency and promote the rapid, buoyant rise of end-member hydrothermal fluids within the fracture networks to form upflow zones (Figure 11). Recent modeling studies indicate that this nonlinear behavior may limit fluid temperatures of vents to ~400°C, even though abundant evidence indicates that the temperature of the heat source may be 100°C–300°C higher (Jupp & Schultz 2000). Circulating seawater-like fluids that intersect the portion of the two-phase curve at conditions less than the critical point (CP) (CP = 298 bars and 407°C for seawater; Bischoff & Rosenbauer 1988) undergo boiling (Figure 6). At temperatures and pressures greater than the CP, seawater-like fluids that intersect the condensation portion of the curve will separate out droplets of brine from a low-salinity vapor (see Fournier 1987 for additional discussion).

The geometry of the upflow zone at depth is not known but may be similar to an artery system in which a fine capillary fracture network progressively feeds fluids into larger, more through-going fractures at shallow crustal levels. Whatever the geometry is, however, it is clear that most end-member hydrothermal fluids pass into the zone of supercritical phase separation (condensation) during their transport to the surface, resulting in the formation of vapor (i.e., fluids with less than seawater salinity) and brines (i.e., fluids with greater than seawater salinity) (Delaney et al. 1987, Kelley & Delaney 1987, Vanko 1988, Kelley et al. 1993, Saccocia & Gillis 1995, Von Damm 1995, Butterfield et al. 1997). Under appropriate conditions, the salinity of the brine and vapor phases are likely to change as the fluids migrate up the conduits. Differences in density and wetting characteristics will promote segregation of the immiscible vapor and brine phases, and with a decrease in pressure the segregated phases will either continue to undergo condensation or boiling (Delaney et al. 1987, Kelley & Delaney 1987, Goldfarb & Delaney 1988, Fox 1990). It is well documented that both of these processes occur in hydrothermal systems at Axial Seamount, at hydrothermal fields along the Endeavour Segment of the Juan de Fuca Ridge, and at venting sites along the East Pacific Rise (Butterfield et al. 1990, 1994; Delaney et al. 1992; Haymon et al. 1993; Von Damm 1995; Lilley et al. 1995; Fornari et al. 1998).

The preservation of 5–20 wt% NaCl equivalent inclusions along healed microfractures within oceanic plutonic rocks suggests that segregation of the vapors and brines occurs deep within these system as well (Delaney et al. 1987, Kelley & Delaney 1987, Fournier 1987, Goldfarb & Delaney 1988, Bischoff & Rosenbauer 1989, Fox 1990, Von Damm 1995, Von Damm et al. 1997). A consequence of this is that density-temperature differences in the separated fluids may result in the establishment of double diffusive convection cells at depth (Bischoff & Rosenbauer 1989). Intermittent release of deep-seated brine and vapor-rich pools during episodic fracturing events appears to be a common process affecting the compositions of fluids venting on the seafloor, where salinities change from <1 wt% NaCl to 7 wt% NaCl over the lifetime of a vent system (Von Damm et al. 1992, 1997; Von Damm 1995; Butterfield et al. 1997). More recent studies suggest that vent fluid salinities may also be affected by the dissolution or precipitation of halite (Berndt & Seyfried 1997, Von Damm 2000).

Volatiles in Hydrothermal Fluids

In addition to elemental changes, the concentrations of H_2, CH_4, and CO_2 may be modified during fluid ascent. These volatile species are incorporated into hydrothermal fluids through direct degassing of magma chambers, by high-temperature leaching from the enclosing host rock, and by inorganic synthesis at high-temperature involving mineral-fluid reactions (Welhan & Craig 1983, Welhan 1988, Lilley et al. 1992, Butterfield et al. 1994, Kelley, 1996, Kelley & Früh-Green 2000). The conditions under which they form and the flux of these gases to the hydrosphere are of great interest because they form nutrients critical to microbial development. The concentration of CO_2 in end-member fluids is typically in the range of 2–20 mmol/kg; however, in volcanically active systems where volcanic gases are directly incorporated into the high-temperature limb of the convection cell, or where boiling occurs, values of up to ~300 mmol/kg have been measured (Lilley et al. 1992, Butterfield et al. 1994). Boiling is of particular importance in that the volatiles will be preferentially incorporated into the vapor phase (Butterfield et al. 1990, 1994; Lilley et al. 1992).

Analyses of hydrothermal fluids in bare-rock hydrothermal environments show that CH_4 is generally a trace component of the fluids (Welhan & Craig 1983, Welhan 1988, Lilley et al. 1992). Isotopic analyses indicate that in basaltic environments some of the CH_4 may be formed by re-equilibration of CO_2 on cooling of the volcanic gases below 700°C, but there is a growing body of evidence from field and experimental studies that in mafic and ultramafic systems mineral-fluid reactions play a critical role in the production of CH_4, H_2, and possibly some hydrocarbon species (Janecky & Seyfried 1986, Kelley 1996, Berndt et al. 1996, Allen et al. 1998, Kelley & Früh-Green 1999, Kelley et al. 2001a, Holm & Charlou 2001, Früh-Green et al. 2002). Intense CH_4 degassing has been observed along the Mid-Atlantic Ridge in crustally attenuated zones in which serpentinized peridotite bodies outcrop on the seafloor (Rona et al. 1987, 1992; Charlou et al. 1992, 1998; Charlou & Donval 1993; Bougault et al. 1993; German et al. 1996; Gracia et al. 2000), pore-waters sampled during ODP Leg 125 at a serpentinized seamount in the Mariana forearc yielded high concentrations of CH_4 and C_2H_6 (Haggerty 1989, Mottl & Haggerty 1989), and CH_4 seeps have been observed emanating from serpentinized bodies in the Zambales ophiolite in the Philippines (Abrajano et al. 1988).

Recent studies show that $CH_4 \pm H_2 \pm$ hydrocarbon-bearing fluids may be common in the plutonic section of the oceanic crust as well as in the mantle. $CH_4 + H_2O \pm H_2 \pm$ graphite(?)-bearing fluid inclusions are pervasive throughout the 1500-m section gabbroic rocks recovered from the Southwest Indian Ridge at Hole 735B that contain up to 40 mol% CH_4. Isotopic, microthermometric, and petrographic analyses of the inclusions indicate that the fluids are a product of seawater alteration of mafic material at a temperature of ~400°C (Vanko & Stakes 1991, Kelley 1996, Kelley & Früh-Green 1999). Formation of CH_4- and H_2-rich fluids in deep-seated hydrothermal systems involves complex reactions that require the infiltration of water and may involve a series of metastable reaction steps during serpentinization (Holloway 1984; Shock 1990, 1992; Allen et al. 1998; Kelley & Früh-Green 1999, Früh-Green et al. 2002). These reactions are commonly accompanied by conditions of extremely low fO_2 at the serpentinization front (Frost 1985, Früh-Green et al. 1996, Kelley 1996, Alt & Shanks 1998, Früh-Green et al. 2002). Reduction accompanies the formation of FeNi alloys in serpentinites, and these alloys and magnetite may act as catalysts enabling Fischer-Tropsch-type reactions ($CO_2 + 4H_2 = CH_4 + 2H_2O$) to form significant amounts of methane, hydrogen, and other hydrocarbons (e.g., Alt & Anderson 1991, Kelley 1996, Berndt et al. 1996, Früh-Green et al. 1996, Allen et al. 1998). Experiments of Berndt et al. (1996) show that alteration of olivine at 300°C and 500 bars leads to elevated H_2 contents and the reduction of dissolved CO_2 to form reduced gaseous species such as methane, ethane, propane, and a significant amount of amorphous carbon or graphite. Continuation of this study by Allen et al. (1998) demonstrates that the H_2 may react with the CO_2-bearing fluids to produce large quantities of formic acid and smaller concentrations of alkane and alkene gases. The carbon source for these reactions is equivocal, however, because similar experiments by McCollom & Seewald (2001) examining the reduction of CO_2 with serpentinized olivine using labeled ^{13}C failed to produce significant quantities of CH_4 and other hydrocarbons.

If the total methane concentrations (0.3–0.6 mmol/kg) in the SWIR samples are representative of gabbroic rocks in other submarine settings, and assuming that plutonic layer 3 is 6-km thick and that it represents ~60% of the oceanic crust, then the plutonic section of the oceanic crust may contain $\sim 10^{19}$ g of abiogenic methane (Kelley & Früh-Green 1999). Based on preliminary studies (Früh-Green et al. 1996; Früh-Green, unpublished data), the shallow mantle may be an even larger reservoir for abiogenically produced methane. If these carbon-bearing fluids are released during subsequent hydrothermal events, they may be an important energy source for subsurface and vent-associated chemosynthetic microbial communities that may include CH_4- and H_2-oxidizers (McCollum & Seewald 2001, Kelley et al. 2001a).

Methane and H_2 production may be significant along extensive sections of the Mid-Atlantic, Arctic, and Indian Ocean ridges. In zones of low magmatic supply, which characterize many segments along these three ridges, serpentinization and unroofing of mantle and deep, hot crustal rocks are significant processes in crustal development. Migration of fluids along deeply penetrating fault systems may intensify hydration of deep-seated mafic/mantle material, leading to significant CH_4 ($+ H_2 +$ hydrocarbons) generation. In intermediate spread crust, this process may also be important during the waning stages of magmatic activity where the brittle-ductile boundary has undergone significant migration into crustal layer 3 (Wilcock & Delaney 1996, Fornari et al. 1998). Limited sampling of plutonic rocks from fast-spreading environments precludes evaluation of the importance of CH_4 generation during fluid-rock interactions. If this process is significant, however, it is likely to occur off-axis because the shallow nature of the brittle-ductile boundary at the ridge axis is likely to prevent fluid penetration into the gabbroic sequence.

HYDROTHERMAL VENTS ON THE SEAFLOOR

The past 20 years has seen new discoveries and accrual of a wealth of information about submarine hydrothermal vents that are now known to occur in all the world's oceans (Figure 1). From investigation of mid-ocean ridges has come documentation of sulfide chimneys that reach >45 m in height, the discovery of a new class of peridotite-hosted systems that support actively venting carbonate towers that rise 60 m above the seafloor, sulfide edifices that grow > 10 m in a year, tube worms that grow >85 cm per year, and abundant new species of animals and microbes with unique metabolisms that do not require energy derived from sunlight (Deming & Baross 1993, Robigou et al. 1993, Lutz et al. 1994, Karl 1995, Fisher 1995, Delaney et al. 1998, Shank et al. 1998, Kaye & Baross 2000, Summit 2000, Van Dover 2000, Kelley et al. 2001a, Reysenbach & Cady 2001, Takai et al. 2001). How such venting systems are established is not well known. In nascent hydrothermal systems, the initial plumes of hot water that rise through the seafloor from the reaction zone must displace the surrounding cooler seawater, which saturates the shallow portions of the oceanic crust. For high-temperature fluids to reach the seafloor, the channels through which this water rises must become progressively insulated by deposition of minerals such as quartz, sulfide, and chlorite (Alt 1995, Kelley et al. 2001b). Presumably, the onset of venting is marked by a period of lower-temperature diffuse flow that lasts until the system is well insulated, but how long this insulation process takes is unclear.

Once a high-temperature venting system is established, the black smokers grow and evolve as venting continues at the seafloor. The examination of stockwork (fossilized plumbing networks) deposits in ophiolites and the large size of some deposits indicate that, in some environments, flow channels may be operative on and off for several thousands of years (Richards & Cann 1989, Hannington et al. 1995, Humphris & Cann 2000, Humphris & Tivey 2000). The upflow zones develop alteration haloes analogous to those in porphyry copper systems, where high-temperature mineral assemblages are focused near the core of the upflow zone, and lower-temperature minerals occur in the outer, shallower portions of the system. However, during the lifetime of a system, individual conduits may close and reform, creating a highly complex stockwork array that records multiple hydrothermal pulses and events.

As the metal-rich, low pH, reduced, 350°C–400°C fluids mix turbulently with oxygen-rich, cold (2°C) seawater, drastic temperature-chemical changes cause minerals such as anhydrite, barite, pyrite, chalcopyrite, and sphalerite to precipitate (Tivey & Delaney 1986; Tivey 1995a,b; Hannington et al. 1995; Tivey et al. 1999). Many of the fine-grained sulfide particles are carried upward into the buoyant, jet-like plumes that vent at more than a meter per second; the particles are carried 100–200 m up into the overlying ocean water, forming broad, extensive hydrothermal plumes (Lilley et al. 1995). Some of these particles sink back to the ocean floor, oxidize, and become hydrothermal sediment, and some are scavenged by microbial communities that live within the plumes (Lilley et al. 1995, Cowen et al. 1998). Sulfide and sulfate minerals not carried away in the hydrothermal plumes are deposited at the vent orifice, causing chimneys to grow upward and outward over time (Figure 12) (Haymon 1983, Tivey & Delaney 1986, Delaney et al. 1992, Robigou et al. 1993, Hannington et al. 1995, Tivey 1995).

Analyses of chimney deposits in a variety of environments have allowed general models of their evolution to be developed (Haymon 1983, Tivey & Delaney 1986, Hannington et al. 1995, Tivey 1995, Tivey et al. 1999, Delaney et al. 2001). In many chimneys, anhydrite ($CaSO_4$) and fine sulfide particles form the initial chimney structure. Anhydrite precipitates from seawater at temperatures of ~150°C, and during seawater mixing with hot hydrothermal fluids, sulfides and anhydrite coprecipitate. With continued growth, this fine-grained, friable structure allows the inner fluids to become insulated from surrounding seawater, turbulent mixing becomes less within the structure, and temperatures rise, allowing sulfides to precipitate. With continued venting, lower-temperature sulfide minerals such as pyrite and sphalerite form an edifice, and at temperatures of ~350°C, chalcopyrite begins to form. Many structures develop strong mineralogical zonations with annular rings of chalcopyrite lining the inner open channels, followed outward by variable mixtures of sphalerite, marcastite, and pyrite. With aging of the structure, conductive cooling of high-temperature fluids that circulate within the pores of the chimney allows precipitation of amorphous silica, which gives the chimney strength (Tivey 1995, Tivey et al. 1999). Intense recrystallization of sulfide minerals is common in most structures, making them analogous to metamorphic rocks.

No data exist on modification of hydrothermal fluid chemistry within the pores during circulation over time. But, it may be that the microbial communities that thrive within the warm, porous interiors significantly modify pore fluid chemistry. In the outer zones minerals such as anhydrite, barite, and clay fill fine pore spaces, indicating infiltration of seawater into the structure.

Numerous observations of these systems show that the size of the edifices varies dramatically with spreading rate, that they exhibit highly variable morphology, and that their ecology varies not only within different oceans, but also at the scale of a local ridge segment (Wilcock & Delaney 1996, Juniper & Tunnicliffe 1997, Van Dover 2000). Much remains to be discovered about these systems. For example, the spacing, growth rates, and mineralogical evolution of black smoker chimneys are not well understood. Black smokers are shaped differently in different spreading environments, even when only a few kilometers separate them (Kelley et al. 2001b). In addition, the relationships between microbial, geochemical, and geophysical conditions over time and space that could reveal controls on microbial growth and survival remain uncharted. In the following sections we discuss four venting areas that provide examples of the diversity of these systems and some of the questions that still need to be explored in these extreme environments.

Slow-Spreading Environment: Trans-Atlantic Geotraverse (TAG)

Along the mid-ocean ridge system, one of the largest single known hydrothermal deposits occurs on the Mid-Atlantic Ridge at 26°08′N. This hydrothermal field known as TAG (Trans-Atlantic Geotraverse) (Figure 13) hosts low-temperature and high-temperature zones of venting and two major areas of extinct sulfide deposits, which have been mapped in a 5 × 5 km area (Rona et al. 1984, 1993; Thompson et al. 1985, 1988; Tivey et al. 1995; Humphris & Tivey 2000). A recent summary by Humphris and Tivey (2000) provides an excellent overview of this system. The TAG mound is the largest single deposit in the area, measuring 200 m in diameter and ~50-m high; it was probably formed by individual venting structures that combined into one deposit over time. Much of the mound is composed of massive sulfide blocks and black and white smoker debris that is variably cemented and hydrothermally recrystallized.

Active venting is maintained by a black smoker complex located on the top of the mound on a 10–15-m tall conical structure that hosts multiple, spire-shaped

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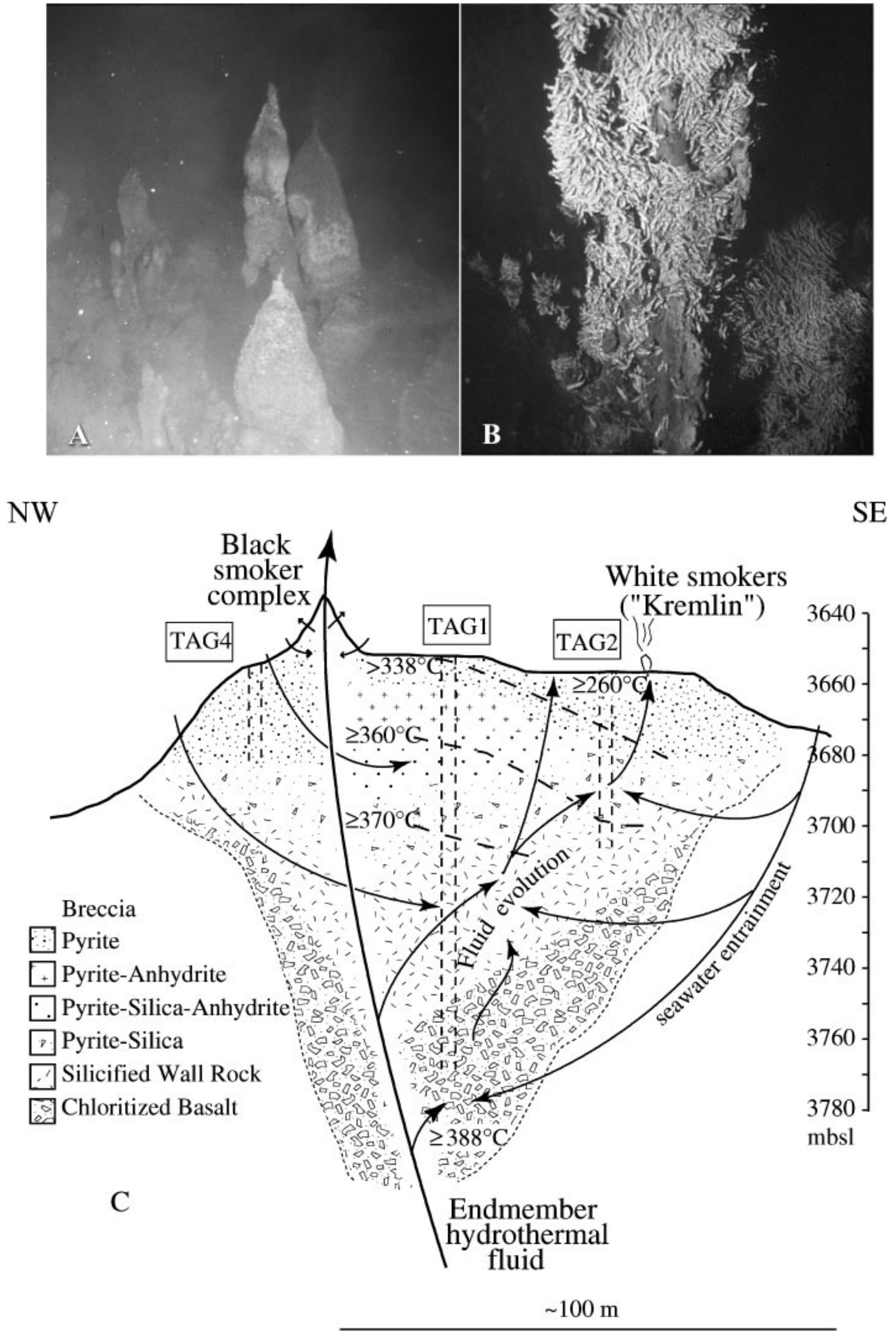
Figure 13 Schematic of the TAG active hydrothermal mound showing lithofacies as defined by the Ocean Drilling Program at sites TAG1-3, during Leg 158. (*a*) Focused flow in narrow, pipe-like regions is believed to cause significant entrainment of seawater into the mound, resulting in anhydrite precipitation. (*b*) Smoker on TAG engulfed by swarming shrimp. (*c*) White smokers in the Kremlin area of TAG. Images courtesy of M.K. Tivey, Woods Hole Oceanographic Institution.


A
B
NW
SE
Black smoker complex
White smokers ("Kremlin")
TAG4
TAG1
TAG2
>338°C
≥260°C
≥360°C
≥370°C
Fluid evolution
seawater entrainment
≥388°C
Endmember hydrothermal fluid
3640
3660
3680
3700
3720
3740
3760
3780
mbsl
Breccia
Pyrite
Pyrite-Anhydrite
Pyrite-Silica-Anhydrite
Pyrite-Silica
Silicified Wall Rock
Chloritized Basalt
C
~100 m

chimneys venting Cu-rich fluids at temperatures of up to 363°C (Figure 13*b*). Hydrothermal venting supports several species of shrimp, which swarm around the structures, commonly completely masking the chimneys from view (Figure 13*c*) (Van Dover 2000). In addition, the area hosts brachyuran crabs, and anemones dominate the periphery of the field (Van Dover 2000). Fluid chlorinities are slightly elevated with respect to seawater values in the black smokers, and white smoker fluids are approximately 70% of seawater chlorinities. Over a nine-year period, the composition of the venting fluids has been remarkably stable (Humphris & Tivey 2000) (Table 1). Fluid inclusion analyses of anhydrite recovered from >100 m below the surface of the mound by drilling show that beneath the mound, fluid temperatures reach 380°C–390°C (Tivey et al. 1998). These data, in concert with petrographic, isotopic, and chemical modeling, indicate that significant entrainment of seawater

TABLE 1 Comparison of a subset of hydrothermal vent compositions

	Units	Seawater	TAG[a] black smoker	TAG[a] white smoker	East[b] Pacific Rise	Endeavor[c]	Lost City[d]
Temp	°C		290–369	270–301	308–403	346–370	40–75
pH		7.5	3–3.8	<3–3	2.06–5.69	4.2–4.5	9.0–9.8
Alk	meq/kg	2.41				−0.994–<2.27	
Cl	mmol/kg	541.5	633.5–659	636	29.9–863	253–505	546–549
H_2S	mmol/kg	0	2.5–3.5	0.5–3	0.374–81.6	0–8.1	0.064
Si	mmol/kg	0.174			2.70–19.8	0.174–17	
Li	μmol/kg	27.5	367–411	352	4.01–1270	160–439	
Na	mmol/kg	461 (2)	543–584	549	22–721	216–461	479–485
K	mmol/kg	9.9	17–20	17–20	−0.974–42.2	13.5–29.1	
Ca	mmol/kg	10.31	26–31	27	−0.803–51.9	13.8–42.9	21.0–23.3
Sr	μmol/kg	87	99–103	91–95	−12.8–197	60–149	
Mn	μmol/kg	.002	666–1000	750–762	61.7–1003	194–550	
Fe	μmol/kg	.005	1640–5590	3830–3840	6.95–4330	177–1362	
Cu	μmol/kg	<0.002	>83–150	3		7–21	
Zn	μmol/kg	<0.002	>36–46	300–400		25–35	
B	μmol/kg	420 (2)				698–798	
NH_3	μmol/kg	<5				500–633	
CO_2	mmol/kg	2.5 (.05)				8.4–22	
SO_4	mmol/kg	28.6			−9.02–13.8		5.9–12.9
CH_4	μmol/kg	4×10^{-7}			28.1–1380	1.8–3.4	0.13–0.28

[a] Data from Humphris & Tivey 2000.

[b] Data from Von Damm 2000.

[c] Data from Butterfield et al. 1994.

[d] Data from Kelley et al. 2001.

occurs beneath the deposit. These fluids are heated during mixing with high-temperature hydrothermal fluids and by conductive heating as the fluids are transported through the underlying channel network (Tivey et al. 1998). The entrainment results in generation of acidic fluids and metal remobilization beneath the deposit.

Abundant Zn-rich, 1–2-m tall, white smokers on the southeastern margin of the mound discharge less vigorously venting fluids at 265°C–300°C (Figure 13*c*). This zone, known as the Kremlin area, hosts 1–2-m-tall spires with bulbous tops composed of sphalerite, amorphous silica, marcasite, and pyrite (Tivey et al. 1995). In addition to these sites, diffusely venting fluids percolate locally through the top and sides of the mound. Magnetic surveys of the area in concert with results from Ocean Drilling Program Leg 158 indicate that the deposit is underlain by a cylindrical pipe or silicified-pyritized stockwork system that is 80–100 m in diameter (Tivey et al. 1996). The mound and its underlying network of channels is believed to contain a total of ~3.9 million tonnes of massive sulfide. It is unclear whether the heat necessary to drive this system is extracted from the ridge axis or from episodic local intrusive activity, but large intersecting faults have played a role by channeling flow to the hydrothermal mound episodically over a 40,000–50,000-year period (Karson & Rona 1990; Humphris & Kleinrock 1996; Kleinrock & Humphris 1996; Lalou et al. 1995, 1998; Bohenenstiehl & Kleinrock 2000). The mound may have only been active 1%–2% of this period, however (Humphris & Cann 2000). Humphris & Cann (2000) speculate that the TAG hydrothermal activity is driven by periods of rapid magma supply (similar to that of Hawaii) and the latent heat of crystallization of magma near the top of the plutonic sequence. The long history of venting at this site and the acidic nature of the fluids has led to a mineralogically zoned deposit and to remobilization of many of the metals.

Fast-Spreading Environment: East Pacific Rise 9°N

In contrast to the large sulfide mounds that may typify deposits on the Mid-Atlantic Ridge, black smokers at the fast-spreading East Pacific Rise in the 9°N locality commonly occur as small, discrete individual structures rarely more than 15-m tall. ARGO-I, 100 kHz, and Alvin data indicate that most venting occurs within the narrow, sinuous central grabens located at the crest of the summit (Haymon et al. 1991, 1993; Fornari & Embley 1995). In this area, the axial summit caldera is approximately 70–200-m wide, and the bounding faults are 8–15-m high. Hydrothermal activity is generally focused into this very narrow zone, and it is well correlated with areas in which recent volcanic activity has been documented or inferred to have taken place. Most of the hydrothermal venting occurs in a zone north of 9°27′N, and over 40 active and 100 inactive sulfide deposits have been mapped (Haymon et al. 1993, Fornari & Embley 1995, Von Damm et al. 1997, Von Damm 2000). Spacing of the vents is highly irregular with some vents a few to 10s of meters apart, whereas others are several hundreds to a few kilometers apart. Temperatures of the vents reach 403°C, some of the highest yet measured for submarine systems (Von Damm 2000). In this volcanically active area, the small size of the deposits is probably due to at least two factors. First, basaltic lava may frequently erupt along fast-spreading systems, which may cover the hydrothermal vents and associated biological communities (Haymon et al. 1991, 1993; Wilcock & Delaney 1996). Second, during diking-eruptive events, as magma moves up from the chamber into the shallow overlying crust, the fluid flow channels established to feed hydrothermal vents may be disrupted. This may cause the vents to shut down until the channels become re-established or to relocate to a new site.

Examination of the 9°N area following the 1991 eruption has provided a wealth of information on the chemical, volatile, and biological evolutions following perturbation events such as eruptions or those associated with earthquake activity. Following the 1991 eruption, time series measurements have been made on many of the vents surrounding this area (Von Damm et al. 1997, 2000; Fornari et al. 1998; Shank et al. 1998). At least one vent near the 1991 eruption site approached the critical temperature of seawater (407°C), and all fluids show evidence for having undergone phase separation (Von Damm et al. 1997, Von Damm 2000). An excellent example of this is provided by examination of a vent called "F vent," which was sampled in 1991 and again in 1994 (Von Damm et al. 1997). Following the eruption, this sulfide chimney was 3–5-m tall and was emitting fluids at 388°C. At the sampling depth of 2580 m (258 bar), the venting fluid was on the two-phase curve and was boiling subcritically. Fluid chlorinities were very low (46.5 mmol/kg versus 540 mmol/kg for seawater), H_2S and CO_2 concentrations were high, and alkali and alkaline Earth cation concentrations were low (Von Damm 2000). It is considered that the end-member fluids involved reflected minimal water-rock interaction.

During the course of a three-week dive period following the eruption, CH_4 concentrations increased from 0.13 to 0.19 mmol/kg, and H_2 increased from 25 to 45 mmol/kg (Lilley & Olson 2001). In contrast, in 1994, fluid temperatures had cooled to 351°C, chlorinities had risen to 846 mmol/kg, H_2S concentrations had dropped dramatically (41 to 8.71 mmol/kg), and CO_2 contents had dropped slightly (15.5 to 11.4 mmol/kg). These data were interpreted to reflect venting of phase-separated vapors associated with the volcanic event. This was followed three years later by venting of the conjugate brines, which had been stored at depth in the crust (Von Damm 2000).

One of the unexpected benefits of this eruption was the opportunity to monitor colonization of a new lava flow by microbial and macrofaunal communities, in concert with characterization of chemical and volatile changes of the venting fluids (Shanks et al. 1998). Newly formed lower-temperature diffuse flow fluids associated with the eruptive event contained extremely high H_2S and Fe concentrations. Methane concentrations in the diffuse fluids were unusually high with concentrations up to nearly 6 mmol/kg (Lilley and Olson 2001). These areas were engulfed by a bloom of sulfur-oxidizing bacteria believed to be derived from the subseafloor (Shank et al. 1998), and thermophilic methanogens were isolated from the 20°C vents (Lilley & Olson 2001). Crabs, copepods, fish, and limpets grazed on the bacteria, and within 11 months vetimentiferan tube worms colonized the site: These were succeeded by domination of a species called *Riftia pachyptila*

21 months later. Revisitation of the site three years later showed that these worms had grown 2 meters. Within three years, mussels also colonized the diffuse flow sites, and the macrofaunal communities resembled those established before the eruptive event. The succession of animals was closely tied to H_2S concentrations in the fluids: Vestimentifera colonization was followed by mussels, and polychaetes and galatheid crabs ended the sequence (Figure 9*b*) (Shank et al. 1998).

This area is also one of the few areas where data exist that allow examination of the linkages among seismic events, fluid chemistry, and temperature. On March 22, 1995, an intense period of seismic activity was measured with over 162 events occurring within a three-hour period (Sohn et al. 1998). Twenty-two days later, a smaller swarm occurred involving at least 25 events. The deepest event was located ~300 m above the top of the axial magma chamber at a depth of 1.1 km, and many of the hypocenters were located in a thin volume of crust with a height of ~300 m. Temperatures recorded at a vent called "Bio9" had been stable at 365°C for approximately one year before the seismic swarm. In one week following this eruption, vent temperatures had risen to 373°C, with a gradual decay back to 365°C occurring over the next 70 days. The delay in temperature rise time has been used to infer that fluids in the upflow limb of the convection cell feeding this vent had a residence time of ~4 days. Prior to the earthquakes, fluid chlorinities were depleted with respect to seawater, but following the seismic event they had increased by 52%. These data are believed to reflect cooling of the rock above the axial magma chamber, which induced large enough stresses to allow fracturing and subsequent penetration of hydrothermal fluids in a column of rock 200–300-m tall (Sohn et al. 1998). Such events may be common in magmatically active areas.

Intermediate-Spreading Environment: Endeavour Segment, Juan de Fuca Ridge

Somewhere between the venting manifestations of TAG and the EPR lies the Endeavour Segment of the Juan de Fuca Ridge. The area has the highest density of hydrothermal venting of any system yet discovered. Active faulting, rather than volcanic activity, along this segment has produced a 1-km wide, 100–200-m deep graben along which there are five high-temperature vent fields (Kelley et al. 2001b). The fields are formed by focused upflow regions, spaced approximately 2–3 kilometers apart (with hints of more) and abundant areas of diffuse flow adjacent to the high temperature venting (Delaney et al. 1992; Robigou et al. 1993; Butterfield et al. 1994; Lilley et al. 1995; Kelley et al. 1998, 2001b; Veirs et al. 1999) (Figure 14). Currently, there are broad intervening zones between vent fields where significant diffuse flow occurs without interspersed high-temperature venting (Figure 15) (Lilley et al. 1995, Delaney et al. 2000, Veirs et al. 1999, Kelley et al. 2001b). From this pattern, a nested type of circulation can be inferred in which the shallow diffuse flow cells are perched within the recharge zones for the deeper higher temperature cells (McDuff et al. 1994, Delaney et al. 1996) (Figures 14 and 15). Several zones of extensive but inactive sulfide deposits

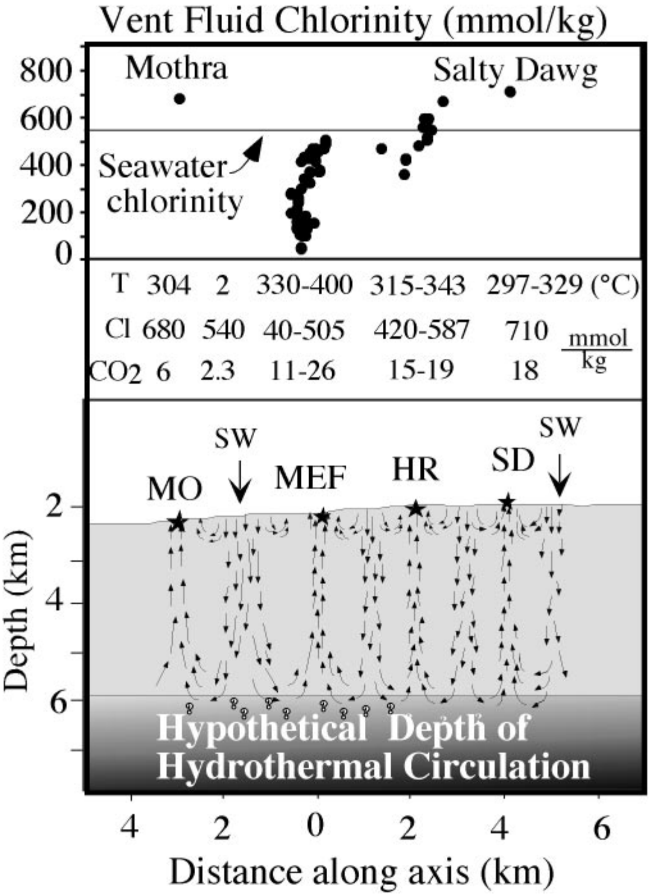


Figure 14 Possible flow distribution for a system such as the Endeavour Segment on the Juan de Fuca Ridge. The regular spacing of the four vent fields supports a working model that the fields represent the surface outflow of subsurface cells along axis. The gradients in fluid temperature and chemistry within the vent fields suggest that the fields could be zones of confluence between two adjacent cells (McDuff et al. 1994, Delaney et al. 1997). The depths of circulation are inferred from earthquake activity (Wilcock et al. 2002) directly beneath the axial valley to depths of 2–4 kilometers below the seafloor. The chemical data require sustained two-phase separation in the subsurface at very high temperatures and boiling at more-shallow crustal levels. Also shown are representative fluid temperatures and ranges in chlorinity (Cl) and methane (CH_4) for fluids in four of the five fields on the Endeavour.

on the valley floor and high on the valley walls indicate that high-temperature venting has been localized elsewhere in the past (Lilley et al. 2000).

The fields, which are generally 400–500-m long, host abundant >20-m-tall sulfide structures on top of which rise abundant smaller black smoker chimneys (Delaney et al. 1992, Robigou et al. 1993, Kelley et al. 2001b). Microseismic and T-phase data show that the Endeavour is seismically very active with extensive on- and off-axis activity (Archer et al. 1996, Wilcock et al. 2002). Earthquakes beneath the median valley are concentrated at depths of 2–3.5 km and show that hydrothermal fluids have penetrated the mid-crust, effectively precluding the presence of a substantial shallow axial magma chamber (Figure 14). Lister (1983) asserted that sustained high-intensity hydrothermal output could not be supported by an active magma chamber but required an active cracking front. Building on this concept, Wilcock & Delaney (1996) suggested that crack penetration well into the lower crust at rates determined by the heat removal could account for formation of large sulfide deposits at active vent sites. This style of hydrothermal activity is likely to be common in systems where the magma chamber has recently solidified, allowing cooling and spreading to control the rate of downward crack propagation.

In four of the fields, the most common structures include large multiflanged irregular sulfide mounds (up to 18–20-m tall) that host multiple vigorously venting black smoker chimneys on their summits (Figures 16 and 17; for video imagery of active black smokers, see www.neptune.washington.edu/vents/video.html) (Tivey & Delaney 1986; Delaney et al. 1984, 1992, 1997; Robigou et al. 1993). Fluids venting from spires, chimneys, and flanges reach temperatures in excess of 400°C (Delaney et al. 1994, Tivey et al. 1990), and temperatures of 360°C are routinely measured (Delaney et al. 1992, 1997; Tivey et al. 1990; Butterfield et al. 1994). Many structures are characterized by stair-step arrays of large sulfide ledges that form an almost tree-like structure. The most spectacular of these structures was "Godzilla" in the High Rise Field (Figure 16*c*), which rose 45 m above the seafloor. It contained 15–16 tiers of ledges or flanges, which extended outward from the main trunk of the edifice 7 m that trapped 330°C fluids (Woods & Delaney 1992, Robigou et al. 1993). This structure collapsed sometime in 1996. Lower-temperature venting of nutrient-rich hydrothermal fluids through the porous chimney walls and flanges support rich and diverse colonies of tube worms, sulfide worms, and palm worms; galatheid crabs; and a variety of snails and limpets (Sarrazin et al. 1997) (Figure 9). On actively venting structures, these animal communities are commonly so dense that the underlying host rock is completely obscured.

The larger deposits are thought to result from long-lived hydrothermal activity fueled by heat extracted from cracking and cooling of the lower crust, a scenario proposed for other large mid-ocean ridge (MOR) deposits, e.g., the TAG hydrothermal mound (Figure 14) (Wilcock & Delaney 1996). The five identified active Endeavour hydrothermal systems exhibit some unusual characteristics relative to other unsedimented MOR vent sites: (*a*) The deposits at Endeavour are large and steep sided and exhibit an abundance of amorphous silica and flanges; and (*b*) the Endeavour vent fluids exhibit very high concentrations of methane and ammonia, consistent with interaction between the fluids and organic matter (Tivey

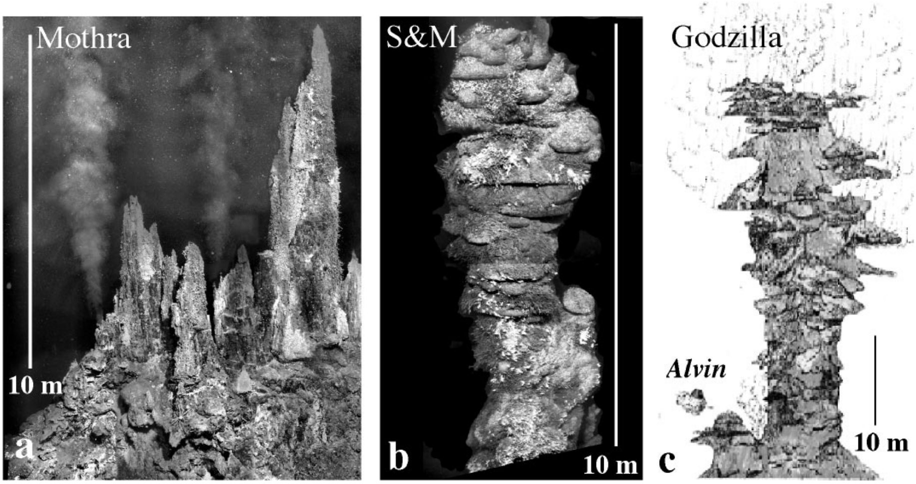


Figure 16 (*a*) Hydrothermal vents in the Faulty Towers complex within the Mothra Hydrothermal Field (MHF), Endeavour Segment of the Juan de Fuca Ridge. Individual spires coalesce to form a linear array of steep-sided pinnacles that vent fluids up to ~300°C. (*b*) In contrast to sulfide edifices in the MHF, sulfide structures in the Main Endeavour Field (MEF) are characterized by ~20-m high mounds that host vigorously venting, 380°C smokers on the mound tops. The structure shown is called S&M for Smoke and Mirrors, and it is characterized by abundant subdued sulfide flanges that trap pools of hydrothermal fluid. (*c*) The largest structure in the Endeavour system, "Godzilla," is located 2-km north of the MEF, in the High Rise Hydrothermal Field (after Robigou et al. 1993). Arrays of large sulfide flanges vent hydrothermal fluids that spill out from under the flanges and also diffuse up through the flange tops. They support dense macrofaunal and microfaunal communities. Godzilla collapsed in 1996 but has since partially regrown (Robigou et al. 1995). Also shown to scale is the submersible Alvin. Scale bars in all three diagrams are equal to 10 m.

& Delaney 1986, Delaney et al. 1992, Lilley et al. 1993). Geochemical calculations indicate that as vent fluids conductively cool with the porous interior of the structures, ammonia-ammonium equilibrium buffers the pH. This equilibria allows more efficient deposition of sulfide minerals and silica from the fluids, which may lead to the formation of larger and stronger edifices (Tivey et al. 1999).

The fields exhibit strong structural control (Delaney et al. 1992, Robigou et al. 1993, Kelley et al. 2001b). In the Main Endeavour Field (MEF), the boundary fault network that forms the western valley wall of the Endeavour Segment is the dominant structure localizing the MEF (Figure 18). This vigorously active vent field is the locus of steep salinity, temperature, and microbial gradients that cover an area approximately 400 m along strike and 150 m across strike (Figure 18). The field contains over 100 actively venting sulfide chimneys. All indications are that the MEF is in a period of active phase separation, and this affects all aspects of the chemistry. The high temperatures (425°C–450°C) required to sustain supercritical

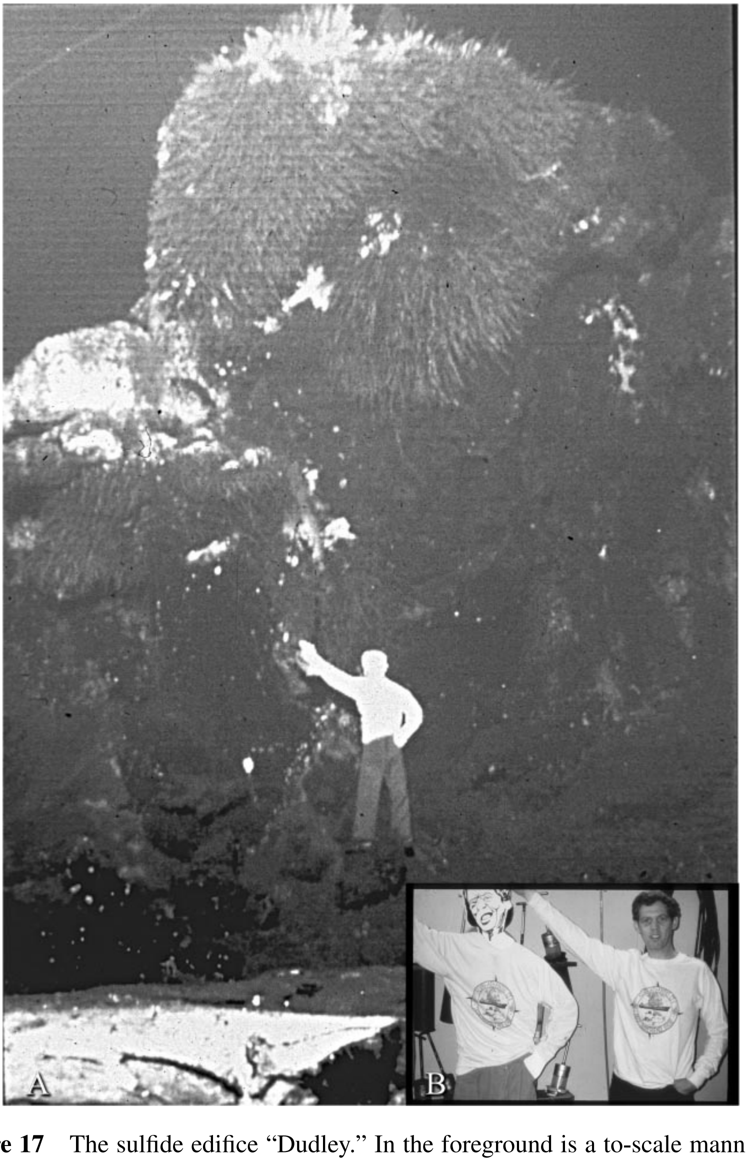
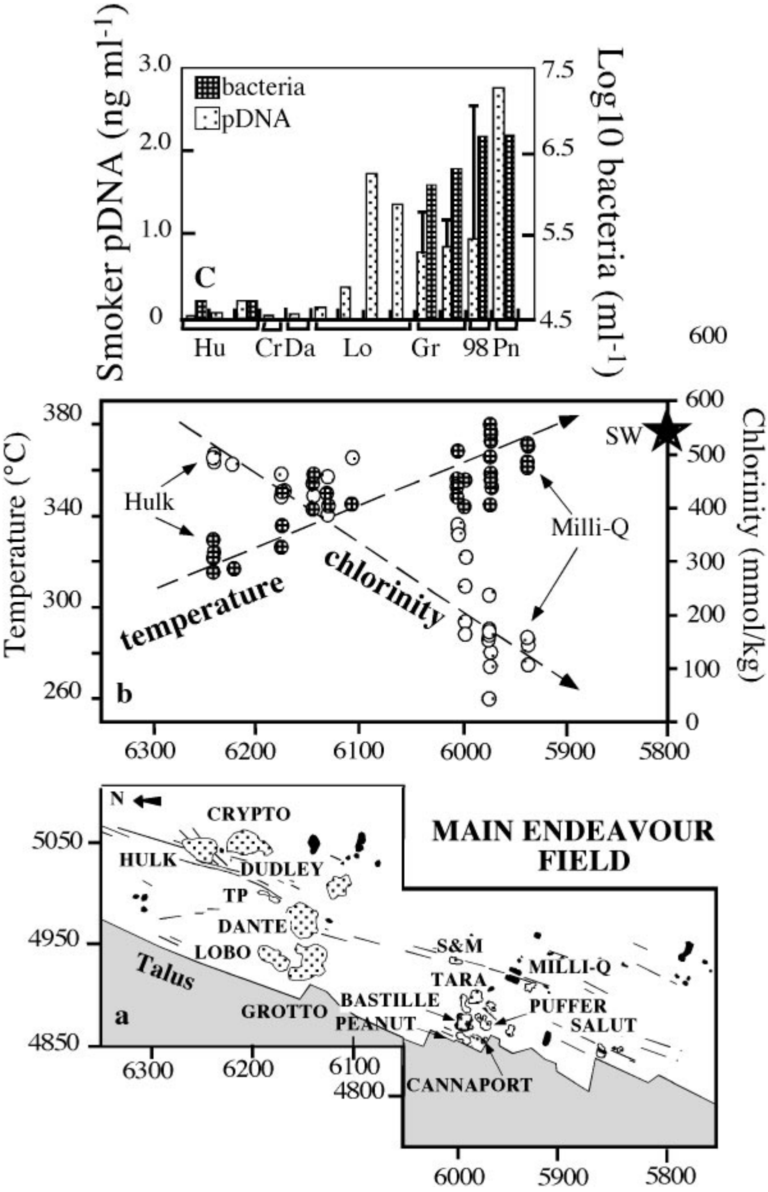


Figure 17 The sulfide edifice "Dudley." In the foreground is a to-scale mannequin of the Alvin pilot, Dudley Foster; Woods Hole Oceanographic Institution. The dense, hair-like growths that cap this edifice are macrofaunal communities dominated by tubeworms (after Robigou et al. 1993).


Smoker pDNA (ng ml-1)
Log10 bacteria (ml-1)
bacteria
pDNA
C
3.0
2.0
1.0
0
7.5
6.5
5.5
4.5
Hu
Cr
Da
Lo
Gr
98
Pn
600
Temperature (°C)
Chlorinity (mmol/kg)
380
340
300
260
600
500
400
300
200
100
0
Hulk
Milli-Q
SW
temperature
chlorinity
b
6300
6200
6100
6000
5900
5800
N
MAIN ENDEAVOUR FIELD
CRYPTO
HULK
DUDLEY
TP
DANTE
LOBO
Talus
GROTTO
BASTILLE
PEANUT
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phase separation at depth may give rise to the observations of variable and extremely high fluid temperatures (405°C) in the Main Field (Delaney et al. 1992).

The processes of phase separation and brine loss are linked to the steep gradients in vent fluid composition and temperature across the MEF (Figure 18). Until 1999, end-member chlorinities ranged from 40 to 505 mmol/kg (Butterfield et al. 1994, 1995) (seawater chlorinity is 540 mmol/kg). Fluid chlorinities step down systematically and incrementally, structure-by-structure, from 330°C at Hulk in the NE to the hottest, most volatile-rich, and lowest chlorinity vents near Bastille (Figure 18*a*,*b*). The hottest fluids are either close to or precisely on the "boiling" curve, and their compositions reflect both supercritical and subcritical processes (Butterfield et al. 1994, Delaney et al. 1997). Until 1999, when the hydrologic system was perturbed by a magnitude 5.0 earthquake, all emergent fluids sampled in the MEF were lower than seawater in chloride, indicating that a brine phase was sequestered at depth (Figure 4*b*) (Butterfield et al. 1994, Delaney et al. 1997, Lilley et al. 2000). An increase in fluid temperatures and salinity following this tectonic event may indicate minor release of this brine pool (Lilley et al. 2000). Brines are also venting 2 km to the south in the Mothra Hydrothermal Field and 6 km to the north in the Salty Dawg Field (Figure 14). Both of these systems are venting fluids at ~300°C (Kelley et al. 2001b).

One of the most interesting aspects of the Endeavour hydrothermal system is the relatively high concentrations of CH_4 and NH_4^+ found in the high-temperature fluids (Figure 14) (Lilley et al. 1993). These high CH_4 and NH_4^+ concentrations may imply subseafloor interaction between hydrothermal fluids and organic material from buried sediments. The CH_4 carbon isotopic compositions ($\delta^{13}CH_4$-55‰ versus PDB) of these fluids are the lightest yet found in a submarine system devoid of sediment. These data in concert with the elevated CH_4 concentrations, which reach values of >900 times background seawater values, likely imply a robust subseafloor methanogen community within the Endeavour system (Lilley et al. 1993).

The unique range of fluid properties associated with phase separation may also affect the microbial communities within the Endeavour fields (Figure 18*c*). For

Figure 18 Gradients in the Main Endeavour Hydrothermal Field. (*a*) Location of active sulfide structures (*stippled*) and inactive sites (*solid*). (*b*) End-member chloride concentrations and corresponding temperatures for vents in the MEF (after Delaney et al. 1997). The temperature-chlorinity data are consistent with formation by supercritical phase separation, phase segregation, and accumulation of residual brine at depth, followed by boiling as the vapor-rich fluids rise through the high-temperature conduits. SW = seawater chlorinity (*cross-filled circles* = temperature, *dotted circles* = chlorinity). (*d*) Smoker pDNA concentrations (particulate DNA) and bacterial counts by epifluorescence microscopy per smoker, ordered to the location of the vents along the NE-SW gradient (after Deming & Baross 1993). Error bars indicate standard deviation of the mean for smokers sampled more than once. Bacterial concentrations show a strong correlation with vent fluid chlorinity and temperature.

example, it has been hypothesized that brine formation and accumulation at depth may play an important role in the development of the halotolerant mesophilic bacteria isolated from Endeavour vents that grow in 20% NaCl (Kaye & Baross 2000). In addition, there appears to be a direct correlation between vent fluid temperature and composition and the quantity of microbial products emitted from the vents (Figure 18*c*) (Deming & Baross 1993). Within the MEF, the highest temperature, lowest chlorinity, and most volatile-rich fluids are associated with the highest-particulate DNA in the vent fluids (Deming & Baross 1993, Delaney et al. 1997). Although it is unclear what the exact linkages are, two possible hypotheses can be posed: (*a*) The elevated volatile concentrations in the highest-temperature fluids allow dense microbial communities to grow within the cooler chimney walls, and/or (*b*) the increased vigor with which the high-temperature fluids flow through the conduits, cracks, and pores in the edifices promote effective stripping of organisms from the sulfide substrate.

Investigation of microbial communities within hydrothermal systems is still exploratory in nature. However, it is clear that the sulfide edifices are habitats for dense and diverse microbial communities. For example, study of a 2-m-sized piece of chimney recovered from a 302°C venting structure called Finn in the Mothra Hydrothermal Field revealed that Archaea comprised 40% of the microorganisms near the exterior of the structure and that these increased to >90% of the intact microbial population near the hot 300°C interior (Schrenk et al. 1999a,b). In contrast, Eubacteria were most abundant near the cooler, more oxygen-rich outside of the edifice. Total cell numbers for microbes within the walls ranged from below 10^5 cells/g to greater than 10^9 cells/g, and they displayed a maximum within 3 to 5 cm of the outer chimney wall (Schrenk et al. 1998, 1999a). Fewer cells were observed near the hot interior. SEM images of preliminary DNA sequencing of these organisms indicate diverse and novel morphologies and evidence for extensive biofilm development. Preservation of silica-encased micron-sized tubes within the walls may reflect fossilization of biofilm-forming communities.

The highest concentration of organisms is spatially associated with increased concentrations of some metals in the sulfides (e.g., Mo, Pb, U, Sb, and As) (Juniper & Fouquet 1988, Zierenbers & Schiffman 1990, Kelley et al. 1999). In mineralogical studies, the interpretation has generally been that the increased concentrations are due to changes in pH associated with seawater migration and mixing of end-member hydrothermal fluids (Hannington et al. 1995). However, there are now many studies in a variety of environments that attest to the importance of microorganisms in influencing the mobilization of metals (Banfield & Hamers 1997; Silver 1994; Tebo, 1995; Eberhard et al. 1995; Hafenbrandl et al. 1996; Schrenk et al. 1998; Edwards et al. 1998, 1999), and such studies raise the possibility that similar microbial-geochemical processes are operative within the walls of sulfide structures.

Results of studies such as these establish that the interaction of metal-rich hydrothermal fluids and cool, oxygenated seawater within submarine sulfide structures creates a variety of conditions that can support microbial growth (McCollom

& Shock 1997). The presence of Archaea in all mineral zones within Finn implies that these organisms may grow or at least survive at temperatures considerably higher than 100°C. The extent to which these communities modify the geochemistry of their local environment and affect the development of hydrothermal systems in general is not yet known. Investigation of structures similar to Finn and of vent habitats as a whole may prove of general significance because an essential component in the search for life in the Solar System and in the search for the origins of life on our planet is the identification and interpretation of key signals for biological activity preserved in the rock record.

The stability of hydrothermal venting in the Endeavour system, in contrast to that of the EPR, has allowed examination of faunal communities that have not been affected by eruptive events. For example, during a five-year time series investigation of a 10–12-m-tall actively venting structure called Smoke and Mirrors (S&M) (Figure 16*b*), six distinct macrofaunal communities were mapped, sampled, and studied (Sarrazin et al. 1997, Sarrazin & Juniper 1999). These communities differed in either species composition or in the abundance of organisms. During the five-year interval, the total colonized surface of the structure increased from 58.6 m^2 in 1991 to 79.7 m^2 in 1995. This increase was correlated with a change in venting style from predominately focused, high-temperature flow to lower-temperature, widespread diffuse flow. Coregistered thermal, fluid, and macrofaunal measurements showed that each faunal community required a distinct habitat in terms of the physico-chemical conditions (Sarrazin et al. 1997, Sarrazin & Juniper 1999). These communities, which contained variable distributions of tubeworms (*Ridgeia piscesae*), polychaetes (*alvinella sulfincola* and *P. palmifomis*), sulfide worms (*Paralvinella sulfincola*), palm worms (*Paralvinella palmiformis*), a blue mat-forming protozoan, limpets, snails, crabs, and polynoids, all showed high temporal-spatial variability over the five-year period that is believed to reflect flow redistribution. In the highest temperature regions, *Paralvinella sulfincola* populated the sulfide substrate. These polycheates promoted deposition of the sulfide mineral marcasite, which provided a suitable substrate for colonization by *palmiformis* (Juniper et al. 1992).

A New Class of Submarine Hydrothermal System: Lost City

The Lost City Field was discovered on December 4, 2000, on the Atlantis massif near the eastern intersection of the Mid-Atlantic Ridge and the Atlantis Fracture Zone 30°N (Kelley et al. 2001a) (Figure 19). This field of active carbonate chimneys occurs at the crest of the south wall of the massif and appears to be the surface expression of warm fluids (40°C–75°C) emanating from fault zones that tap a region of active (exothermic) serpentinization in the underlying peridotites. This is the first major occurrence of active carbonate-magnesium hydroxide chimneys along a mid-ocean ridge, although other carbonate chimneys have been described in fjords and along continental margins (Buchardt et al. 1997, Seaman 1998, Kulm & Suess 1990). Deep-towed geochemical mapping (German et al. 1996, Gracia

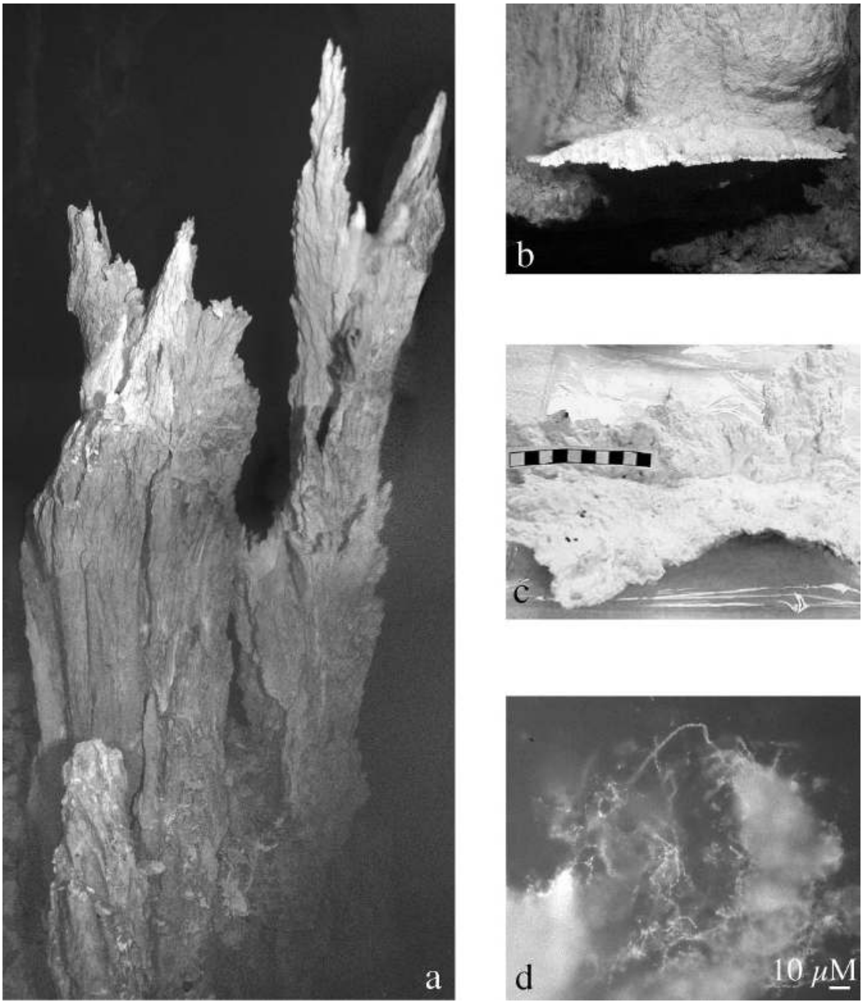

Figure 19 Carbonate hydrothermal deposits and microorganisms from the periodotite-hosted hydrothermal field "Lost City." (*a*) Photomosaic of extinct carbonate chimney imaged by the remotely operated camera Argo (after Kelley et al. 2001a). (*b*) Actively venting, ~2-m-wide carbonate flange growing from the side of a 60-m-tall edifice named Poseidon. Diffuse, 55°C fluids spill out from up under the flange lip, promoting thickening and outward growth. Dense microbial communities of filamentous bacteria are common in these active areas of diffuse flow. (*c*) Flange sample composed of aragonite [$CaCO_3$], calcite [$CaCO_3$], with trace brucite [$Mg(OH_2)$]. Scale bar is equal to 10 cm. (*d*) Photomicrograph of DAPI-stained cells attached to flange sample shown in *c*. Cells exhibit diverse morphologies and show densities of 10^7 cells/g of carbonate material (Kelley et al. 2001a). Hyperthermophiles, thermophiles, and mesophiles thrive within the porous walls of the structures.

et al. 2000) hints that similar structures with distinctive fluid chemistry may be widespread along the rift mountains of the MAR. For example, the Saldanha Field just north of the Rainbow Vent Field is at a depth of 700 m and in a setting that is remarkably similar to the Lost City Field, with diffuse flow being emitted from a nearly flat-topped, peridotite platform (Barriga et al. 1998). This type of venting is very different chemically and probably biologically from all other known serpentinite-hosted vents on the MAR that are driven by magmatic heat (Table 1). In other peridotite systems such as Rainbow, the chemistry of the fluid (e.g., how pH, elevated H_2S) and resulting sulfide deposits indicate interaction with basaltic/gabbroic material as well as reaction with peridotite (Janecky & Seyfried 1986, Wetzel & Shock 2000, Donval et al. 1997). At present the Lost City is the only known major active field that is solely sustained by exothermic serpentinization processes (Kelley et al. 2001a).

Investigations of the south wall of the Atlantis massif (Cann et al. 1997, Blackman et al. 1998) resulted in the discovery and initial documentation of the Lost City Field. The Lost City Field rests on a terrace at a water depth of 700–800 m and is underlain by a diverse suite of mafic and ultramafic basement rocks that crop-out on the cliffs immediately below the edge of the scarp. The hydrothermal deposits overlie and fill fractures in the capping carbonate unit and thus clearly postdate that unit. The field extends for at least 400 m across the terrace and hosts at least 30 active and inactive pinnacle-like vent structures. Just to the south, cliffs composed of basement material show extensive areas of active and inactive white hydrothermal precipitates. These deposits fill fractures and form hundreds of cascading shelf-like flanges that protrude as much as 2 m from the cliff face. Similar densely veined serpentinites (ophicalcites) are known from ancient ophiolites (Treves & Harper 1994) including Archean ($>$3000 Ma old) examples (de Wit et al. 1987). Collectively, these types of assemblages may represent a linkage to hydrothermal and possibly biological activity at the time of the oldest known life on Earth.

Within the field, active and inactive vents form spires, mounds, pinnacles, and flanges built atop material derived from older, collapsed vent structures. Large isolated pinnacles are commonly 10–30-m tall. The most spectacular of the pinnacles is a giant columnar edifice named Poseidon that rises 60 m above the seafloor. The top of this composite structure is actively venting 75°C fluid. On this and other large pinnacles, flanges exhibit delicate concave-down forms that trap reflective pools of 40°C–55°C vent fluid. Jagged, superimposed clusters of stalagmite-like structures rise several meters from the tops of some flanges. The carbonate chimneys are strikingly similar to ikaite ($CaCO_3 \cdot 76H_2O$) columns found in the Ikka Fjord of Greenland (Buchardt et al. 1997, Seaman 1998).

Preliminary analyses of material from the chimneys indicate that they are composed of variable mixtures of calcite [$CaCO_3$], aragonite [$CaCO_3$], and brucite [$Mg(OH)_2$] (Figure 19) (Kelley et al. 2001a). Silica is only a trace component within the chimney minerals, and no sulfides have been detected. The active vent samples are composed of very delicate branching "fingers" of carbonate, while flange samples show fibrous, botryoidal to colliform structures (Figure 19*c*). All of the samples are extremely porous and some exhibit delicate structures similar to those of wasp nests. Initial results from Lost City show that the fluid chemistry is very different from that of black smoker systems. The fluids have pHs of 9.0–9.8 (versus 7.8 for ambient seawater), and they are low in metals, silica, and H_2S (Kelley et al. 2001a). Methane and hydrogen are elevated with respect to seawater values. Ca is enriched more than twofold in the fluids, but K is within 3% of the ambient seawater value. The mineralogy and chemistry of the fluids are consistent with production through peridotite-dominated fluid-rock interaction. These reactions result in an alkaline fluid, which upon mixing with seawater, precipitates carbonate and hydroxide minerals (Kelley et al. 2001a). Model calculations indicate that this mixing process has a high potential for synthesis of organic compounds (Shock & Schulte 1998).

Active structures within the Lost City Field are typically awash in buoyantly rising mixtures of warm vent fluid and cooler seawater. The diffuse vents support dense microbial communities that include both Archael and Eubacterial lineages. On actively venting surfaces, these colonies commonly form white to light gray colored filamentous strands several centimeters in length (Figure 19*d*). Enrichment culturing of chimney material under aerobic and anaerobic conditions yields microorganisms in the hyperthermophilic (780°C), thermophilic (50°C, 70°C), and mesophilic (25°C) temperature regimes in media designed for methanogens, methane-oxidation, and heterotrophy (Kelley et al. 2001c). Such findings are consistent with the presence of elevated CH_4, H_2, and other hydrocarbons in peridotite-hosted systems (Kelley et al. 2001a, Holm & Charlou 2001). The morphology of the cells is diverse, and cell counts reach up to 10^7 cells/g of carbonate material. In contrast to the dense microbial communities that inhabit the diffusely venting sites, based on the limited submersible observations, macrofaunal assemblages that typify most known high-temperature axial vent environments are rare within the Lost City Field (Van Dover 2000). Their paucity is likely due to the low metal-sulfur concentration of the venting fluid. Animals observed during the single dive to the Lost City included a few crabs, sea urchins, and abundant sponges and corals.

There is a growing consensus that geochemical and geological processes are intimately linked with microbial activity and diversity within submarine systems. The production of fluids enriched in CH_4 and H_2 during serpentinization should support moderately thermophilic methane- and hydrogen-oxidizing microorganisms, as well as sulfate-reducing bacteria (Nishihara et al. 1990, Sorokin et al. 2000). Lost City offers an important opportunity to examine this hypothesis. This new class of peridotite-hosted hydrothermal system, on 1–1.5-Ma crust, shows that volcanic activity is not necessary to drive hydrothermal flow; instead, a large component of the heat may be obtained from exothermic serpentinization reactions. This, coupled with the observation that inside-corner highs similar to the Atlantis Massif are common along slow-spreading and ultra-slow-spreading mid-ocean ridges, indicates that a much larger portion of the oceanic crust may support chemosynthetic microbial populations than has been previously recognized (Kelley et al. 2001a,c).

The Lost City Field may provide insights into hydrothermal processes of early Earth and the life forms that they supported (Kelley et al. 2001a,c). The reducing conditions associated with serpentinization of ultramafic material may be similar to conditions present in the Hadean Ocean 4.5–3.8 billion years ago. In addition, model calculations suggest that disequilibrium mixing of ultramafic-derived fluids with early ocean water favors the synthesis of numerous organic compounds (Shock & Schulte 1998). Such a warm, high-pH, organic-rich environment may have been an extremely suitable habitat for the emergence of thermophilic to hyperthermophilic organisms.

Lost City may serve as an important guide in the search for life on other planets as well. It has been argued that all rocky, volcanic planets that have had liquid water present during some part of their evolution are suitable candidates for life (e.g., Russell et al. 1994, Shock 1996). The propensity for serpentinite-hosted systems like Lost City to (*a*) be driven by the heat from exothermic water-rock reactions at depth and (*b*) synthesize organic compounds during hydrothermal fluid-seawater mixing indicates that wet, ultramafic environments may also provide excellent habitats for life.

BIOLOGICAL COMMUNITIES AT VENTS

We have given an overview of the physico-chemical setting of submarine hot springs and the life that they support. In the following sections, we present a review of faunal and microbial habitats, the kinds of organisms that thrive in the fluids and rocks, and their unique nutritional requirements. Different vent environments (e.g., subseafloor, sulfide edifices, plumes) offer contrasting habitat conditions for micro- and macrofaunal communities (Figure 20). These environments span a range of conditions including almost all of the extremes in temperature, Eh, and heavy metal concentrations that are currently believed to limit where life on Earth can exist. The microbial communities exploit the diverse range of electron acceptors and electron donors and the variety of carbon sources that exist within the many submarine biotopes. The macrofaunal communities, in turn, exploit the physiological versatility of vent microbes by either directly feeding on microbes or entering into symbiotic associations with sulfur or methane oxidizing bacteria. Moreover, the macro- and microfauna have adapted to habitat conditions that include flowing water, porous spaces within basalt and sulfides, and the surfaces of rocks and animals. A common characteristic of vent organisms is their ability to take advantage of the carbon and energy sources provided by hydrothermal processes while evolving mechanisms to counteract the toxic effects of high concentrations of heavy metals or short-term exposure to lethal high temperatures. The microbes can derive their carbon and energy from solid minerals and/or utilize volatile dissolved species such as H_2S, CO_2, H_2, and CH_4 (Table 2).

Some of the most abundant animals at vents derive their nutrition from sulfur- and/or methane-oxidizing bacterial endosymbionts that live in specialized internal organs (Childress & Fisher 1992, Nelson & Fisher 1995, Van Dover 2000). Other

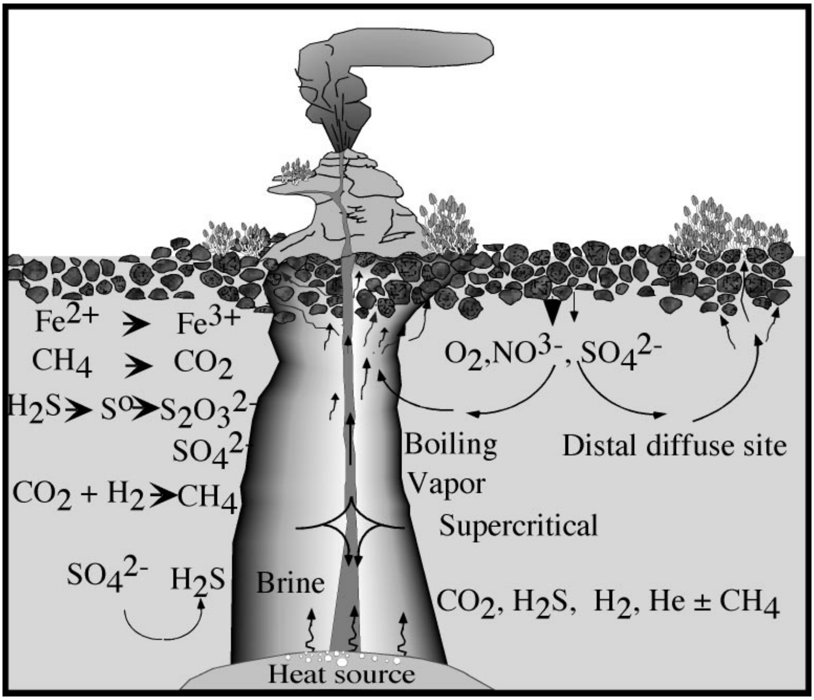

Figure 20 Chemical-volatile reservoirs and chemical transformations in submarine hydrothermal systems. Degassing of basaltic melts and fluid-rock reactions release reduced volatiles and chemicals into the overlying hydrothermal systems. Complex oxidation-reduction reactions during mixing with seawater and by microbial processes modify fluid-volatile compositions in the shallower portion of the system (after Butterfield et al. 1997).

animals may exploit the ability of some bacteria to oxidize and precipitate toxic metals. For example, the polychaete worms, *Alvinella* and *Paralvinella* species, have specific groups of filamentous bacteria attached to their outer dorsal surfaces that are believed to be symbiotic with the worms (Cary et al. 1997, Gaill et al. 1997). While the nature of the symbiotic relationship between the bacteria and worms is not understood, it is assumed that because these microbes can tolerate high concentrations of cadmium, arsenic, and copper (Jeanthon & Prieur 1990) they may be involved in protecting the worm from the toxic effects of heavy metals (Alayse-Danet et al. 1987).

The microbial communities occupy both aerobic and anaerobic environments having in situ temperatures that range from ambient seawater temperature (2°C) to temperatures greater than 110°C (Figures 10 and 20) (Baross & Deming 1995, Karl 1995, Stetler 1996). In general, increases in ambient temperature are accompanied by decreases in available oxygen and increases in hydrothermally derived

TABLE 2 Concentration and source of biologically important chemical species in submarine hydrothermal vent environments[a]

Chemical species	Vent fluids conc/kg SW	Seawater conc/kg	Sources in vents	Biological significance
CO_2	3.9–215 mmol	2.3 mmol	Magma degassing, water/rock reactions, fermentation	Carbon source for chemoautotrophs and methanogens
CH_4	0.05–4.5 mmol	0.3 nmol	Magma degassing, reduction of CO_2, methanogenesis	Aerobic and anaerobic microbial oxidation
H_2	0.1–50 mmol	0.3 nmol	Magma degassing, water/rock reactions, microbial fermentation	Methanogenesis; aerobic and anaerobic oxidation by microorganisms
S (as H_2S)	3–110 mmol	Not detected 28 mmol (as SO_4^{2-})	Water/rock reactions, chemical reduction to anhydrate, microbial reduction of SO_4^{2-}	H_2S is the primary energy source for aerobic chemoautotrophs including symbionts; oxidized sulfur species reduced by high diversity of microorganisms; present in some amino acids and Fe-S clusters as protein cores
N (as NH_3 or NH_4^+)	$<$0.01–1 mmol[a]	$<$0.01 mmol 30 μ mol (as NO_3^-)	Organic-N in buried sediments, possibly N_2-fixation by microorganisms and/or chemical reduction of N_2[b]	A source of nitrogen for subsurface microorganisms; oxidation to NO_3^- or NO_2^- by nitrifying bacteria
P (as PO_4^{2-})	0.5 μ mol	2.5 μ mol	Water/rock reactions (P_2O_5 in basalts), SW PO_4^{2-}	All organisms require P for nucleic acids, energy reactions and fatty acids; animals and aerobic microbes use SW-PO_4^{2-} and/or detrital organic PO_4^{2-} compounds
Fe	0.009–18 mmol as Fe(II)	$<$1 nmol	Water/rock reactions (12% iron in crust), major component of sulfides as pyrite	Energy source for Fe(II) oxidizing bacteria. Fe(III) as electron acceptor for specific groups of vent microbes. Trace element required by all organisms
Mn	0.1–4.5 mmol as Mn(III)	$<$1 nmol	Water/rock reactions	Energy source for Mn(III) oxidizing bacteria. Trace element required by all organisms
Si	2.7–23 mmol	0.16 mmol	Water/rock reactions, SW entrainment, major component of outer layers of sulfide deposits	Some evidence for microbially mediated Si precipitation in sulfides

(*Continued*)

TABLE 2 (*Continued*)

Chemical species	Vent fluids conc/kg SW	Seawater conc/kg	Sources in vents	Biological significance
Zn	2–100 μmol	0.01 μmol	Water/rock reactions, major component of sulfides as pyrite	Trace element required for key enzymes including alkaline phosphatase and RNA polymerase
Cu	0.02–44 μmol	0.007 μmol	Water/rock reactions, major component of sulfides as chalopyrite	Trace element required for enzymes including oxidative enzymes involved in electron transfer; component of haemocyanin in arthropods; toxic in μ mol concentrations
Co	20–200 nmol	0.03 nmol	Water/rock reactions	Trace element required by all organisms usually involving enzymes requiring B_{12} coenzymes (contain Co)
Cd	1–180 nmol	<1 nmol	Water/rock reactions	Toxic to all organisms in nmol levels; binds to S, N centers of proteins and DNA
Pb	9–359 nmol	0.01 nmol	Water/rock reactions	Toxic to all organisms in nmol levels
Mo	1–33 nmol	<1 nmol	Water/rock reactions	Trace element required for specific enzymes including nitrogenase
W[c]	<0.01–2.1 μmol	<1 nmol	Water/rock reactions	Trace element required for specific enzymes by hyperthermophilic archaea
Ni[c]	<0.01–53 μmol	<1 nmol	Water/rock reactions	Important component in coenzymes (F-430) of methanogens and enzymes of hyperthermophilic archaea

[a] Chemical data from Butterfield et al. 1995; Elderfield & Schultz 1996; Lilley et al. 1993; Von Damm 1990, 1995.

[b] There are experimental data for the reduction of N_2 to NH_3 under hydrothermal vent conditions (Brandes et al. 1998).

[c] Data from high temperature fluids from nine different sites at Endeavour on the Juan de Fuca Ridge (Baross & Adams, unpublished).

chemical compounds and elements. These shifts are also reflected in the microbial communities with strictly anaerobic organisms dominating environments exceeding 50°C. The macrofaunal communities are generally restricted to temperatures less than 30°C, although some of the polychaete worms found on active sulfides might be able to grow at temperatures greater than 50°C, which is the upper temperature limit for growth of known metazoans (Cary & Stein1998, Cary et al. 1998b). While the animal communities are restricted to aerobic environments, many of the animals are adapted to grow in low concentrations of oxygen by producing high volumes of specialized hemoglobin with a high affinity for oxygen.

HYDROTHERMAL CHEMISTRY AND THE VENT FOOD WEB

There is a strong link between the major element and volatile chemistry of vent fluids and microbial diversity (Gugliandolo et al. 1999, Jannasch 1995, Karl 1995). At vent environments, the predominant energy and carbon sources utilized by microbes originate de novo as a result of hydrothermal processes (Table 1). Thus, chemical energy replaces light as the fuel that supports the primary producers in vent environments; the gases derived from volcanoes fuel life on and within the seafloor. Only O_2, the key electron acceptor for all animals and aerobic microorganisms, and possibly some organic compounds, originate from pelagic photosynthesis. The primary producers use CO_2 as their main carbon source, although there are organisms at vents that utilize CH_4 and organic compounds. The aerobic microorganisms use O_2 or NO_3^- as the electron acceptor and derive their energy from the oxidation of reduced sulfur compounds, CH_4, H_2, NH_4^+, or organic compounds (Table 3). The oxidation of reduced sulfur compounds is the most important of these processes and is the basis of most of the dominant symbiotic associations:

$$S^{2-}(HS^-, H_2S, S^\circ) + CO_2 + O_2 + H_2O \rightarrow SO_4^{2-} + [CH_2O].$$

The oxidized forms of sulfur from this reaction can vary depending on the organism, and other environmental conditions can include $S_2O_3^{2-}$ and H_2SO_4. The different animals at vents feed either directly on these microbes, or they derive their carbon and nitrogen indirectly from symbiotic associations. Methane oxidizers are the only other group of bacteria that enter into symbiotic associations with vent animals (Cary et al. 1998, Cavanaugh et al. 1987, Streams et al. 1997), although like hydrogen-oxidizing and ammonia-oxidizing bacteria, they are present on the surfaces of animals and rocks and in hydrothermal plumes (Mevel et al. 1996, de Angelis et al. 1991, Huber et al. 1992). Various reactions involved with these organisms include:

$$CH_4 + O_2 \rightarrow [CH_2O] + H_2O$$

$$4H_2 + O_2 + CO_2 \rightarrow [CH_2O] + 3H_2O$$

$$NH_3 + O_2 + CO_2 \rightarrow [CH_2O] + HNO_3.$$

Bacterial methane and hydrogen oxidation have been measured in samples recovered from hydrothermal plumes (McLaughlin 1998, McLaughlin et al. 1996, de Angelis et al. 1993, Huber et al. 1992) and detected in gene libraries of vent samples, but they to date have not been studied in isolated culture. Similarly, most observations of iron and manganese oxidation bacteria have been from either microscopic examination of rock surfaces and in sulfides or by their activity in recovered hydrothermal plume samples. The metal-oxidizing microbes that have been isolated usually require organic compounds for growth and metal oxidation.

TABLE 3 Microbial metabolic processes at hydrothermal vent environments

Conditions	Electron donor	Electron acceptor	Carbon source	Metabolic process	Biotopes	Thermal groups of microorganisms[a]
AEROBIC	HS^-, S°, $S_2O_3^{2-}$, $S_4O_6^{2-}$	O_2, possibly NO_3^-	CO_2	Sulfur oxidation	Diffuse-flow vent fluids, outer zone of sulfides and some basalts, microbial mats, smoker plume fluid, symbionts of tube-worms, clams and mussels, gut flora of heterotrophic macrofauna	Mesophilic bacteria (α, γ proteobacteria), ε-proteobacteria in microbial mats at vents presumed to be S-oxidizers but not yet cultured, acidophilic S-oxidizing archaea exist but not yet found in vents
	H_2	O_2, possibly NO_3^-	CO_2	Hydrogen oxidation	Diffuse-flow vent fluids, smoker plumes	Mesophilic bacteria detected by activity measurements
	Fe^{2+}, Mn^{2+}	O_2	CO_2	Metal oxidation	Diffuse-flow vent fluids, outer zone of sulfides and some basalts, microbial mats, surface of tubes and shells of some animals	Diverse mesophilic bacteria
	CH_4 and other C_1 compounds	O_2	CH_4, CH_3OH, CO, CO_2	Methanotrophy and methylatrophy	Diffuse-flow vent fluids, outer zone of sulfides, surface of tubes and shells of some animals, smoker plume fluid, symbionts for some animals	Mesophilic β-proteobacteria
	NH_4^+, NO^{2-}	O_2	CO_2	Nitrification	Limited data, diffuse-flow vent fluids	Mesophilic bacteria
	Organic compounds	O_2, NO_2^-	Organic compounds	Heterotrophy	Ubiquitous at vents	Many different genera of mesophilic and thermophilic bacteria

ANAEROBIC	H_2	S°, SO_4^{2-}, $S_2O_3^{2-}$	CO_2	Sulfur and sulfate reduction	Diffuse-flow vent fluids, sulfide structures, microbial mats, sediments (Guaymas, sedimented-ridges)	Mesophilic and thermophilic bacteria and hyperthermophilic archaea
	H_2	CO_2	CO_2, possibly formate and acetate	Methanogenesis	Ubiquitous in anaerobic biotopes	Mesophilic, thermophilic, and hyperthermophilic archaea
	H_2	NO_3^-	CO_2	Hydrogen oxidation	Diffuse-flow fluids	Identified from molecular analyses of vent samples
	Organic acids	Fe^{3+} (iron oxyhydroxides)	Organic acids	Iron reducers	Crustal fluids from new eruptions, subsurface fluids, and sediments	Mesophilic bacteria and hyperthermophilic archaea
	CH_4	SO_4^{2-}?	CH_4?	Anaerobic methane oxidation	Measured in methane hydrate sediments and from enrichment culture with high-temperature hydrothermal fluids	Evidence that the acetoclastic methanogen, Methanosarcina spp., oxidizes CH_4 anaerobically
	Organic compounds	S°, SO_4^{2-}	Organic compounds	Sulfur and sulfate reduction	Commonly isolated hyperthermophilic archaea isolated from diffuse-flow vent fluids, sulfides and guts of sulfide-dwelling animals	Mesophilic and thermophilic bacteria and hyperthermophilic archaea
	Organic compounds	Organic compounds	Organic compounds	Fermentation	Ubiquitous in anaerobic biotopes; include both obligate and facultative anaerobes	Mesophilic and thermophilic bacteria and hyperthermophilic archaea
	fatty acids, alcohols or H_2	CO, fatty acids, alcohols CO_2	CO, fatty acids, alcohols	Acetogenesis (produce acetate)	Limited data from vents	Unknown taxa at vents

[a] Mesophile, defined by their optimum growth temperature which is approximately 37°C, frequently grows from 5°C–10°C to 45°C–50°C; thermophile grows at 50°C and above; hyperthermophile grows optimally at 80°C or above. Maximum growth temperature measured for a pure culture is 113°C.

There are also a diverse group of aerobic heterotrophic microorganisms in vents that utilize a wide variety of organic compounds including organic acids, carbohydrates, and fatty acids (Karl 1995). Some of these organisms are mixotrophic and can grow autotrophically (use of CO_2 as the primary inorganic-carbon substrate that is reduced and fixed to organic carbon) or heterotrophically (obtaining energy from the oxidation of organic compounds).

Some of the best-studied organisms at vents are anaerobic (Table 3) because most vent habitats that exceed 50°C are depleted in O_2 and NO_3^- (Lilley et al. 1993). Included in this group are both bacteria and archaea, some of which are capable of growing at temperatures exceeding 90°C (Summit 2000, Baross & Deming 1995, Deming & Baross 1993, Holden et al. 1998, Huber et al. 2000, Jannasch et al. 1992). The three most common metabolic groups of anaerobes include the sulfate reducers, fermenters, and methanogens. Sulfate reduction has been observed in diffuse flow vents and in hot Guaymas sediments (Lilley et al. 1983, Jørgensen et al. 1992). Sulfate reduction can occur chemolithotrophically (using energy from chemical reactions involving inorganic compounds and CO_2 as the only carbon source) and heterotrophically and by different thermal groups of both bacteria and archaea:

$$\text{Chemolithotrophic } SO_4^{2-} \text{ reduction: } CO_2 + SO_4^{2-} + 6H_2 \rightarrow [CH_2O] + S^{2-} + 5H_2O.$$

$$\text{Heterotrophic } SO_4^{-} \text{ reduction: } CH_3COOH + SO_4^{2-} \rightarrow 2CO_2 + S^{2-} + 2H_2O.$$

The heterotrophic sulfate reducers commonly utilize acetate as their carbon source but can also utilize a limited number of other low molecular weight organic acids. Like sulfate reduction, methanogenesis occurs over the entire temperature growth range for microorganisms (<0°C to 110°C). All methanogens are archaea and generally reduce CO_2 to methane, although a few species can utilize acetate and formate:

$$2CO_2 + 6H_2 \rightarrow [CH_2O] + CH_4 + 3H_2O.$$

Methanogens have been isolated or detected using molecular methods from most high-temperature anaerobic vent habitats. The best-studied methanogens are hyperthermophiles capable of growing at temperatures greater than 80°C. These organisms are extraordinarily fast growing, and some species have doubling times of less than 30 min at their optimum growth temperature. Typically, low levels of hydrogen in vent fluids will correlate with high levels of methane, suggesting extensive methanogenesis (Lilley et al. 1983, 1993). Another important group of organisms are the anaerobic heterotrophic archaea. Most of these organisms have complex nutrient requirements including amino acids and elemental sulfur. It is presumed that the major source of organic material for these organisms comes from dead and/or pyrolyzed animals and other microbes (Baross & Deming 1995). These archaea are commonly used as indicators for the existence of hot biotopes in the subseafoor and sulfides because they usually have minimum growth temperatures that are higher than 50°C (Holden et al. 1998; Summit & Baross 1998, 2001). Recently, anaerobic archaea were isolated from the subseafloor that are capable of coupling the utilization of acetate with the reduction of Fe(III) to magnetite. These organisms represent a new genus within the Thermococcales (Summit & Baross 1998, Summit 2000).

In addition to carbon and energy sources and electron acceptors and donors, there are other chemical species that are required by organisms. These include a source of nitrogen and phosphorus and a wide variety of transition metals including iron, manganese, molybdenum, tungsten, nickel, and zinc (Table 2). Iron and manganese concentrations exceeding 1 mM are commonly measured in hydrothermal fluids from most vent environments, whereas iron concentrations approaching 20 mM have been detected along the Southern Juan de Fuca Ridge (Butterfield & Massoth 1994; Elderfield & Schultz 1996; Evans et al. 1988; Von Damm 1990, 1995).

In contrast to metals, the concentration of nitrogen compounds varies considerably, presumably depending on the amount of organic material present. It is believed that the ammonia measured in submarine vent environments is derived from buried organic nitrogen. This may be equivocal because ammonia may be abiotically synthesized under vent conditions (Brandes et al. 1998). Measurable ammonia is present in diffuse flow fluids at the Endeavour. This has been interpreted by Lilley et al. (1993) to be derived from buried organic nitrogen in sediments covered by basaltic flows. Other vents along the Juan de Fuca Ridge, the East Pacific Rise, and the Mid-Atlantic Ridge do not have measurable ammonia. The only nitrogen present is N_2 derived from seawater or possibly organic nitrogen from decaying or pyrolyzed animals or microbes. It is presumed that if there is an active microbial community associated with the subseafloor at vents, a significant portion of the community will have to chemically incorporate N_2. Only some bacteria and a few species of methanogenic archaea are capable of fixing N_2. Preliminary molecular data from microbial communities at Axial Volcano on the Juan de Fuca Ridge show a surprisingly high diversity of the nitrogen fixation gene that include both bacteria and archaea (Mehta & Baross 2000).

Much less is known about the concentration and types of phosphorus present in most hydrothermal vent environments other than the levels of dissolved phosphate in seawater and the presence of phosphorus as apatite (P_2O_5) in basalt. It is not known if there are subseafloor microbes that are capable of extracting phosphorus from basalt.

All organisms have requirements for a variety of trace metals. These metals are incorporated as metal clusters in enzymes and other proteins and in coenzymes such as B_{12} and the flavin F_{430} in methanogens (Table 3). It is interesting that many of the proteins found in vent archaea are associated with Fe-S clusters and that iron is also required for key enzymes including the enzymes involved in nitrogen fixation. Many of the hyperthermophilic archaea have a requirement for tungsten for five key groups of enzymes involved in their metabolism (Adams & Kletzen 1996, Roy et al. 1999). Tungsten imparts a greater thermal stability for the enzymes than molybdenum (Kletzen & Adams 1996). The discovery of tungsten enzymes in vent hyperthermophiles underscores the intimate link between hydrothermal chemistry and the nutritional needs of vent organisms.

Much remains to be explained about the relationship between the chemistry of vent environments and the nutrition and metabolism of the microorganisms they support. Little is known about the source reactions or rates of synthesis of ammonia and other nitrogen compounds, S° and other S-electron acceptors, and organic compounds in vent environments and the role of organisms in their production and consumption (Baross & Deming 1995). Are there sources of organic compounds and nitrogen other than buried organic material such as abiotic synthesis at high temperature? All evidence suggests that petroleum hydrocarbons and organic acids, including all of the amino acids, can be synthesized from volcanic volatiles and metal catalysts with heat as the energy source (see Corliss et al. 1981 for reference list, Amend & Shock 1998, Hennet et al. 1992, Marshall 1994, Simoneit 1993, Shock & Shulte 1998, McCollum & Seewald 2001). While there is some controversy about the stability of amino acids at vent temperatures and pressures (Miller & Bada 1988, Qian et al. 1993), based on thermodynamic models, there is also evidence that amino acids enter into metastable equilibrium at different high temperatures (Shock 1990, 1993).

A model by Wächtershäuser (1988, 1998) proposed the abiotic synthesis of organic compounds, including the intermediates in metabolic pathways, under hot hydrothermal vent conditions associated with pyrite (FeS_2). These metastable equilibrium reactions are dependent on the fugacity of oxygen and hydrogen (Helgeson & Amend 1994). Both acetate and pyruvate have been synthesized under simulated hydrothermal vent conditions (Cody et al. 2000, Huber & Wächtershäuser 1997). One of the frequently overlooked properties of most hydrothermal vent systems, which is particularly germane to the questions concerning the thermal stability of organic compounds and, by inference, to the possibility of an extensive hot subsurface biosphere, is that they are open systems. That is, the input of seawater and output of hydrothermal fluid is continuous during fluid transit through the ocean crust, with seawater circulating through gradients in chemical species, pH, Eh, and temperatures from ambient seawater (2°C–4°C) to greater than 400°C (Baross & Hoffman 1985, Shock 1990, Baross 1998).

These systems are much like chemical reactors. Specific organic compounds may be synthesized at temperatures where proteins denature. They are also likely to be advected rapidly into lower-temperature regimes that favor stability and perhaps reactivity with other organic compounds. Current models of heat flow associated with submarine volcanic systems indicate that most hydrothermal circulation is associated with diffuse flow on the flanks of ridges and not with the more dramatic outflow associated with black smokers (Mottl & Wheat 1994, Wheat & Mottl 2000, Butterfield et al. 2001). Diffuse flow environments reflect steep subsurface gradients in temperature. They should provide good sites to search for evidence of abiotic organic synthesis for subsequent utilization by subsurface dwelling hyperthermophiles.

MICROBIOLOGY—THE ORGANISMS

It has become increasingly clear that there is an extraordinarily high diversity of microorganisms associated with submarine hydrothermal vent environments (e.g., Baross & Deming 1985; de Angelis et al. 1991; Hedrick et al. 1992; Karl 1995; Harmsen et al. 1997a,b; Adams 1999; Resenbach et al. 2000; Takai 2001). In part, this is because of the diverse number of biotopes associated with vent environments that span so many extremes in physical and chemical conditions. However, little is known about most of these organisms other than their phylogeny based on small subunit ribosomal RNA sequences because only a few species have been cultured and characterized. The development of new molecular techniques has revolutionized our ability to study microbial ecology without isolating organisms (Pace 1997, Hugenholtz et al. 1998, Huber et al. 2000, Jeanthon 2000). Moreover, the creative pairing of molecular methods with geochemical techniques is leading to a better understanding of the physiology of organisms without prior culturing (Orphan et al. 2001).

Although most of the microbial diversity at vents includes both bacteria and archaea only characterized by molecular methods, this high diversity is also reflected in cultured bacteria and archaea that include different thermal classes. The important primary producers in vent food webs are the bacteria that oxidize sulfur, methane, hydrogen, and iron. The sulfur-oxidizing bacteria represent the dominant CO_2-utilizing microbes in vent environments (Jannasch 1995). They are the key symbionts associated with tubeworms and mollusks, and they are a significant fraction of the free-living organisms in diffuse-flow fluids and in microbial mats. Included in this group of bacteria are *Thiobacillus*, *Thiomicrospira*, *Ferrobacillus*, and the large mat-forming filamentous Beggiatoa species that can exceed 50 μm in diameter (Nelson et al. 1989, Karl 1995, Wirsen et al. 1998). Other putative sulfur-oxidizing bacteria have been identified in microbial mats using molecular methods (Moyer et al. 1998, Longnecker & Reysenbach 2001). The halotolerant bacteria, *Halomonas* and *Marinomonas* spp., are among the most abundant groups of bacteria in low-temperature vent fluids. These organisms can grow in salt concentrations up to 25%, and they grow on a large number of organic compounds (Kaye & Baross 2000). Some of these organisms also have the capacity to tolerate up to 3-mM Cd. It is not known if the ability to grow in high salt concentrations reflects widespread brine environments below seafloor.

Data based on molecular techniques show high diversity of bacteria and archaea in high-temperature environments and in diffuse-flow vents. There is somewhat less diversity in microbial mats. In general, it is difficult or impossible to infer physiological characteristics of many of the organisms detected by molecular methods. This is particularly true for the environmental archaea because only hyperthermophiles and halophiles have been cultured. Most of the thermophilic and hyperthermophilic bacteria and archaea isolated from vents are anaerobic; however, there are anaerobic sulfate reducers, heterotrophs, and methanogens that can exist at both low seawater temperatures and at temperatures near or exceeding 100°C (Karl 1995).

Hyperthermophiles from vents and other geothermal environments have received considerable attention because they are of interest for (*a*) their ability to grow and survive at the most extreme conditions of high temperatures and low pH, (*b*) their phylogenetic position as the most ancient of extant organisms, and (*c*) their biotechnology applications. Most of the hyperthermophiles isolated from hydrothermal vent environments are archaea and are represented by exclusively anaerobic heterotrophs and methanogens. Because the isolation and characterization of hyperthermophilic microorganisms from vent and other thermal environments is an extremely active endeavor, there are 31 genera and more than 100 species described (Adams 1999, Baross & Holden 1996, Stetter 1999). Marine hyperthermophiles require salt, and among those species tested, increased hydrostatic pressure can extend upward the optimal and maximal growth temperatures (Deming & Baross 1993; Pledger et al. 1994; Holden & Baross 1993, 1995) and increase the thermal stability of enzymes (Adams 1993, Michels et al. 1996, Summit et al. 1998). Most of the heterotrophic species, such as *Thermococcus*, *Pyrococcus*, *Hyperthermus*, and *Staphylothermus* have maximal growth temperatures less than 105°C. *Pyrodictium* and the methanogen *Methanopyrus* species grow at 110°C (Stetter et al. 1990), and *Pyrolobus fumarii* grows at 113°C, which is the highest temperature for growth of a pure culture (Blöchl et al. 1997).

Most hyperthermophiles are strict anaerobes; only three species utilize O_2. There are also species of hyperthermophiles that use nitrate as an electron acceptor under anoxic conditions. The use of S° as an electron acceptor is a hallmark of heterotrophic hyperthermophiles; for most species, S° is an obligate requirement. Archaeoglobus species use SO_4^{2-} or $S_2O_3^{2-}$, whereas *Pyrodictium occultum* and *Thermoproteus tenax* can use $S_2O_3^{2-}$ in addition to S°. On the other hand, *Pyrobaculum aerophilum* is inhibited by sulfur and uses organic compounds as both electron acceptors and donors (Völkl et al. 1993). Some species of *Thermococcus*, *Pyrococcus*, *Pyrodictium*, and *Thermoporoteus* can grow without sulfur, with carbohydrates serving as electron acceptors. While S° reduction is known to play a role in the energy metabolism of hyperthermophilic heterotrophs, the exact mechanism is not known (Kelly & Adams 1994).

A new genus within the order Thermococcales is capable of growing on acetate utilizing Fe(III) as the electron acceptor and forming magnetite (Summit & Baross 2001). Other groups of iron reducers from vents have also recently been described (Slobodkin & Wiegel 1997, Slobodkin et al. 2001, Summit 2000). A number of hyperthermophilic archaea, notably *Thermoproteus* and *Sulfolobus* species and *Acidianus infernus*, fix CO_2 through the reductive citric acid pathway. The reaction pathway is thought to be one of the most ancient of metabolic pathways. In contrast, all of the methanogens utilize a reductive acetyl CoA pathway (a pathway of autotrophic CO_2 fixation) to reduce CO_2 to methane.

Some classes of microbes are easily distinguished and can be used as microbial habitat tracers. For example, if microorganisms that live only at high temperature (50°C–100°C) are present in low-temperature venting fluids, those microbes must have been carried from below the seafloor (Holden et al. 1998, Summit & Baross 1998). One excellent indicator of subseafloor ecosystems are Thermococcales. They are cosmopolitan and have been isolated from all hydrothermal environments thus far sampled. They are Archaea and members of the kingdom Euryarchaeota (Woese et al. 1990, Woese 1998). All are strict anaerobes, heterotrophic, and utilize carbohydrates by a glycolytic pathway that includes some unusual enzymes (Adams 1999, Mukund & Adams 1995). Most species have a requirement for amino acids, peptides, and elemental sulfur (Baross & Holden 1996). *Pyrococcus* and *Thermococcus* are the two genera within the Thermococcales, and at the present time there are approximately 30 species described. *Thermococcus* and *Pyrococcus* spp. are routinely cultured from near-vent sites, from samples of sulfide rocks, from alvinellid worms, and occasionally from hot fluid samples (Baross & Deming 1995, Jannasch et al. 1992). They are hardy, surviving even in low-temperature oxic conditions (Baross, unpublished observations). Moreover, because the Thermococcales are heterotrophic, they are known to utilize a wide range of organic substrates and produce diverse hydrolytic enzymes; one species is capable of degrading chitin (Adams 1999, Adams & Kelly 1998, Connaris et al. 1991, Gantelet & Duchiron 1999, Cornec et al. 1998, Huber & Stetter 1998, Legin et al. 1998, Uhl & Daniel 1999).

An excellent example of Thermococcales as environmental indicators is the study by Holden et al. (1998). Thermococcales were cultured at levels above background from two 5°C–30°C, basalt-hosted diffuse-flow systems at the eruption sites following the 1993 CoAxial event (Holden et al. 1998). These organisms were entrained in fluids that were 20°C to 50°C below their optimum growth temperature (Holden et al. 1998, Delaney et al. 1998). These findings required the presence of a hot, subseafloor biotope. Thermococcales were also isolated from "event plume" water following the 1996 North Gorda eruption (Summit & Baross 1998) and from diffuse-flow fluids following the 1998 eruption at Axial Volcano, Juan de Fuca Ridge (Huber et al. 2002). These hyperthermophiles are commonly isolated from low-temperature diffuse vents associated with more stable, long-term vent environments such as the Main Endeavour Field (Summit 2000). *Thermococcus* species have been detected in all diffuse-flow vents at Axial and Endeavour but can vary in abundance by more than three orders of magnitude at different sites.

Recently, it was shown that Thermococcales isolated from the subseafloor on the Juan de Fuca Ridge were different from similar organisms isolated from nearby sulfide structures, based on both molecular phylogenetic data and physiological characteristics (Summit & Baross 2001). Similarly, Thermococcales isolated from geographically distinct vent sites and different biotopes within vent fields show distinct protein patterns and growth characteristics (Holden et al. 2001). This implies that these organisms adapt to a range of environmental conditions. Considering the high diversity of bacteria and archaea in high-temperature environments that have been identified from small subunit RNA sequences but have not been cultured (Barns et al. 1994, DeLong 1998, Ferris et al. 1997, Takai & Horikoshi 1999, Takai et al. 2001), it is clear there is still much to learn about their physiological adaptation to vent environments.

HYDROTHERMAL VENT MICROBIAL HABITATS

Submarine environments that support life at vents include sulfide mounds, smokers, sediments, microbial mats, animal symbionts, outer surfaces of animals and rocks, plumes resulting from smokers, diffuse-flow vents, and the subseafloor. These environments show great variation in physical characteristics and in the kinds, and concentrations of carbon and energy sources (Shock 1990, Deming & Baross 1993, Karl 1995). Hydrothermal plumes have near ambient seawater temperature and low levels of nutrients, whereas steep gradients in temperature, oxygen, and nutrient concentrations are hallmarks of sulfide structures and the subseafloor crustal environment (Figure 21). Similar variability is seen in the abundance and diversity of microbes in these habitats (Table 4). For example, the highest numbers

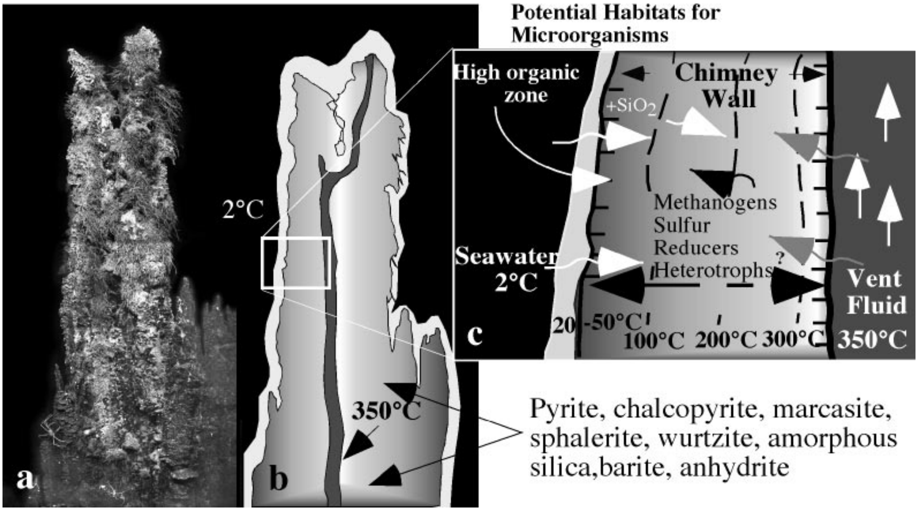

Figure 21 Steep gradients in temperature, oxygen, and nutrient concentrations are hallmarks of sulfide structures (and the subseafloor crustal environments). (*a*) Photomosaic of the diffusely venting hydrothermal structure "Flying Buttress" in the Mothra Hydrothermal Field, Endeavour Segment, Juan de Fuca Ridge. The outer surface of this 8-m-tall sulfide edifice hosts a diverse and dense macrofaunal and microbial community. (*b*) Schematic of the interior of a hydrothermal chimney showing an open conduit through which 350°C hydrothermal fluids flow. The outer portions of some chimneys are steeped in warm mixtures of hydrothermal fluid and seawater, which support life on the outer surfaces of active chimneys. (*c*) Steep thermal and chemical gradients exist within the sulfide walls on scales of centimeters to several meters (after McCollom & Shock 1997). Gradients within the structure walls bound the limits to life. Examination of recovered sulfides shows that the porous, water-saturated outer walls of the sulfide chimneys host abundant microbial communities that can grow at temperatures >90°C and that they tolerate high concentrations of toxic metals.

TABLE 4 Numbers and metabolic diversity of microorganisms in vent environments

Samples	Number of microorganisms[a]	Metabolic and/or phylogenetic groups
Diffuse-flow fluids (2°C–80°C)	10^5–$>10^9$ ml^{-1}; high numbers from Galapagos particles	Extremely high diversity of bacteria and archaea and include aerobes and anaerobes (see Table 1)
Smoker fluids (250°C–400°C)	Not detected to 10^7 ml^{-1}; high numbers correlate with evidence of phase separation[b]	Hyperthermophilic methanogens and heterotrophic archaea isolated; evidence for other hyperthermophilic archaea and bacteria from molecular data[c]
Hydrothermal vent plume water (2°C in horizontal plume)	$\sim 10^5$–$>10^6$ ml^{-1}	H_2-, CH_4-, and Mn^{2+}-oxidizing bacteria detected by activity measurements; *Halomonas* spp. isolated[d]
Deep SW surrounding vents (2°C)	10^3–$<10^5$ ml^{-1}	Limited diversity of bacteria and archaea detected and enumerated using molecular methods
Sulfide structures	$>10^8$ per gram of sulfide on outer layers; 10^5 per gram in interior	Outer layers have a mixture of archaea and bacteria and include metal oxidizers and methanogens; inner layers contain only archaea of unknown physiologies[e]
Subsurface crust	Numbers are unknown	Different thermal groups of bacteria and archae detected from new eruptions; unique archaea isolated from subsurface fluids[f]
Microbial mats	$>10^8$ bacteria per gram	High numbers of sulfur-oxidizing bacteria including *Beggiatoa* spp. and uncultured ε-proteobacteria[g]
Sediments	Surface of Guaymas sediments similar to microbial mats; numbers range from in sedimented ridges[h]	Same as for microbial mats in surface layer with sulfate-reducing bacteria and archaea dominating the deeper layers

(*Continued*)

TABLE 4 (*Continued*)

Samples	Number of microorganisms[a]	Metabolic and/or phylogenetic groups
Animal endosymbionts	∼10^{10} per gram tissue	Sulfide-oxidizing bacteria most common in hydrothermal vent animals whereas methane-oxidizing bacteria found at some cold seeps
Outer surfaces of animals	Probably similar to microbial mats	Methane oxidizers found on surface shells of some limpets and worm tubes[i]; filamentous metal-oxidizing bacteria found on rear surfaces of Alvinella worms[j]

[a] Numbers usually determined by epifluorescence microscopy or quantitative lipid analyses.

[b] Baross & Deming 1995.

[c] Takai et al. 2000.

[d] Cowen et al. 1986, 1998; Lilley et al. 1995; Kaye & Baross 2000.

[e] Harmsen et al. 1997a, Schrenk et al. 1999a.

[f] Delaney et al. 1998; Summit & Baross 1998, 2001.

[g] Jannasch 1995, Longnecker & Reysenbach 2001, Nelson et al. 1989, Moyer et al. 1995.

[h] Parkes et al. 1994, Summit et al. 2000.

[i] De Angelis et al. 1991.

[j] Cary & Stein 1998.

of organisms are detected in the outer surface of sulfide and animals, in sediments, and in the animal structures that house the endosymbiotic bacteria.

LIFE WITHIN SULFIDE EDIFICES

Some of the most extensively studied thermal environments at submarine hydrothermal vent sites are those of the black smokers and related sulfide structures. The microbial diversity in sulfides based on molecular data includes both high-temperature bacteria and archaea (Takai & Horikoshi 1999, Takai et al. 2001). A particularly favorable niche for microorganisms is that of sulfide ledges or flanges, which are characteristic of sulfide structures in the Endeavour system (Delaney et al. 1992, Robigou et al. 1993, Delaney et al. 1997). Hyperthermophilic archaea have been detected in discrete mineral layers within these flanges, where they are estimated to exceed 10^8 cells per gram of sulfide (Figure 22) (Baross & Deming

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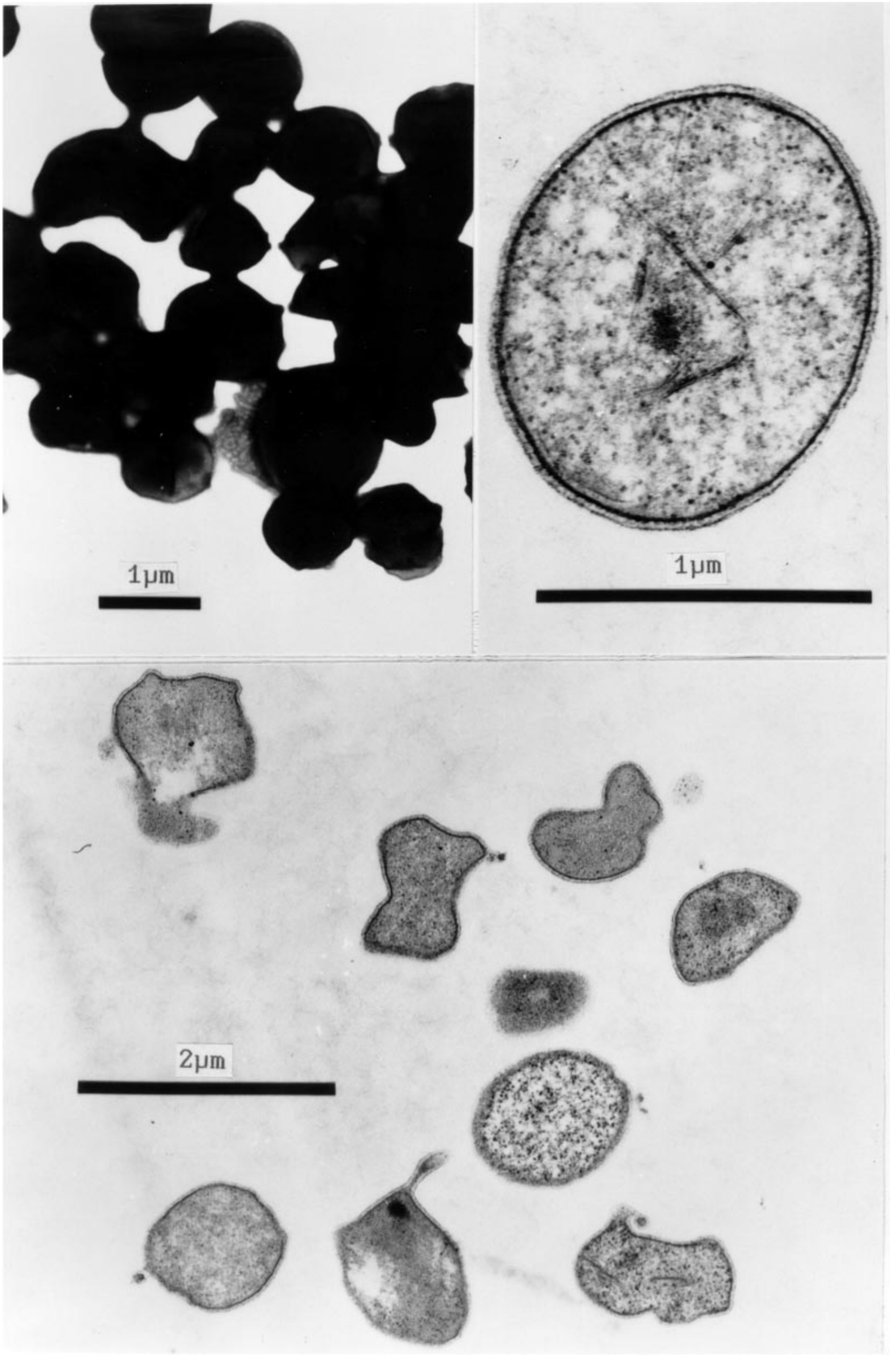
Figure 22 Transmission electron micrographs of *Pyrococcus endeavourii* strain ES4 cultured at 80°C in an organic rich medium. (*a*) Platinum shadow showing a regular-sized coccoid morphology typical of exponential-phase cultures. (*b*,*c*) Electron micrographs of ultra-thin sections of ES4 (Pledger & Baross 1991).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1995, Hedrick et al. 1992, Pledger & Baross 1991). The hyperthermophiles isolated from within these structures include sulfur-dependent heterotrophs and methanogens (Pledger & Baross 1991, Takai et al. 2000). In addition, the surfaces of black smoker and flange sulfides commonly harbor high numbers of several species of polychaete worms including *Alvinella* and *Paralvinella* spp. (Sarrazin et al. 1997, Sarrazin & Juniper 1997). Heterotrophic hyperthermophiles have been isolated from the guts of these animals, suggesting that the polychaetes may derive a portion of their nutrition from hyperthermophiles (Baross & Deming 1995, Pledger & Baross 1989). Alternatively, hyperthermophiles may be a normal component of the gut flora of these polychaetes growing at the low end of their temperature growth range, which is approximately 50°C (Figure 23) (Holden et al. 2001).

Sulfide structures from the Juan de Fuca Ridge have been observed to harbor morphologically diverse groups of bacteria and archaea (Hedrick et al. 1992) including filamentous microbes that appear to be involved in the deposition of silica and metal oxides and in the oxidation of sulfides (Juniper & Tebo 1995, Juniper & Sarrazin 1995). In 1998, four large active and inactive sulfide structures (up to 2 m in length and weighing up to 1800 kg) were recovered from the Mothra Hydrothermal Field on the Endeavour Segment of the Juan de Fuca Ridge (Kelley et al. 1998a, 1999, 2001; Delaney et al. 2001). One of the goals of this program was to obtain a better understanding of the microbial ecology of sulfide chimneys and how the microbial communities manifest their association with the rock and fluid geochemistry in these dynamic environments (Delaney et al. 2001).

Results from this study indicate that microorganisms are ubiquitous in all of the active sulfide structures recovered. Hyperthermophilic archaea were cultured from within the walls of all four of the samples (Delaney et al. 2001). In addition, a preliminary transect from within the hot interior (302°C) to the cool outer walls (2°C) of the Finn structure showed extensive microbial communities and gradients in abundance: Values ranged from 10^5 cells/g in the warm interior to $>10^8$ cells/g in the outer walls (Schrenk et al. 1998, 1999a,b; Kelley et al. 1999). The highest microbial concentrations were associated with enrichments in many trace elements (As, Au, Ag, Th, Sb, etc.) (Kelley et al. 1999). Metal-tolerant hyperthermophiles were also cultured. Within Finn, there is a diversity of microorganisms. Within well-defined mineral zones, the microbial community changes from predominantly bacteria and archaea in the outer surfaces to archaea in the hot interior (Schrenk et al. 1999a,b; Kelley et al. 1999). The 16S rDNA sequence data from the high biomass outer layer of Finn correspond to both autotrophic and heterotrophic microorganisms, whose growth encompasses high-temperature and more moderate-temperature domains. A portion of these sequences corresponds to organisms not yet in culture whose metabolism is unknown.

HYDROTHERMAL PLUMES

Hydrothermal plumes are enriched with methane and manganese, which have been shown to be oxidized by bacteria (Cowen et al. 1986; de Angelis et al. 1993; Lilley et al. 1995; Winn et al. 1986, 1995). Microbial-volatile reactions could be a locally

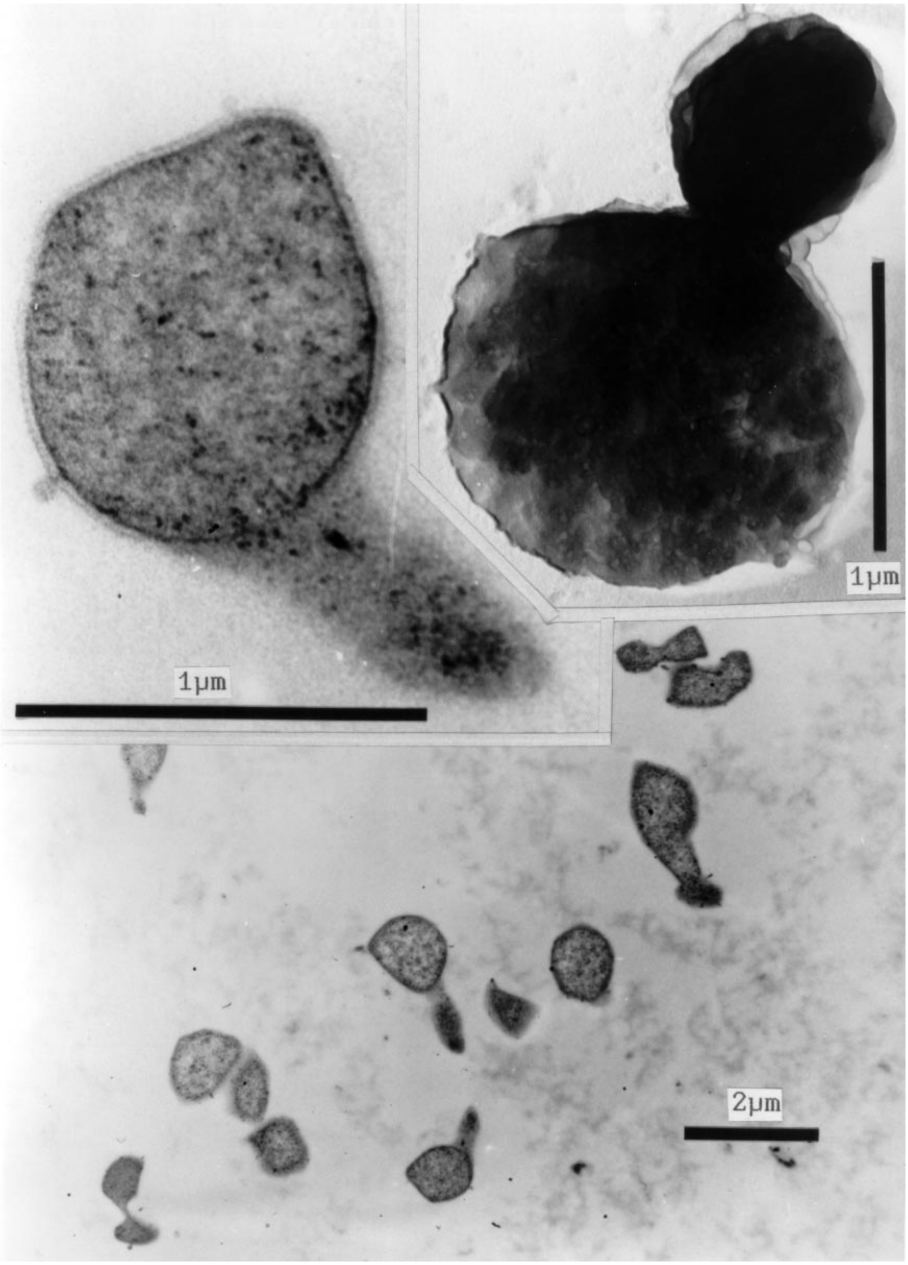


Figure 23 Transmission electron micrographs of *Thermococcus paralvinelleii* strain ES1 cultured at 80°C in an organic rich medium. (*a*) Platinum shadow showing the budding morphology typical of actively growing cultures. (*b*,*c*) Electron micrographs of an ultra-thin section of ES1 (Pledger & Baross 1989).

significant source of organic carbon. For example, the amount of organic carbon generated from methane oxidation in Endeavour plumes is estimated to be 1.5 times the amount of primary produced detrital carbon sinking to plume depths (de Angelis et al. 1993). Recent modeling by McCollum (2000) suggests that most of the primary productions in early plume development is from sulphur and H_2 oxidation.

Microbes have also been cultured or detected by microscopic and biochemical methods in hot smoker fluids at Endeavour. A correlation was observed between the increasing incidence of microbes and the degree to which the hydrothermal fluid had undergone phase separation (Baross & Deming 1995, Deming & Baross 1993). The total number of microbes in vent fluids ranges from 10^7 to 10^9 per liter. In general, within the hyperthermophilic microbial community, the numbers of cultured heterotrophs exceed methanogens by an order of magnitude.

The diffuse-flow vent fluids show great variations in the number of hyperthermophiles, ranging from undetectable levels ($<10^2$ per liter) to greater than 10^5 per liter. Novel microorganisms have also been isolated from diffuse-flow fluids, including halotolerant bacteria capable of growing in 25% salt and 3-mM Cd (Kaye & Baross 2000). Phylogenetic analyses of diffuse-flow samples from Axial show a very diverse community of both bacteria and archaea (Huber et al. 2002). The highest number of unique taxa is found in the fraction of microbes that are attached to particles. The particle-attached microbes are believed to be more indicative of subseafloor microbes because cultured microbes from the subsurface form biofilms within the cracks of crustal rocks (Summit 2000). The dominant archaea were Crenarchaeota, which did not resemble any cultured organism or any environmental sequence. These Crenarchaeota appear to be very diverse at both the genus and species levels. The Euryarchaeota detected were all related to *Methanococcus* species. The dominant bacterial sequences included methanotrophs and sulfur oxidizers. While *Thermococcus* and *Methanococcus* are the most commonly isolated species of hyperthermophiles from subseafloor biotopes, these initial phylogenetic analyses showed a high diversity of archaea that were not related to these cultured groups. Results to date support the hypothesis that subseafloor microbes associated with hydrothermal systems may have phylogenetic, nutritional, physiological, and bioenergetic characteristics that reflect the physical and geochemical properties of their habitat (Holden et al. 2001, Summit & Baross 2001).

SEDIMENT-HOSTED ENVIRONMENTS AND MICROBIAL MATS

Very high densities of microorganisms have been detected in microbial mats and in Guaymas sediments (Table 3). Sulfate reduction was measured within temperature gradients in Guaymas sediments, and three peaks of activity were observed at 35, 80, and 106°C (Jørgensen et al. 1990, 1992). The rate of sulfate reduction ranged from 32 nmol cm^{-3} day^{-1} at 90°C to 1563 nmol cm^{-3} day^{-1} at 70°C; activity was detected at 120°C (Elsgaard et al. 1994). The hyperthermophilic sulfate reducer, *Archaeoglobus profundus*, was isolated from these sediments (Burggraf et al. 1990). Microbes have also been observed in deep marine sediments over 500 m below the seafloor (Cragg & Parkes 1994; Cragg et al. 1990, 1992), and they have been detected in hot sediments along ridges (Cragg & Parks 1994, Summit et al. 2000). Sulfate reducers have been cultured from these samples (Barnes et al. 1998), and the sediments show the potential for microbial sulfate reduction (Parkes et al. 1994). Microbial concentrations in the sediments decrease with depth (Cragg & Parks 1994).

Most of the reports on microbial mats involve phylogenetic analyses, fatty acid analyses of the microbial community (Hedrick et al. 1992; Longnecker & Reysenbach 2001; Moyer et al. 1995, 1998), or microscopic observations (Jannasch & Wirsen 1981, Nelson et al. 1989). High densities of microbes and microbial CO_2-fixing activity and methane oxidation have also been observed on the surfaces of rocks and animal shells (Baross & Deming 1985, de Angelis et al. 1991, Tuttle 1985).

VENT MACROFAUNA

Macrofaunal communities at deep-sea hydrothermal vents are geographically isolated and generally ephemeral on timescales of months to decades because the microbial primary producers in the vents are dependent on discharging hydrothermal fluids. Vent animals exploit these primary producers in several ways, including symbiotic associations, direct consumption of microbes, as predators of other animals, or as scavengers and parasites (Cavanaugh 1993, Fisher 1995, Cary et al. 1997, Van Dover 2000). The predominant symbiont-carrying invertebrates include several species of vestimentiferan tubeworms, clams, and mussels (Childress & Fisher 1992, Cary et al. 1998a, Distel et al. 1995, see Van Dover 2000 for a review). Other vent-specific animals include limpets and shrimp that graze on microbial mats, various deposit-feeding polychaete worms, limpets and amphipods that can extract microbes from sulfides, and several groups of suspension feeders, including anemones and serpulid polychaetes. Some species of crab are predators of other animals. However, there are few predators at vents and little evidence that lethal predation plays a significant role in vent ecology (Voight 2000).

More than 440 species of animals have been observed globally in vent environments, of which more than 90% are endemic to vents. Specific regional variation in species composition is recognized with invertebrate faunas defining six biogeographic provinces (Van Dover et al. 2000). In general, the highest species diversity of animals is observed at the fast- and intermediate-spreading areas. The possible explanation for this is the correlation between increasing spreading rates and increased hydrothermal activity, as measured by plume incidence and an increased vent habitat area (Juniper & Tunnicliffe 1997). Approximately 100 species have been described from the fast-spreading East Pacific Rise, and approximately 80 species have been identified from the Northeast Pacific representing 64 genera and 45 families (Tunnicliffe et al. 1998). In contrast, there are only 35 species identified from the Mid-Atlantic Ridge. Most of the species from the Northeast Pacific are endemic to this location and are not found at any other vent site. Similarily, some of the dominant species found at the East Pacific Rise, including mussels, crabs, and fish, are not found at Juan de Fuca sites. Macrofaunal communities at most vent sites are dominated by species with endosymbiotic bacteria, such as vestimentiferans, mussels, and clams. However, this is not the case at Endeavour. Here, the abundant vestimentiferan communities coexist with a wide variety of other macrofauna without endosymbionts (Tunnicliffe 1988). At the Mid-Atlantic Ridge site, mussels are the only animals with endosymbionts, and tubeworms are absent. The vent fields at the Mid-Atlantic Ridge appear to show a continuous range in the distribution of dominant macrofauna, from shrimp-dominated to mussel-dominated assemblages (Desbruyeres et al. 2000, 2001). This variation at different vent sites may be attributable to high concentrations of heavy metals, which apparently have a negative impact on the filter-feeding mussels, rather than geographical or physical characteristics of the environments (Desbruyeres 2000). The fauna at the TAG site is predominately swarming shrimp (*Rimicaris exoculata*) that have unusual photoreceptors. One explanation for the existence of these eyelike structures is to allow the shrimp to detect thermal radiation associated with hot vent fluids, thus serving as a mechanism to locate feeding habitats (Van Dover et al. 1989, 2000).

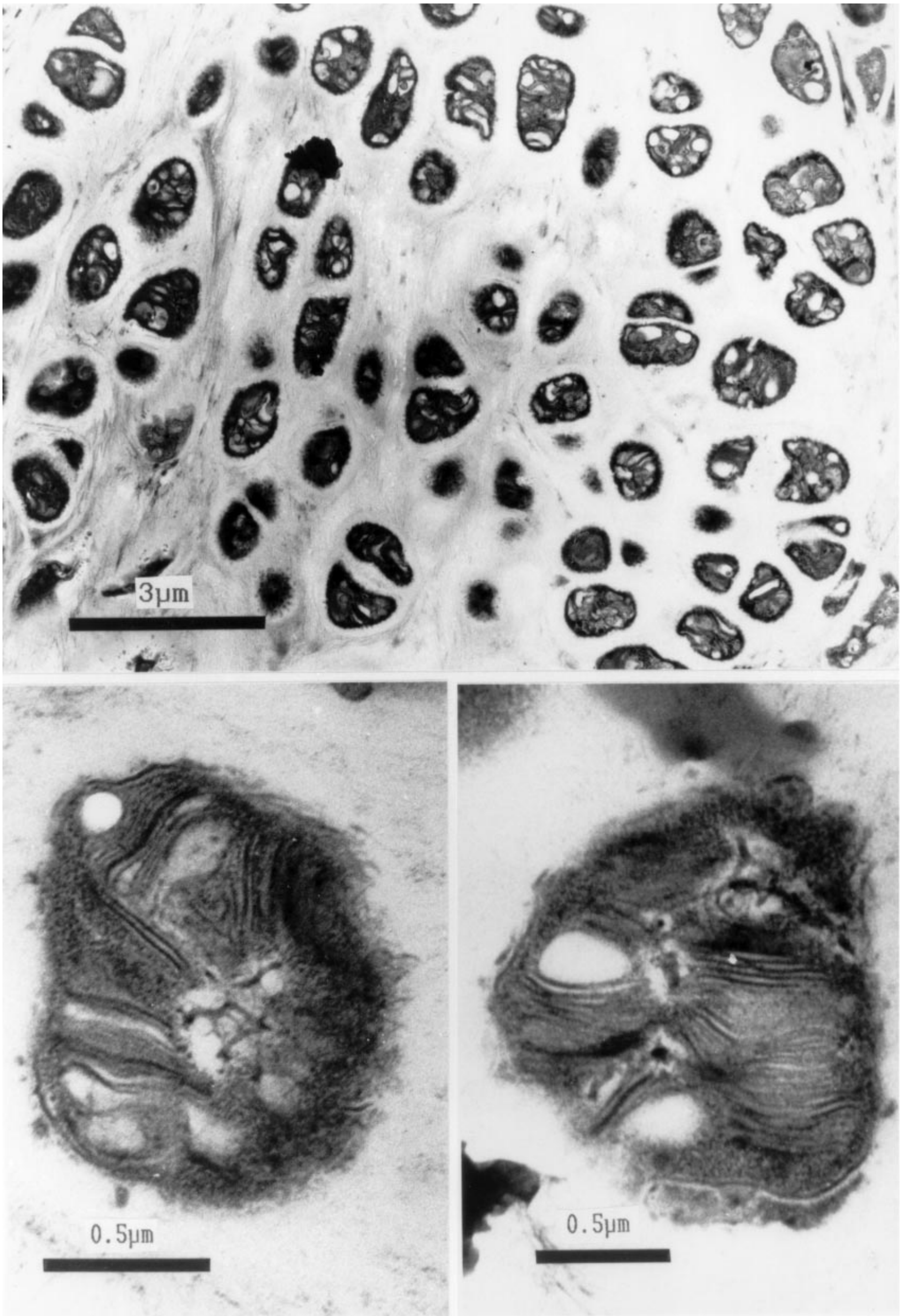
Significant attention has been given to the geographical distribution of vent fauna because of their importance to investigation of genetic exchange between Pacific and Atlantic fauna. A recent field investigation focused on the Central Indian Ridge (Figure 1) to examine (*a*) the hypothesis that the Indian Ocean Ridge system may serve as a conduit for exchange and (*b*) the possibility that, because of its remoteness, this area might support independently evolved, previously unknown species (Van Dover et al. 2001). At the Kaireri field and newly discovered Edmond vent field, Van Dover et al. (2001) found fauna similar to both the Pacific and Atlantic vents, with most organisms having evolutionary affinities with the Western Pacific vent faunas. The dominant shrimp at this site, however, most closely resembled those from the Mid-Atlantic Ridge.

The different vent environments offer many contrasting habitat conditions for macrofaunal communities. The large sulfide structures at Endeavour are ideally suited for studying species successions and overall productivity over time and space (Sarrazin et al. 1997) and the effect of tube-dwelling polychaetes on mineralization processes (Juniper et al. 1992, Juniper & Sarrazin 1995). There are also diffuse-flow vents on the Juan de Fuca Ridge, Galapagos, and the East Pacific Rise. These sites support dense populations of animals that depend on sulfide for their source of energy. The Endeavour, Axial, CoAxial, and Cleft vent sites along the Juan de Fuca Ridge show wide variations in chemical composition, including chloride, ammonia, and temperature (Butterfield et al. 1990, 1997; Lilley et al. 1993). Moreover, seismic events occur regularly and appear to affect the temperature and chemistry of vents located tens of kilometers away (Johnson et al. 2000). The high frequency of eruption events and ability to detect and follow these events have provided the unprecedented opportunity to study the colonization by animals and the early stages of community development and productivity at these newly formed vent sites (Tunnicliffe et al. 1997). Similarly, these eruption events provide one of the best opportunities to detect and characterize subseafloor microbial communities ejected from crust (Delaney et al. 1998, Holden et al. 1998, Summit & Baross 1998). So far the only evidence of eukaryotes from the subseafloor are microscopic observations of single-cell protists from diffuse-flow fluids at CoAxial following the 1992 eruption (Holden et al. 1998).

Extremely dense filamentous microbial communities have been observed on tubes of *Ridgeia piscesae* and on the surfaces of other animals and rocks from Juan de Fuca vents (Fisher 1996) and the East Pacific Rise (Baross & Deming 1985, Juniper & Tebo 1995). In addition, an active methanotrophic microbial community has been observed on most animal and rock surfaces tested from Endeavour (de Angelis et al. 1991) (Figure 24). Evidence from stable carbon and nitrogen analyses indicates that vent animals without endosymbionts are not nutritionally linked to animals with endosymbionts, and it is presumed that they feed on free-living microbes or microbial biofilms (Fisher et al. 1994, Van Dover & Fry 1994). Based on δ^{13}C data, the primary source of organic carbon for the shrimp at the Mid-Atlantic Ridge is bacteria attached to their gills (epibionts) and not free-living bacteria (Rieley et al. 1999).

The vent animals with endosymbiotic bacteria are thought to be the principal source of new carbon in vents. This is also reflected in the densities and large size of tubeworms and clams at vents. Carbon production by the tubeworm *Riftia pachyptila* on the East Pacific Rise can exceed 1g C m^{-2} day^{-1} (Shillito et al. 1999). This is consistent with growth rate measurements based on increase in tube length for *R. pachyltila*, which can exceed 85 cm $year^{-1}$ (Lutz et al. 1994). This is the fastest reported growth rate for a vestimentiferan tubeworm and an extraordinary growth rate for a deep-sea animal (Lutz et al. 1994). *Ridgeia piscesae* from the Juan de Fuca Ridge increase their tube length at a rate of 30–50 cm $year^{-1}$ (Tunnicliffe et al. 1990). In contrast, the vestimentiferan tubeworm *Lamellibrachia* sp. from hydrocarbon seeps requires 170 to 250 years to grow to a length of 2 m (Bergquist et al. 2000). The growth rates for the giant clam, *Calyptogena magnifica*, and the mussel, *Bathymodiolus thermophilis*, range from <1 to 6 cm $year^{-1}$ (Turner & Lutz 1984).

Hydrothermal vent environments can be viewed as deep-sea islands (Tunnicliffe et al. 1998). The extent of a vent field can vary but generally does not exceed 1 km. In contrast, oceanic ridge segments can approach 1000 km in length. These distances pose problems for the dispersal of animal larvae and the mechanisms for larval dispersal (Mullineaux & France 1995, Van Dover 2000, Van Dover et al. 2001). In a recent report, Marsh et al. (2001) looked at the dispersal potential of *Riftia pachyptila* larvae based on their life span under in situ conditions. It was estimated that the average lifespan for the larvae was 38 days, which translated into short dispersal distances of approximately 100 km. Deep-ocean currents are the most important factor in larval dispersal.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ORIGIN OF LIFE AT VENTS

It is tempting to conclude from molecular phylogenetic trees (Woese et al. 1990) that hyperthermophiles evolved more than four billion years ago in deep-sea hydrothermal vent environments and particularly in the subsurface associated with these hot springs (Corliss et al. 1981, Baross & Hoffman 1985, Baross 1998). During the early Archaean era, when life arose, subsurface environments would have offered these early anaerobic microbial communities refuge from the regular bombardment of large planetesimal bodies, estimated to be of a magnitude that would have regularly evaporated the oceans between 4.4 and 3.7 billion years (Ga) (Sleep et al. 1989, Oberbeck & Fogelman 1990). These impacts could also have resulted in oceanic and atmospheric temperatures locally and episodically approaching 100°C during the first several hundred million years after Earth's accretion (4.4 to approximately 3.7 Ga) (Schwartzman et al. 1993, Oberbeck & Mancinelli 1994).

Because we know that diverse microbial ecosystems existed at 3.5 Ga (Schopf & Klein 1992) and that organic chemical and stable carbon isotope data indicate CO_2-fixing microbial ecosystems at 3.8 Ga (Schidlowski 1988), it is highly probable that the origin of life and early evolution of prokaryotes occurred in or on a hotter Earth. During this period in Earth's history, tectonism and volcanism were significantly elevated over present levels, creating a reducing ocean chemically dominated by volcanically produced volatiles and metals (Bickle 1978, Kadko et al. 1995, Russell & Hall 1996, Russell et al. 1998). Life must have evolved in less than 500–600 million years after accretion of the Earth, a period when there were no continents and the chemical and physical properties of the oceans were most strongly influenced by tectonic activity. The alternative explanation is that life arose somewhere other than Earth: on another planet, in the upper atmosphere, or associated with comets or other planetesimal bodies. Regardless of how life became established on Earth, this pioneering organism(s) would likely have to live in hot anaerobic environments that have chemical properties similar to the hot fluids associated with present-day submarine hydrothermal systems. The recent detection of diverse microbial species in various subsurface environments (Cragg & Parks 1994, Fisk et al. 1998, Summit & Baross 1998, Torsvik et al. 1998) points to the physiological versatility of microbes while offering the exciting opportunity

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Figure 24 Transmission electron micrographs of an ultra-thin section from scraping of the outer surface of vent limpet *Lepetodrilus fucensis* shells. These shells showed very high rates of methane oxidation when incubated with methane and air. The upper panel shows extensive colonization of limpet shells by a single morphotype of microorganisms. The lower panels are high magnifications of individual cells showing the presence of stacked intracytoplasmic membranes typical of Type 1 methylotrophic bacteria (de Angelis et al. 1991).

of searching on Earth for microbes, including hyperthermophilic archaeal species that may possess genetic sequences and phenotypic characteristics unusually close to those of the ancestor of all extant organisms.

The discovery of hydrothermal vent environments has led to theories and models about chemical and biochemical evolution, and the origin and early evolution of life and microbial ecosystems at hydrothermal vent environments (Baross & Hoffman 1985, Corliss et al. 1981, Russell et al. 1998, Wächtershäuser 1998). Moreover, one of the predictions from global phylogenetic models based on 16S rRNA sequence analyses is that the most ancient of extant organisms were anaerobic hyperthermophiles that inhabited volcanic environments. A ramification of the bolide impact models for the early Archaean (3.5–4.3 billion years ago) is that the deep-sea benthic or subsurface environments were the most stable sites for life and early microbial ecosystems to evolve (Sleep et al. 1989, Baross 1998). This conclusion is strengthened by evidence from models indicating that ridge lengths were greater and hydrothermal systems were more prevalent during the Archaean than at present. The implications are that metabolic characteristics of microorganisms that can use the carbon and energy sources derived from the reaction of hot water with rock will be analogous to Archaean vent microorganisms and by inference would be analogous to putative microorganisms on other solar bodies where there is evidence for hydrothermal activity either in the past or at present.

NEW INSIGHTS AND FUTURE RESEARCH DIRECTIONS

The discovery of submarine hydrothermal vents in the late 1970s and the recent recognition of a potentially vast, as yet unexplored hot microbial biosphere associated with active volcanism along the global mid-ocean ridge spreading center system have fundamentally shifted concepts of how planets and life may coevolve. A number of powerful new concepts, and derivative questions, are in much sharper focus than they were only a decade ago. The universal nature of the basic physical-chemical processes involved in the early evolution of rocky, water-bearing planets are compatible with support of, and perhaps conducive to, generation of life forms supported by processes that do not require photosynthesis. For example, many young planets of carbonaceous chondrite composition, with sufficient mass and internal heat to separate a metallic core, would simultaneously experience planet-wide decompressional melting in the presence of primordial volatiles resulting in primitive basaltic volcanism releasing water, carbon, and sulfur compounds to the near surface environment. This out-gassing and subsequent condensation will result in formation of a primordial ocean. Catalytic interactions between an ocean-saturated porous volcanic crust, and volcanically driven fluid circulation may be an inevitable consequence of this overall process. Indeed, depending upon how common these processes are and how long they last on a given body, production of self-replicating carbon compounds (life) may be a cosmic imperative rather than a rare event.

Possibly as important, the deep-sea vents and the porous underlying volcanic crust are potential refuges for primitive microbial life forms threatened by the vigorous postaccretion bombardment of Earth in the first 500 to 700 million years of planetary history. Furthermore, despite the seemingly unstable nature of episodic volcanic activity, conditions existing in a volcanically active submarine crust should represent an enduring spectrum of environments, many of which would be conducive to the support of a variety of chemosynthetic metabolic activity. Some form of submarine volcanism has almost certainly been operative on Earth from the early stages of its planetary history. The conditions associated with modern submarine volcanic systems may therefore be viewed as covering a spectrum from rock-dominated to fluid-dominated systems associated with a broad range of temperatures, pressures, and nutrient availability. Indeed, certain portions of the modern subsurface microbial biosphere are likely to be environmentally similar (or identical) to those in the earliest Archaean Period when life existed on Earth. If so, developing new approaches to studying such ocean-dominated crustal systems will provide essential new information about geobiocomplexity on our own planet, while providing critically needed, novel insights into how we might explore for life on other planets.

During the past 20 years, it has become clear that answers to a host of basic scientific questions about underwater, volcanic habitats on Earth will require bold new interdisciplinary approaches using remote, in situ, interactive research facilities. This is particularly true regarding the intimate interactions among microbiological communities and the ever-changing chemical and physical processes operating at the interfaces between the deep ocean and its underlying volcanically active crust. Although some of these interactions can be identified and studied, in general, we are ignorant of the complex interplay among microbes and vent environments. This is particularly true for the subseafloor biosphere where many recently posed questions are unanswered and unapproachable by existing, single discipline techniques of inquiry.

Far-reaching questions include: What are the dimensions of the subsurface biosphere? How far does the biosphere extend off the ridge axis? Is the biosphere composed of individual biotopes, or are they linked by geophysical factors such as seismically induced cracking or diking events? What kinds of organisms inhabit the subseafloor, and how do they affect the chemical fluxes and the alteration mineralogy? What is the carbon productivity, the total biomass, and the cycling time of the subsurface biosphere? How important is detrital carbon as fuel for subsurface microbes? The keys to approaching these questions will require direct observations and sampling of the rocky subsurface. We must also understand fluid flow in the crust and make direct measurements of key physical, chemical, and biological parameters simultaneously over vast horizontal and vertical dimensions for extended periods of time.

The future of research at vent environments will take advantage of new methods and technology from many different disciplines. For example, the combination of newly developed molecular methods to better understand the diversity of microbial communities that are recalcitrant to culturing, the discovery that microbes occupy habitats thought to be free of life, and the isolation of microbes with novel metabolisms have redefined and greatly broadened the scope of microbiology. Moreover, the ability to rapidly sequence the complete genome of organisms will inevitably lead to a better appreciation of the metabolic diversity of life and also help to identify at the genetic level how microbes have indeed coevolved with the environment. Coupled with these discoveries, new instruments for sampling environments such as deep crustal rock, for making in situ physical and chemical measurements, and the ability to make models with large and diverse databases will certainly lead for the first time to an understanding of ecosystems at broad spatial and temporal scales that span the age of Earth.

Innovative changes are currently taking place in the ocean sciences in terms of how we approach the study of the entire oceanic system. In contrast to the traditional expeditionary approaches utilized over the past 150 years in the ocean sciences, we are entering a new era of scientific-technical investigations of the oceans. Many of the questions posed by the expeditionary science cannot be answered solely with that approach. We must learn to operate routinely within all of ocean space using break-through technologies that include high-speed communication at broadband widths, extensive power on or near the seafloor, sophisticated robotic systems, and a wide variety of novel, durable sensor packages that will allow real-time continuous remote interactive science to be conducted below sea level anywhere on Earth. Such new approaches involving a real-time presence via fiber optic systems such as NEPTUNE (Delaney et al. 2000) will dramatically expand the kinds of questions that we can investigate. Episodic events like volcanic eruptions and earthquake activity will be explored immediately using sophisticated robotic systems bearing novel sensor suites capable of identifying genomic information in situ.

The potential significance of volcanically supported microbial biomes to issues related to the origin of life and the possibility of life on other planets is a major driving force for continuing the exploration of these dynamic systems here on Earth. The greater intergration of microbiology with Earth sciences at hydrothermal vents is already having profound implications, not only for understanding early life on Earth and the coevolution of microbes with their environment, but also offers an approach and an Earth-based laboratory that will aid in the hunt for extant or extinct life on other solar bodies.

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LITERATURE CITED

Abrajano TA, Sturchio NC, Bohlke JK, Lyon GL, Poreda RJ, et al. 1988. Methane-hydrogen gas seeps, Zambales ophiolite, Philippines: deep or shallow origin? *Chem. Geol.* 71:211–22

Adams MWW. 1999. The biochemical diversity of life near and above 100°C in marine environments. *J. Appl. Microbiol.* 85(Suppl. S): S108–17

Adams MWW. 1993. Enzymes and proteins from organisms that grow near and above 100°C. *Annu. Rev. Microbiol.* 47:627–58

Adams MWW, Kelly RM. 1998. Hyperthermophilic enzymes: finding them and using them. *Trends Biotechnol.* 16:329–32

Adams MWW, Kletzen A. 1996. Oxidoreductase-type enzymes and redox proteins involved in fermentative metabolisms of hyperthermophilic archaea. *Adv. Protein Chem.* 48: 101–80

Aharonov E, Whitehead JA, Kellemen PB, Spiegelman M. 1995. Channelling instability of upwelling melt in the mantle. *J. Geophys. Res.* 100:20433–50

Alayse-Danet AM, Debruyères D, Gaill F. 1987. The possible nutritional or detoxification role of the epibiotic bacteria of alvinellid polychaetes: review of current data. *Symbiosis* 4:51–62

Allen DA, Berndt ME, Seyfried WE Jr, Horita J. 1998. Inorganic reduction of CO_2 to HCOOH, CH_4, and other reduced carbon compounds with application to subseafloor hydrothermal systems. *Eos Trans. Am. Geophys. Union* 79:58–59

Alt JC. 1995. Subseafloor processes in mid-ocean ridge hydrothermal systems. See Humphris et al. 1995, pp. 178–93

Alt JC, Anderson TF. 1991. Mineralogy and isotopic composition of sulfur in layer 3 gabbros from the Indian Ocean, Hole 735B. *Proc. Ocean Drill. Program Sci. Results* 118:113–25

Alt JC, Honnorez J, Laverene C, Emmermann R. 1986. Alteration of a 1 km section through the upper oceanic crust, DSDP Hole 504B: the mineralogy, chemistry, and evolution of seawater-basalt interactions: *J. Geophys. Res.* 91:10309–55

Alt JC, Laverene C, Vanko DA, Tartarotti P, Teagle DAH, et al. 1996. Hydrothermal alteration of a section of upper oceanic crust in the eastern equatorial Pacific: a synthesis of results from Site 504 (DSDP Legs 69, 70, and 83 and ODP Legs 111, 137, 140, and 148). *Proc. Ocean Drill. Program Sci. Results* 148:417–34

Alt JC, Shanks WC. 1998. Sulfur in serpentinized peridotites. Serpentinization processes and microbial sulfate reduction. *J. Geophys. Res.* 103:9917–29

Amend JP, Shock EL. 1998. Energetics of amino acid synthesis in hydrothermal ecosystems. *Science* 281:1659–62

Alt JC, Teagle DAH. 2000. Hydrothermal alteration and fluid fluxes in ophiolites and oceanic crust. In *Ophiolites and Oceanic Crust: New Insights from Field Studies and the Ocean Drilling Program*, ed. Y Dilek, E Moores, D Elthos, A Nicoals, pp. 273–82. Geol. Soc. Am. Spec. Pap. 349. Boulder, CO: Geol. Soc. Am. 552 pp.

Archer SD, Wilcock WSD, Purdy GM. 1996. Microearthquake activity associated with hydrothermal circulation on the Endeavour Segment of the Juan de Fuca Ridge. *Eos Trans. Am. Geophys. Union* 77:727

Auzende J-M, Ballu V, Batiza R, Bideau D, Charlou J-L, et al. 1996. Recent tectonic, magmatic and hydrothermal activity on the East Pacific Rise between 17°S and 19°S: submersible observations. *J. Geophys. Res.* 101:17995–18000

Baker ET. 1998. Patterns of event and chronic hydrothermal venting following a magmatic intrusion: new perspectives from the 1996 Gorda Ridge eruption. *Deep-Sea Res. II* 45: 2599–618

Baker ET, German CR, Elderfield H. 1995a. Hydrothermal plumes over spreading-center axes: global distributions and geological inferences. See Humphris et al. 1995, pp. 47–71

Baker ET, Lavelle JW, Feely RA, Massoth GJ, Walker SL, et al. 1989. Episodic venting of hydrothermal fluids from the Juan de Fuca Ridge. *J. Geophys. Res.* 94:9237–50

Baker ET, Lupton JE. 1990. Changes in submarine hydrothermal ^{3}He/heat ratios as an indicator of magmatic/tectonic activity. *Nature* 346:556–58

Baker ET, Massoth GJ, Feely RA. 1987. Cataclysmic hydrothermal venting on the Juan de Fuca Ridge. *Nature* 329:149–51

Baker ET, Massoth GJ, Feeley RA, Embley RW, Thomson RE. 1995b. Hydrothermal event plumes from the Co-Axial seafloor eruption site, Juan de Fuca Ridge. *Geophys. Res. Lett.* 22:147–50

Ballard RD, van Andel T. 1977. Project FAMOUS: operational techniques and American submersible observations. *Geol. Soc. Am. Bull.* 88:495–506

Ballhaus C, Frost BR. 1994. The generation of oxidized CO_2-bearing basaltic melts from reduced CH_4-bearing upper mantle sources. *Geochim. Cosmochim. Acta* 58:4931–40

Banfield JF, Hamers RJ. 1997. Processes at minerals and surfaces with relevance to microorganisms and prebiotic synthesis. In *Geomicrobiology: Interactions Between Microbes and Minerals. Reviews in Mineralogy*, ed. JF Banfield, KH Nealson, PH Ribbe, 35:81–122. Washington, DC: Mineral. Soc. Am. 448 pp.

Barnes SP, Bradbrook SD, Cragg BA, Marchesi JR, Weightman JC, et al. 1998. Isolation of sulfate-reducing bacteria from deep-sediment layers of the Pacific Ocean. *Geomicrobiol. J.* 15:67–83

Barns SM, Fundyga RE, Jeffries MW, Pace NR. 1994. Remarkable archaeal diversity detected in Yellowstone National Park hot spring environment. *Proc. Natl. Acad. Sci. USA* 91:1609–13

Baross JA. 1998. Do the geological and geochemical records of the early Earth support the prediction from global phylogenetic models of a thermophilic cenancestor? See Wiegel & Adams 1998, pp. 1–18

Baross JA, Deming JW. 1985. The role of bacteria in the ecology of black-smoker environments. *Biol. Soc. Wash. Bull.* 6:355–71

Baross JA, Deming JW. 1995. Growth at high temperatures: isolation and taxonomy, physiology, and ecology. See Karl 1995, pp. 169–217

Baross JA, Hoffman SE. 1985. Submarine hydrothermal vents and associated gradient environments as sites for the origin and evolution of life. *Orig. Life* 15:327–45

Baross JA, Holden JF. 1996. Overview of hyperthermophiles and their heat-shock proteins. *Adv. Protein Chem.* 48:1–34

Baross JA, Summit M, Holden JF. 1997. Is there a microbial biosphere in the subsurface? *JOI/USSAC Newsl.* 10:8–11

Barriga FJAS, Fouquet Y, Biscoito MJ, Chalou J-C, Costa RLP, et al. 1998. Discovery of the Saldanha hydrothermal field on the FAMOUS segment of the MAR (36°30N). *Eos Trans. Am. Geophys. Union* 79:67

Bell DR, Rossman GR. 1992. Water in Earth's mantle: the role of nominally anhydrous minerals. *Science* 255:1391–97

Bergquist DC, Williams FM, Fisher CR. 2000. Longevity record for deep-sea invertebrate. *Nature* 403:499–500

Berndt ME, Allen DE, Seyfried WE Jr. 1996. Reduction of CO_2 during serpentinization of olivine at 300°C and 500 bar. *Geology* 24: 351–54

Berndt ME, Seyfried WE Jr. 1997. Calibration of Br/Cl fractionation during subcritical phase separation of seawater. Possible halite at 9 to 10°N East Pacific Rise. *Geochim. Cosmochim. Acta* 61:2849–54

Berndt ME, Seyfried WE, Janecky DR. 1988. Plagioclase and epidote buffering of cation ratios in mid-ocean ridge hydrothermal fluids: experimental results in and near the supercritical region. *Geochim. Cosmochim. Acta* 53:2283–300

Bickle MJ. 1978. Heat loss from the Earth: a constraint on Archaean tectonics from the relation between geothermal gradients and the rate of plate production. *Earth Planet. Sci. Lett.* 40:301–15

Bischoff JL, Rosenbauer RJ. 1988. Liquid-vapor relations in the critical region of the system NaCl-H_2O from 380°C to 415°C: a refined determination of the critical point and two-phase boundary of seawater. *Geochim. Cosmochim. Acta* 52:2121–26

Bischoff JL, Rosenbauer RJ. 1989. Salinity variation in submarine hydrothermal systems by layered double-diffusive convection. *J. Geol.* 97:613–23

Björnsson A, Johnsen G, Sigurdsson S, Thorbergsson G, Tryggvason E. 1979. Rifting of the plate boundary in North Iceland, 1975–1978. *J. Geophys. Res.* 84:3029–38

Blackman DK, Cann JR, Janssen B, Smith DK. 1998. Origin of extensional core complexes: evidence from the Mid-Atlantic Ridge at Atlantis Fracture Zone. *J. Geophys. Res.* 103: 21315–34

Blöchl E, Rachel R, Burggraf R, Hafenbrandl S, Jannasch HW, Stetter KO. 1997. *Pyrolobus fumarii*, gen. and sp. nov., represents a novel group of archaea, extending the upper temperature for life to 113°C. *Extremophiles* 1: 14–21

Bodnar RJ, Beane RE. 1980. Temporal and spatial variations in hydrothermal fluid characteristics during vein filling in preore cover overlying deeply-buried porphyry copper-type mineralization at Red Mountain, Arizona. *Econ. Geol.* 75:876–93

Bohenenstiehl DR, Kleinrock MC. 2000. Fissuring near the TAG active hydrothermal mound, 26°N on the Mid-Atlantic Ridge. *J. Volcano. Geotherm. Res.* 98:33–48

Bougault H, Charlou J-L, Fouquet F, Needham HD, Vaslet N, et al. 1993. Fast- and slow-spreading ridges: structure and hydrothermal activity, ultramafic topographic highs, and CH_4 output. *J. Geophys. Res.* 98:9643–51

Brandes JA, Boctor NZ, Cody GD, Cooper BA, Hazen RM, et al. 1998. Abiotic nitrogen reduction on the early Earth. *Nature* 395:365–67

Bryan WB, Humphris SE, Thompson G, Casey JF. 1994. Comparative volcanology of small axial eruptive centers in the MARK area. *J. Geophys. Res.* 99:2973–84

Bryan WB, Moore JG. 1976. Compositional variations in young basalts in the Mid-Atlantic Ridge rift valley near 36°49′N. *Geol. Soc. Am. Bull.* 88:556–70

Buatier MD, Monnin C, Früh-Green GL, Karpoff AM. 2001. Fluid-sediment interactions related to hydrothermal circulation in the eastern flank of the Juan de Fuca Ridge. *Chem. Geol.* 175:343–60

Buchardt B, Seaman PG, Duwel L, Thorbjorn L, Vous M, et al. 1997. Submarine columns of ikaite tufa. *Nature* 390:129–30

Buck WR, Delaney PT, Karson JA, Lagabrielle Y, eds. 1998. *Faulting and Magmatism at Mid-Ocean Ridges, Geophysical Monogr. 106*. Washington, DC: Am. Geophys. Union. 348 pp.

Buck WR, Su W. 1989. Focused mantle upwelling below mid-ocean ridges due to feedback between viscosity and melting. *Geophys. Res. Lett.* 16:641–44

Burggraf S, Jannasch HW, Nicolaus B, Stetter KO. 1990. *Archaeoglobus profundus* sp. nov., represents a new species within the sulfate-reducing archaebacteria. *Syst. Appl. Microbiol.* 13:24–28

Burnham CW. 1979. Magma and hydrothermal fluids. In *Geochemistry of Hydrothermal Ore Deposits*, ed. HL Barnes, pp. 71–133. New York: Wiley

Butterfield DA, Jonasson IR, Massoth GJ, Feely RA, Roe KK, et al. 1997. Seafloor eruptions and evolution of hydrothermal fluid chemistry. *Philos. Trans. R. Soc. London Ser. A* 355:369–86

Butterfield DA, Massoth GJ. 1994. Geochemistry of the North Cleft Segment vent fluids—temporal changes in chlorinity and their possible relation to recent volcanism. *J. Geophys. Res.* 99:4951–68

Butterfield DA, Massoth GJ, McDuff RE, Lupton JE, Lilley MD. 1990. Geochemistry of hydrothermal fluids from Axial Seamount hydrothermal emissions study vent field, Juan de Fuca Ridge: subseafloor boiling and subsequent fluid-rock alteration. *J. Geophys. Res.* 95:12895–921

Butterfield DA, McDuff RE, Mottl M, Lilley MD, Massoth GJ, et al. 1994. Gradients in the compositions of hydrothermal fluids from the Endeavour Ridge vent field. *J. Geophys. Res.* 99:9561–83

Butterfield DA, Nelson BK, Wheat CG, Mottl MJ, Roe KK. 2001. Evidence for basaltic Sr in midocean ridge-flank hydrothermal systems and implications for the global oceanic Sr isotope balance. *Geochim. Cosmochim. Acta* 65:4141–53

Butterfield DA, Roe KK, Massoth GJ, Embley RW, McDuff RE, et al. 1995. Spatial and temporal variability in hydrothermal vent fluid composition along the Juan de Fuca Ridge. *Eos Trans. Am. Geophys. Union* 76:420

Calvert AJ. 1995. Seismic evidence for a magma chamber beneath the slow-spreading Mid-Atlantic Ridge. *Nature* 377:410–14

Caroll MR, Holloway JR, eds. 1994. *Volatiles and Magmas. Rev. Mineral.* 30:479–517. Washington, DC: Mineral. Soc. Am. 517 pp.

Cann JR, Strens MR. 1989. Modeling peridodic megaplume emission by black smoker systems. *J. Geophys. Res.* 94:12227–37

Cann JR, Blackman DK, Smith DK, McAllister E, Janssen B, et al. 1997. Corrugated slip surfaces formed at ridge-transform intersections on the Mid-Atlantic Ridge. *Nature* 385:329–32

Cannat M, Ceuleneer G, Fletcher J. 1997. Localization of ductile strain and the magmatic evolution of gabbroic rocks drilled at the Mid-Atlantic Ridge (23°N). *Proc. Ocean Drill Program Sci. Results* 153:77–98

Cannat M, Chatin F, Whitechurch H, Ceuleneer G. 1997. Gabbroic rocks trapped in the upper mantle at the Mid-Atlantic Ridge. *Proc. Ocean Drill. Program Sci. Results* 153:242–64

Carroll MR, Holloway JR. 1994. *Volatiles in Magmas. Reviews in Mineralogy*, ed. MR Carroll, JR Holloway, PH Ribbe, Vol. 30. Washington, DC: Mineral. Soc. Am. 517 pp.

Cary SC, Cottrell MT, Stein JL, Camacho F, Desbruyeres D. 1997. Molecular identification and localization of filamentous symbiotic bacteria associated with the hydrothermal vent annelid *Alvinella pompejana. Appl. Environ. Microbiol.* 63:1124–130

Cary SC, Fisher CR, Felbeck H. 1998a. Mussel growth supported by methane as sole carbon and energy source. *Science* 240:78–80

Cary SC, Shank T, Stein J. 1998b. Worms bask in extreme temperatures. *Nature* 391:545–46

Cary SC, Stein JL. 1998. Spanning the thermal limits: an extreme eurythermal symbiosis. *Cah. Biol. Mar.* 39:275–78

Casey JF. 1997. Comparison of major- and trace-element geochemistry of abyssal peridotites and mafic plutonic rocks with basalts from the MARK region of the Mid-Atlantic Ridge. *Proc. Ocean Drill. Program Sci. Results* 153:181–242

Cathles LM. 1993. A capless 350°C flow zone model to explain magaplumes, salinity variations, and high-temperature veins in ridge axis hydrothermal systems. *Econ. Geol.* 88: 1977–88

Cavanaugh CM. 1993. Symbiotic chemoautotrophic bacteria in marine invertebrates from sulphide-rich habitats. *Nature* 302:58–61

Cavanaugh CM, Levering PR, Maki JS, Lidstrom ME, Mitchell R. 1987. Symbiosis of methylotrophic bacteria and deep-sea mussels. *Nature* 325:346–48

Chadwick WW Jr, Embley RW. 1994. Lava flows from a mid-1980s submarine eruption on the Cleft Segment, Juan de Fuca Ridge. *J. Geophys. Res.* 99:4761–76

Chadwick WW Jr, Embley RW. 1998. Graben formation associated with recent dike intrusions and volcanic eruptions on mid-ocean ridges. *J. Geophys. Res.* 103:9807–825

Chadwick WW Jr, Embley RW, Fox CG. 1991. Evidence for volcanic eruption on the southern Juan de Fuca Ridge between 1981 and 1987. *Nature* 350:416–18

Chadwick WW Jr, Embley RW, Fox CG. 1995. SeaBeam depth changes associated with recent lava flows, CoAxial segment, Juan de Fuca Ridge: evidence for multiple eruptions between 1981–1993. *Geophys. Res. Lett.* 22: 167–70

Chadwick WW Jr, Embley RW, Shank TM. 1998. The 1996 Gorda Ridge eruption: geologic mapping, sidescan sonar, and SeaBeam comparison results. *Deep-Sea Res. II* 45: 2547–69

Charlou JL, Bougault H, Appriou P, Nelsen T, Rona P. 1992. Different TDM/CH_4 hydrothermal plume signatures: TAG site at 26°N and serpentinized ultrabasic diapir at 15°05 on the Mid-Atlantic Ridge. *Geochim. Cosmochim. Acta* 55:3209–23

Charlou JL, Donval J-P. 1993. Hydrothermal methane venting between 12°N and 26°N along the Mid-Atlantic Ridge. *J. Geophys. Res.* 98:9625–42

Charlou JL, Fouquet YA, Bougault H, Donval J-P, Etoubleau J, et al. 1998. Intense CH_4 degassing generated by serpentinization of ultramafic rocks at the intersection of the 15°20′N fracture zone and the Mid-Atlantic Ridge. *Geochim. Cosmochim. Acta* 62:2323–33

Cherkaoui ASM, Wilcock WSD, Baker ET. 1997. Thermal fluxes associated with the 1993 diking event on the CoAxial segment, Juan de Fuca Ridge. *J. Geophys. Res.* 102: 24887–902

Childress JJ, Fisher CR. 1992. The biology of hydrothermal vent animals: physiology, biochemistry and autotrophic symbiosis. *Oceanogr. Mar. Biol. Annu. Rev.* 30:337–41

Christenson GL, Purdy GM, Fryer GJ. 1994. Seismic constraints on shallow crustal emplacement processes at the fast spreading East Pacific Rise. *J. Geophys. Res.* 99: 17957–73

Christie DM, Carmichael ISE, Langmuir CH. 1986. Oxidation states of mid-ocean ridge basalt glasses. *Earth Planet. Sci. Lett.* 79: 397–411

Cody GD, Boctor NZ, Filley TR, Hazen RM, Scott JH, et al. 2000. Primordial carbonylated iron-sulfur compounds and the synthesis of pyruvate. *Science* 289:1337–39

Connaris HD, Cowan A, Sharp RJ. 1991. Heterogenity of proteinases from the hyperthermophilic archaeobacterium *Pyrococcus furiosus. J. Gen. Microbiol.* 137:1193–99

Corliss JB, Baross JA, Hoffman SE. 1981. An hypothesis concerning the relationship between submarine hot springs and the origin of life on Earth. *Oceanol. Acta* 4:59–69

Corliss JB, Dymond J, Gordon LI, Edmond JM, von Herzen RP, et al. 1979. Submarine thermal springs on the Galapagos Rift: *Science* 203:1073–83

Cornec L, Robineau J, Rolland JL, Dietrich J, Barbier G. 1998. Thermostable esterases screened on hyperthermophilic archael and bacterial strains isolated from deep-sea hydrothermal vents: characterization of esterase activity of a hyperthermophilic archaeum, *Pyrococcus abyssi. J. Mar. Biotechnol.* 6:104–10

Cowen JP, Bertram MA, Baker ET, Feely RA, Massoth GJ, Summit M. 1998. Geomicrobial transformation of manganese in Gorda Ridge event plumes. *Deep-Sea Res. II* 45:2713–37

Cowen JP, Massoth GJ, Baker ET. 1986. Bacterial scavenging of Mn and Fe in a mid- to far-field hydrothermal particle plume. *Nature* 322:169–71

Cragg BA, Harvey SM, Fry JC, Herbert RA, Parkes RJ. 1992. Bacterial biomass and activity in the deep sediment layers of the Japan Sea, Hole 798B. *Proc. Ocean Drill. Program Sci. Results* 127:761–76

Cragg BA, Parkes RJ. 1994. Bacterial profiles in hydrothermally active deep sediment layers from Middle Valley (NE Pacific), Sites 857 and 858. *Proc. Ocean Drill. Program Sci. Results* 112:509–16

Cragg BA, Parkes RJ, Fry JC, Jeerbert RA, Wimpenny JWT, Getliff JM. 1990. Bacterial biomass and activity profiles within deep sediment layers. *Proc. Ocean Drill. Program Sci. Results* 112:607–19

Cragg BA, Summit M, Parkes RJ. 2000. Bacterial profiles in a sulfide mound (Site 1035) and an area of active fluid venting (Site 1036) in hot hydrothermal sediments from Middle valley (Northeast Pacific). *Proc. Ocean Drill. Program Sci. Results.* 169:1–18. http://

www-odp.tamu.edu/publications/169_SR/VOLUME/CHAPTERS/SR169_02.pdf

Curewitz D, Karson JA. 1998. Geological consequences of dike intrusion at mid-ocean ridge spreading centers. See Buck et al. 1998, pp. 117–36

Davis EE, Chapman DS, Forster CB. 1996. Observations concerning the vigor of hydrothermal circulation in young volcanic crust. *J. Geophys. Res.* 101:2927–42

Davis EE, Chapman DS, Mottl MJ, Bentkowski WJ, Dadey K, et al. 1992. FlankFlux: an experiment to study the nature of hydrothermal circulation in young oceanic crust. *Can. J. Earth. Sci.* 29:925–52

de Angelis MA, Lilley MD, Olson EJ, Baross JA. 1993. Methane oxidation in deep-sea hydrothermal plumes of the Endeavour Segment of the Juan de Fuca Ridge. *Deep-Sea Res.* 40:1169–86

de Angelis MA, Reysenbach A-L, Baross JA. 1991. Surfaces of hydrothermal vent invertebrates: sites of elevated microbial methane oxidation activity. *Limnol. Oceanogr.* 36: 570–77

Delaney JR, Heath GR, Howe B, Chave AD, Kirkham H. 2000. NEPTUNE: Real-time ocean and Earth sciences at the scale of a tectonic plate. *Oceanography* 13:71–79

Delaney JR, Kelley DS, Lilley MD, Butterfield DA, Baross JA, et al. 1998. The quantum event of oceanic crustal accretion: impacts of diking at mid-ocean ridges. *Science* 281:222–30

Delaney JR, Kelley DS, Lilley MD, Butterfield DA, McDuff RE, et al. 1997. The Endeavour Hydrothermal System I: cellular circulation above an active cracking front yields large sulfide structures, "fresh" vent water, and hyperthermophilic archae. *RIDGE Events* 8: 11–19

Delaney JR, Kelley DS, Mathez EA, Yoerger DR, Baross JA, et al. 2001. Edifice Rex Sulfide Recovery Project: analysis of a sulfide-microbial habitat from a submarine hydrothermal system. *Eos Trans. Am. Geophys. Union* 82:67–73

Delaney JR, Lilley MD, McDuff RE, Baross JA. 1988. Standing pools of 350°C fluid and large seafloor sulfide structures. *Eos Trans. Am. Geophys. Union* 69:1497–98

Delaney JR, Lilley MD, McDuff RE, Kelley DS, Wilcock WS, et al. 1996. Cellular hydrothermal circulation in a submarine system. *Eos Trans. Am. Geophys. Union* 77:756

Delaney JR, McDuff RE, Lupton JE. 1984. Hydrothermal fluid temperatures of 400°C on the Endeavour Segment, northern Juan de Fuca. *Eos Trans. Am. Geophys. Union* 65:973

Delaney JR, Mogk DW, Mottl MJ. 1987. Quartz-cemented breccias from the Mid-Atlantic Ridge: samples of a high-salinity hydrothermal upflow zone. *J. Geophys. Res.* 92:9175–92

Delaney JR, Muenow DW, Garcia MO. 1978. Abundance and distribution of water, carbon and sulfur in the glassy rims of submarine pillow basalts. *Geochim. Cosmochim. Acta* 42:581–94

Delaney JR, Robigou V, McDuff RE, Tivey MK. 1992. Geology of a vigorous hydrothermal system on the Endeavour Segment, Juan de Fuca Ridge. *J. Geophys. Res.* 97:19663–82

DeLong E. 1998. Microbiology—archaeal means and extremes. *Science* 280:542–43

Deming JW, Baross JA. 1993. Deep-sea smokers: windows to a subsurface biosphere. *Geochim. Cosmochim. Acta* 57:3219–30

Desbruyeres D, Almeida A, Biscoito M, Comtet T, Khripounoff A, et al. 2000. A review of the distribution of hydrothermal vent communities along the northern Mid-Atlantic Ridge: dispersal vs. environmental controls. *Hydrobiologia* 444:201–16

Desbruyeres D, Biscoito M, Caprais JC, Colaco A, Comtet T, et al. 2001. Variations in deep-sea hydrothermal vent communities on the Mid-Atlantic Ridge near the Azores plateau. *Deep-Sea Res. I* 48:1325–46

de Wit MJ, Hart RA, Hart RJ. 1987. The Jamestown ophiolite complex, Barberton mountain belt: a section through 3.5 Ga oceanic crust. *J. Afr. Earth Sci.* 6:681–730

Dick HJB, Meyer PS, Bloomer S, Kirby S, Stakes D, et al. 1991. Lithostratigraphic evolution of an in-situ section of oceanic crust. *Proc. Ocean Drill. Program Sci. Results* 118:439–538

Dick HJB, Natland JH. 1996. Late-stage melt evolution and transport in the shallow mantle beneath the East Pacific Rise. *Proc. Ocean Drill. Program Sci. Results* 147:103–34

Dick HJB, Natland JH, Alt JC, Bach W, Bideau D, et al. 2000. A long in-situ section of the lower ocean crust: results of ODP Leg 176 drilling at the Southwest Indian Ridge. *Earth Planet. Sci. Lett.* 179:31–51

Distel DL, Lee HK, Cavanaugh K-W. 1995. Intracellular coexistence of methano- and thioautotrophic bacteria in a hydrothermal vent mussel. *Proc. Natl. Acad. Sci. USA* 92: 9598–602

Dixon JE, Stolper EM. 1995. An experimental study of water and carbon dioxide solubilities in mid-ocean ridge basaltic liquids. Part II. Applications to degassing. *J. Petrol.* 36:1633–46

Dixon JE, Stolper E, Delaney JR. 1988. Infrared spectroscopic measurements of CO_2 and H_2O in Juan de Fuca Ridge basaltic glasses. *Earth Planet. Sci. Lett.* 90:87–104

Dixon JE, Stolper EM, Holloway JR. 1995. An experimental study of water and carbon dioxide solubilities in mid-ocean ridge basaltic liquids. Part I. Calibration and solubility models. *J. Petrol.* 36:1607–31

Donval JP, Charlou JL, Douville E, Knoery J, Fouguet Y. 1997. High H_2 and CH_4 content in hydrothermal fluids from Rainbow site newly sampled at $36^\circ 14'$N on the AMAR segment, Mid-Atlantic Ridge (diving FLORES cruise, July 1997). Comparisons with other MAR dives. *Eos Trans. Am. Geophys. Union* 78:832

Dunn RA, Toomey DR. 2001. Crack-induced seismic anisotropy in the oceanic crust across the East Pacific Rise ($9^\circ 30'$N). *Earth Planet. Sci. Lett.* 189:9–17

Dunn RA, Toomey DR, Detrick RS, Wilcock WSD. 2001. Continuous mantle melt supply beneath an overlapping spreading center on the East Pacific Rise. *Science* 291:1955–58

Dziak RP, Fox CG, Schreiner AE. 1995. The June-July 1993 seismo-acoustic event at CoAxial segment, Juan de Fuca Ridge: evidence for a lateral dike injection. *Geophys. Res. Lett.* 22:135–38

Eberhard C, Wirsen CO, Jannasch HW. 1995. Oxidation of polymetalic sulfides by chemolithoautotrophic bacteria from deep-sea hydrothermal vents. *Geomicrobiol. J.* 13:145–64

Edwards KJ, Goebel B, Rodgers TM, Schrenk MO, Cardona MM, et al. 1999. Environmental conditions, microbial populations, and the role of attachment in oxidative dissolution of pyrite at Iron Mt. *Geomicrobiol. J.* 16:155–79

Edwards KJ, Schrenk MO, Hamers RJ, Banfield JF. 1998. Microbial oxidation of pyrite: experiments using microorganisms from an extreme acidic environment. *Am. Mineral.* 83:1444–53

Einarsson P, Brandsdottir B. 1980. Seismological evidence for lateral magma intrusion during the 1978 delfation of the Krafla Volcano in NE Iceland. *J. Geophys.* 47:160–65

Elderfield H, Schultz A. 1996. Mid-ocean ridge hydrothermal fluxes and the chemical composition of the ocean. *Annu. Rev. Earth Planet. Sci.* 24:191–224

Elsgaard MF, Jorgensen BB, Alayse AM, Jannasch HW. 1994. Microbial sulfate reduction in deep-sea sediments at the Guaymas Basin hydrothermal vent area: influence of temperature and substrates. *Geochim. Cosmochim. Acta* 58:3335–43

Elthon D. 1989. Pressure of origin of primary mid-ocean ridge basalts. In *Magmatism in the Ocean Basins*, ed. AD Sauders, MJ Norry, pp. 125–36. Boulder, CO: Geol. Soc. Spec. Publ. 42

Embley RW, Chadwick WW Jr. 1994. Volcanic and hydrothermal processes associated with a recent phase of seafloor spreading at the northern Cleft segment: Juan de Fuca Ridge. *J. Geophys. Res.* 99:4741–60

Embley RW, Chadwick WW Jr, Jonasson IR, Butterfield DA, Baker ET. 1995. Initial results of the response to the 1993 CoAxial event: relationships between hydrothermal and volcanic processes. *J. Geophys. Res.* 22: 143–46

Embley RW, Chadwick WW, Perfit MR, Smith MC, Delaney JR. 2000. Recent eruptions on the CoAxial segment of the Juan de Fuca Ridge: implications for mid-ocean ridge accretion processes. *J. Geophys. Res.* 105: 16501–25

Escartin J, Hirth G, Evans B. 1997. Effects of serpentinization on the lithospheric strength and the style of normal faulting at slow-spreading ridges. *Earth Planet. Sci. Lett.* 151:181–89

Evans WC, White LD, Rapp JB. 1988. Geochemistry of some gases in hydrothermal fluids from the southern Juan de Fuca Ridge. *J. Geophys. Res.* 93:15305–13

Falloon TJ, Green DH. 1987. Anhydrous partial melting of MORB pyrolite and other peridotite compositions at 10 kbar: implications for the origin of primitive MORB glasses. *Contrib. Mineral. Petrol.* 37:181–219

Ferris MJ, Nold SC, Revsbech SC, Ward DM. 1997. Population structure and physiological changes within a hot spring microbial mat community following disturbance. *Appl. Environ. Microbiol.* 63:1367–74

Fine GJ, Stolper EM. 1986. Dissolved carbon dioxide in basaltic glasses: concentrations and speciation. *Earth Planet. Sci. Lett.* 76: 263–78

Fisher AT. 1998. Permeability within basaltic oceanic crust. *Rev. Geophys.* 36:143–82

Fisher AT, Becker K, Narasimhan TN, Langseth MG, Mottl MJ. 1990. Passive, off-axis convection on the southern flanks of the Costa Rica Rift. *J. Geophys. Res.* 95:9343–70

Fisher CR. 1995. Toward an appreciation of hydrothermal-vent animals: their environment, physiological ecology, and tissue stable isotope analyses. See Humphris et al. 1995, pp. 297–316

Fisher CR. 1996. Ecophysiology of primary production at deep-sea vents and seeps. In *Deep-Sea and Extreme Shallow-Water Habitats: Affinities and Adaptations—Biosystematics and Ecology Ser. F* 11:313–36

Fisher CR, Childress JJ, Macko SA, Brooks JM. 1994. Nutritional interactions in Galapagos hydrothermal vent communities: influence from stable carbon and nitrogen isotope analyses. *Mar. Ecol. Prog. Ser.* 103:45–55

Fisk MR, Giovannoni SJ, Thorseth IH. 1998. Alteration of oceanic volcanic glass: textural evidence for microbial activity. *Science* 281: 978–80

Fornari DJ, Embley RW. 1995. Tectonic and volcanic controls on hydrothermal processes at the mid-ocean ridge: an overview based on near-bottom and submersible studies. In interaction of vent biota and hydrothermal deposits: present evidence and future experimentation. See Humphris et al. 1995, pp. 1–46

Fornari DJ, Shank T, Von Damm KL, Gregg TKP, Lilley M, et al. 1998. Time-series temperature measurements at high-temperature hydrothermal vents, East Pacific Rise 9°49′–51′N: evidence for monitoring a crustal cracking event. *Earth Planet. Sci. Lett.* 160: 419–31

Forsyth DW, Scheirer DS, Webb SC, Dorman RM, Orcutt JA, et al. 1998. Imaging the deep seismic structure beneath a mid-ocean ridge; the MELT experiment. *Science* 280:1215–18

Fouquet YA, Wafik P, Cambon P, Mevel C, Meyer G, et al. 1993. Tectonic setting and mineralogical and geochemical zonation in the Snake Pit sulfide deposit (Mid-Atlantic Ridge at 23°N). *Econ. Geol.* 88:2018–36

Fournier RO. 1987. Conceptual models of brine evolution in magmatic-hydrothermal systems. *US Geol. Surv. Prof. Pap.* 1350:1487–506

Fournier RO. 1999. Hydrothermal processes related to movement of fluid from plastic into brittle rock in the magmatic-epithermal environment. *Econ. Geol.* 94:1193–212

Fox CG. 1990. Consequences of phase separation on the distribution of hydrothermal fluids at ASHES vent field, Axial Volcano, Juan de Fuca Ridge. *J. Geophys. Res.* 95:12923–26

Fox CG, Chadwick WW Jr, Embley RW. 1992. Detection of changes in ridge-crest morphology using repeated multibeam sonar surveys. *J. Geophys. Res.* 97:11149–62

Fox CG, Chadwick WW Jr, Embley RW. 2001. Direct observation of a submarine volcanic eruption from a sea-floor instrument caught in a lava flow. *Nature* 412:727–29

Fox CG, Dziak RP. 1998. Hydroacoustic detection of volcanic activity on the Gorda Ridge, February–March 1996. *Deep-Sea Res. II* 45: 2513–30

Fox CG, Radford WE, Dziak RP, Lau T-K, Matsumoto H, Schreiner AE. 1995. Acoustic detection of a seafloor spreading episode on the Juan de Fuca Ridge using military hydrophone arrays. *Geophys. Res. Lett.* 22: 131–34

Francheteau J, Armijo R, Cheminee L, Hekinian R, Lonsdale P, et al. 1992. Dyke complex of the East Pacific Rise exposed in the walls of Hess Deep and the structure of the oceanic crust. *Earth Planet. Sci.* 111:109–21

Frost BR. 1985. On the stability of sulfides, oxides, and native metals in serpentinite. *J. Petrol.* 26:31–63

Früh-Green GL, Connolly JAD, Kelley DS, Plas A, Grobety B. 2002. Serpentinization of oceanic peridotites: implications for geochemical cycles and biological activity. In *The Subseafloor Biosphere at Mid-Ocean Ridges*, *Geophys. Monogr.*, ed. WSD Wilcock, DS Kelley, JA Baross, C Cary, E DeLong. Washington, DC: Amer. Geophys. Union

Früh-Green GL, Plas A, Lecuyer C. 1996. Petrologic and stable isotope constraints on hydrothermal alteration and serpentinization of the EPR shallow mantle at Hess Deep (Site 895). *Proc. Ocean Drill. Program Sci. Results* 147:255–91

Gaill F, Desbruyeres D, Prieur D. 1997. Bacterial communities associated with "Pompei worms" from the East Pacific Rise hydrothermal vents: SEM, TEM observations. *Microb. Ecol.* 13:129–39

Gantelet H, Duchiron F. 1999. A new pullanase from a hyperthermophilic archaeon for starch hydrolysis. *Biotechnol. Lett.* 21:71–75

Gerlach TM, Nordlie BE. 1975. The C-O-H-S gaseous system, Part 1: composition limits and trends in basaltic gases. *Am. J. Sci.* 275: 353–76

German CR, Parson LM, HEAT Scientific Team. 1996. Hydrothermal exploration near the Azores Tiple Junction: tectonic control of venting at slow-spreading ridges? *Earth Planet. Sci. Lett.* 138:93–104

Gillis KM. 1995. Controls on hydrothermal alteration in a section of fast-spreading oceanic crust. *Earth Planet. Sci. Lett.* 134:473–89

Gillis KM, Banerjee NR. 2000. Hydrothermal alteration patterns in supra-subduction zone ophiolites. In *Ophiolites and Oceanic Crust: New Insights from Field Studies and the Ocean Drilling Program*, ed. Y Dilek, E Moores, D Elthon, A Nicolas, pp. 283–97. Geol. Soc. Am. Spec. Pap. 349. Boulder, CO: Geol. Soc. Am. 552 pp.

Gillis KM, Meyer PS. 2001. Metasomatism of oceanic gabbros by late stage melts and hydrothermal fluids: evidence from the rare Earth element composition of amphiboles. *Geochem. Geopys. Geosys.* 2:1525–2027

Gillis KM, Muehlenbachs K, Stewart M, Gleeson T. 2001. Fluid flow patterns in fast-spreading East Pacific Rise crust. *J. Geophys. Res.* 106:26311–29

Gillis KM, Roberts MD. 1999. Cracking at the magma-hydrothermal transition: evidence from the Troodos Ophiolite, Cyprus. *Earth Planet. Sci. Lett.* 169:227–44

Gillis KM, Robinson PT. 1985. Low-temperature alteration of the extrusive sequence, Troodos ophiolite, Cyprus. *Can. Miner.* 23: 431–41

Gillis KM, Robinson PT. 1990. Patterns and processes of alteration in lavas and dykes of the Troodos Ophiolite, Cyprus. *J. Geophys. Res.* 95:21523–48

Gillis KM, Thompson G, Kelley DS. 1993. A view of the lower crustal component of hydrothermal systems at the Mid-Atlantic Ridge. *J. Geophys. Res.* 98:19597–619

Gold TH. 1992. The deep, hot biosphere. *Proc. Natl. Acad. Sci. USA* 89:6045–49

Goldfarb MS, Delaney JR. 1988. Response of two-phase fluids to fracture configurations within submarine hydrothermal systems. *J. Geophys. Res.* 93:4585–94

Gracia E, Charlou JL, Radford-Knoery J, Parson LM. 2000. Non-transform offsets along the Mid-Atlantic Ridge south of the Azores (39°N–34°N): ultramafic exposures and hosting of hydrothermal vents. *Earth Planet. Sci. Lett.* 177:89–103

Grassia GS, Mclean KM, Glenat P, Bauld J, Sheehy J. 1996. A systematic survey for thermophilic fermentative bacteria and archaea in high-temperature petroleum reservoirs. *FEMS Microbiol. Ecol.* 21:47–58

Green DH, Fallon TJ, Taylor WR. 1987. Mantle-derived magmas-roles of variable source peridotite and variable C-H-O fluid compositions. In *Magmatic Processes: Physicochemical Principles*, ed. BO Mysen, Spec. Publ. No. 1:139–63. Geochem. Soc.

Green DH, Ringwood AE. 1967. The genesis of basaltic magmas. *Contrib. Mineral. Petrol.* 15:103–90

Gregg TKP, Fornari DJ. 1998. Long submarine lava flows. Observations and results from numerical modeling. *J. Geophys. Res.* 103: 27517–31

Gregg TKP, Fornari DJ, Perfit MR, Haymon RM, Fink JH. 1996. Rapid emplacement of a mid-ocean ridge lava flow on the East Pacific Rise at 9°46′–51′N. *Earth Planet. Sci. Lett.* 144:E1–6

Gregg TKP, Fornari DHJ, Perfit R, Ridley WI, Kurz MD. 2000. Using submarine lava pillars to record mid-ocean ridge eruption dynamics. *Earth Planet Sci. Lett.* 178:195–214

Gugliandolo C, Italiano F, Maugeri TL, Inguaggiato S, Caccamo D, et al. 1999. Submarine hydrothermal vents of the Aeolian Islands: relationship between microbial communities and thermal fluids. *Geomicrobiol. J.* 16:105–17

Gustafson LB, Hunt JP. 1975. The porphyry copper deposit at El Salvador, Chile. *Econ. Geol.* 70:857–912

Hafenbrandl D, Keller M, Dirmeier R, Rachel R, Ronagel P, et al. 1996. *Ferroglobus pacidus* gen. a novel hyperthermophilic archaeum that oxidizes Fe^{2+} at neutral pH under anoxic conditions. *Arch. Microbiol.* 166: 308–14

Haggerty JA. 1989. Fluid inclusion studies of chimneys associated with serpentinite seamounts in the Mariana Forearc. *Proc. 2nd Pan-Am. Conf. Fluid Inc.,* p. 29

Hannington MD, Jonasson IR, Herzig PM, Petersen S. 1995. Interaction of vent biota and hydrothermal deposits: present evidence and future experimentation. See Humphris et al. 1995, pp. 115–57

Harmsen HJM, Prieur D, Jeanthon C. 1997a. Distribution of microorganisms in deep-sea hydrothermal vent chimneys investigated by whole-cell hybridization and enrichment culture of thermophilic subpopulations. *Appl. Environ. Microbiol.* 63:2876–83

Harmsen HJM, Prieur D, Jeanthon C. 1997b. Group-specific 16s rRNA targeted oligonucleotide probes to identify thermophilic bacteria in marine hydrothermal vents. *Appl. Environ. Microbiol.* 63:4061–68

Haymon RM. 1983. Growth history of black smoker hydrothermal chimneys. *Nature* 301: 695–98

Haymon RM, Fornari DJ, Edwards M, Carbotte SM, Wright D, et al. 1991. Hydrothermal vent distribution along the East Pacific Rise crest (9°09′–54′N) and its relationship to magmatic and tectonic processes on fast spreading mid-ocean ridges. *Earth Planet. Sci. Lett.* 104:513–34

Haymon RM, Fornari DJ, Von Damm KL, Lilley MD, Perfit MR, et al. 1993. Volcanic eruption of the mid-ocean ridge along the east Pacific Rise crest at 9°45′–52′N: direct submersible observations of seafloor phenomena associated with an eruption event in April, 1991. *Earth Planet. Sci. Lett.* 119:85–101

Hedrick DB, Pledger RJ, White DC, Baross JA. 1992. In situ microbial ecology of hydrothermal vent sediments. *FEMS Microbiol. Ecol.* 101:1–10

Helgeson HC. Amend JP. 1994. Relative stabilities of biomolecules at high temperatures and pressures. *Thermochim. Acta* 245:89–119

Hennet RJ, Holm NG, Engel MH. 1992. Abiotic synthesis of amino acids under hydrothermal conditions and the origin of life: a perpetual phenomenon? *Naturwissenschaften* 79:361–65

Hirth GH, Escartin J, Lin J. 1998. The rheology of the lower oceanic crust: implications for lithosphere deformation at mid-ocean ridges. See Buck et al. 1998, pp. 291–303

Hirth G, Kohlstedt DL. 1996. Water in the oceanic upper mantle: implications for rheology, melt extraction and the evolution of the lithosphere. *Earth Planet. Sci. Lett.* 144:93–108

Holden JF, Summit M, Baross JA. 1998. Thermophilic and hyperthermophilic microorganisms in 3–30°C fluids following a deep-sea volcanic eruption. *FEMS Microbiol. Ecol.* 25:33–41

Holden JF, Baross JA. 1995. Enhanced thermotolerance by hydrostatic pressure in the deep-sea hyperthermophile *Pyrococcus* strain ES4. *FEMS Microbiol. Ecol.* 18:27–34

Holden JF, Baross JA. 1993. Enhanced thermotolerance and temperature-induced changes in protein composition in the hyperthermophilic archaea ES4. *J. Bacteriol.* 175:2839–43

Holden JF, Takai K, Summit M, Bolton S, Zyskowski JA, et al. 2001. Diversity among three novel groups of hyperthermophilic deep-sea *Thermococcus* species from three sites in the Northeastern Pacific Ocean. *FEMS Microbiol. Ecol.* 36:51–60

Holloway J. 1984. Graphite-CH_4-H_2O-CO_2 equilibria at low-grade metamorphic conditions. *Geology* 12:455–58

Holloway JR, Blank JG. 1994. Application of experimental results to C-O-H species in natural melts. See Caroll & Holloway 1994, pp. 187–230

Holloway JR, O'Day PA. 2000. Production of CO_2 and H_2 by diking-eruptive events at mid-ocean ridges: implications for abiotic organic synthesis and global geochemical cycling. *Int. Geol. Rev.* 42:673–83

Holm NG, Charlou JL. 2001. Initial indications of abiotic formation of hydrocarbons in the Rainbow ultramafic hydrothermal system, Mid-Atlantic Ridge. *Earth Planet. Sci. Lett.* 191:1–8

Hooft EE, Detrick RS, Kent GM. 1997. Seismic structure and indicators of magma budget along the Southern East Pacific rise. *J. Geophys. Res.* 102:27319–40

Huber JA, Butterfield DA, Baross JA. 2002. Temporal changes in archaeal diversity and chemistry in a mid-ocean ridge subseafloor habitat. *Appl. Environ. Microbiol.*

Huber H, Stetter KO. 1998. Hyperthermophiles and their possible potential in biotechnology. *J. Biotechnol.* 64:39–52

Huber R, Eder W, Heldwein S, Wanner G, Huber H, et al. 1998. *Thermocrinis ruber* gen. nov., sp. nov., a pink-filament-forming hyperhthermophilic bacterium isolated from Yellowstone national Park. *Appl. Environ. Microbiol.* 64:3576–83

Huber R, Huber H, Stetter KO. 2000. Towards the ecology of hyperthermophiles: biotopes, new isolation strategies and novel metabolic properties. *FEMS Microbiol. Rev.* 24:615–23

Huber R, Stoffers P, Cheminee JL, Richnow HH, Stetter KO. 1990. Hyperthermophilic archaebacteria within the crater and open-sea plume of erupting MacDonald Seamount. *Nature* 345:179–82

Huber R, Wächtershäuser G. 1997. Activated acetic acid by carbon fixation on (Fe,Ni)S under primordial conditions. *Science* 276:245–47

Huber R, Wilharm T, Huber D, Trincone A, Burggraf S, et al. 1992. *Aquifex pyrophilus*, new genus new species, represents a novel group of marine hyperthermophilic hydrogen-oxidizing bacteria. *System. Appl. Microbiol.* 15:340–51

Hugenholtz P, Goebel BM, Pace NR. 1998. Impact of culture-independent studies on the emerging phylogenetic view of microbial ecology. *J. Bacteriol.* 180:4765–74

Humphris SE, Cann JR. 2000. Constraints on the energy and chemical balances of the modern TAG and ancient Cyprus seafloor sulfide deposits. *J. Geophys. Res.* 105:28477–88

Humphris SE, Kleinrock MC. 1996. Detailed morphology of the TAG active hydrothermal mound: insights into its formation and growth. *Geophys. Res. Lett.* 23:3443–46

Humphris SE, Thompson G. 1978. Hydrothermal alteration of oceanic basalts by sea water. *Geochim. Cosmochim. Acta* 42:107–25

Humphris SE, Tivey MK. 2000. A synthesis of geological and geochemical investigations of the TAG hydrothermal field: insights into fluid flow and mixing process in a hydrothermal system. In *GSA Memoir/Special Publication on Ophiolites and Oceanic Crust: New Insights from Field Studies and the Ocean Drilling Program*, ed. Y Dilek, E Moores, D Elthon, A Nicholas. Boulder, CO: Geol. Soc. Am. 552 pp.

Humphris SE, Zierenberg RA, Mullineau LS, Thomson RE, eds. 1995. *Seafloor Hydrothermal Systems: Physical, Chemical, Biological, and Geological Interactions*. Geophys. Monogr. 91. Washington, DC: Am. Geophys. Union. 466 pp.

Jambon A. 1994. Earth degassing and large-scale geochemical cycling of volatile elements. See Caroll & Holloway 1994, pp. 479–517

Janecky DR, Seyfried WE Jr. 1986. Hydrothermal serpentinization of peridotite within the oceanic crust: experimental investigations of mineralogy and major element geochemistry. *Geochim. Cosmochim. Acta* 50:1357–78

Jannasch HW. 1995. Microbial interaction with hydrothermal fluids. See Humphris et al. 1995, pp. 273–96

Jannasch HW, Wirsen CO. 1981. Morphological survey of microbial mats near deep-sea thermal vents. *Appl. Environ. Microbiol.* 41: 528–38

Jannasch HW, Wirsen CO, Molyneaux BJ, Langworthy TA. 1992. Comparative physiological studies on hyperthermophilic archaea isolated from deep-sea hydrothermal vents with emphasis on *Pyrococces* strain GB-D. *Appl. Environ. Microbiol.* 58:3472–81

Jeanthon C. 2000. Molecular ecology of hydrothermal vent microbial communities. *Antonie Van Leeuwenhoek.* 77:117–33

Jeanthon C, Prieur D. 1990. Susceptibility to heavy metals and characterization of heterotrophic bacteria isolated from two hydrothermal vent polychaete annelids, *Alvinella pompejana* and *Alvinella caudate*. *Appl. Environ. Microbiol.* 56:3308–14

Johnson HP, Hutnak M, Dziak RP, Fox CG, Urcuyo I. 2000. Earthquake-induced changes in a hydrothermal system on the Juan de Fuca Mid-Ocean Ridge. *Nature* 407:174–77

Johnson KTM, Dick HJB, Shimizu N. 1990. Melting in the oceanic upper mantle: an ion microprobe study of diopsides in abyssal peridotites. *J. Geophys. Res.* 95:2661–78

Jørgensen BB, Isaksen MF, Jannasch HW. 1992. Bacterial sulfate reduction above 100°C in deep-sea hydrothermal vent sediments. *Science* 258:1756–57

Jørgensen BB, Zawaki LX, Jannasch HW. 1990. Thermophilic bacterial sulfate reduction in deep-sea sediment at the Guaymas Basin hydrothermal vent site. *Deep-Sea Res.* 37:695–710

Jousselin D, Nicolas A, Boudier F. 1998. Detailed mapping of a diapir below a paleo-spreading center in the Oman Ophiolite. *J. Geophys. Res.* 103:18153–70

Juniper SK, Fouquet Y. 1988. Filamentous iron-silica deposits afrom modern and ancient hydrothermal sites. *Can. Mineral.* 26:859–69

Juniper SK, Jonasson IR, Tunnicliffe V, Southward AJ. 1992. Influence of a tube-building polychaete on hydrothermal chimney mineralization. *Geology* 20:895–98

Juniper SK, Martinea P, Sarrazin J, Gelinas Y. 1995. Microbial-mineral floc associated with nascent hydrothermal activity on CoAxial Segment, Juan de Fuca Ridge. *Geophys. Res. Lett.* 22:179–82

Juniper SK, Sarrazin J. 1995. Interaction of vent biota and hydrothermal deposits: present evidence and future experimentation. See Humphris et al. 1995, pp. 178–93

Juniper SK, Tebo BM. 1995. Microbe-metal interactions and mineral deposition at hydrothermal vents. See Karl 1995, pp. 219–53

Juniper SK, Tunnicliffe V. 1997. Crustal accretion and the hot vent ecosystem. *Philos. Trans. R. Soc. London Ser. A* 355:459–74

Jupp T, Schultz A. 2000. A thermodynamic explanation for black smoker temperatures. *Nature* 403:880–83

Kadko D, Baross J, Alt J. 1995. The magnitude and global implications of hydrothermal flux. See Humprhis et al. 1995, pp. 446–66

Kappel ES, Ryan WBF. 1986. Volcanic episodicity and a non-steady state rit valley along northeast Pacific spreading centers: evidence from SeaMARCI. *J. Geophys. Res.* 91:13925–40

Karl DM, ed. 1995. *The Microbiology of Deep-Sea Hydrothermal Vents*. Boca Raton, FL: CRC Press. 299 pp.

Karson JA. 1998. Internal structure of oceanic lithosphere: a perspective from tectonic windows. See Buck et al. 1998, pp. 177–218

Karson JA. 2002. Geologic structure of Uppermost Oceanic Crust from fast- to intermediate-rate Mid-Ocean Ridges. *Annu. Rev. Earth Planet. Sci.* 30:347–84

Karson JA, Dick HJB. 1983. Tectonics of ridge-transform intersections at the Kane Fracture Zone. *Mar. Geophys. Res.* 6:51–91

Karson JA, Lawrence RM. 1997. Tectonic setting of serpentinite exposures on the western midian valley wall of the MARK area in the vicinity of Site 920. *Proc. Ocean Drill. Program Sci. Results* 153:5–21

Karson JA, Rona PA. 1990. Block tilting, transfer faults, and structural control of magmatic and hydrothermal proceses in the TAG area, Mid-Atlantic Ridge 26°N. *Geol. Soc. Am. Bull.* 102:1635–45

Karson JA, Thompson G, Humphris SE, Edmond JM, Bryan WB, et al. 1987. Along-axis variations in seafloor spreading in the MARK area. *Nature* 328:681–85

Kaye J, Baross JA. 2000. High incidence of halotolerant bacteria in Pacific hydrothermal vent and pelagic environments. *FEMS Microbiol. Ecol.* 32:249–60

Kelemen PB, Aharonov E. 1997. Periodic formation of magma fractures and generation of layered gabbros in the lower crust beneath oceanic spreading centers. See Buck et al. 1998, pp. 267–89

Kelemen PB, Braun M, Hirth G. 2000. Spatial distribution of melt conduits in the mantle beneath oceanic spreading ridges: observations from the Ingalls and Oman ophiolites. *Geochem. Geophys. Geosyst.* 1:1–17

Kelemen PB, Dick HJB, Quick JE. 1992. Formation of harzburgite by pervasive melt/rock reaction in the upper mantle. *Nature* 358:635–41

Kelemen PB, Dick HJB. 1995. Focused melt flow and localized deformation in the upper mantle: juxtaposition of replacive dunite and ductile sher zones in the Josephine peridotite, SW Oregon. *J. Geophys. Res.* 100:423–38

Kelemen PB, Hirth G, Shimizu N, Spiegelman M, Dick HJB. 1997. A review of melt migration processes in the adiabatically upwelling mantle beneath oceanic spreading ridges. *Philos. Trans. R. Soc. London Ser. A* 355:283–318

Kelemen PB, Whitehead JA, Aharonov E, Jordahl KA. 1995. Experiments on flow focusing in soluble porous media, with applications to melt extraction from the mantle. *J. Geophys. Res.* 100:475–96

Kelley DS. 1996. Methane-rich fluids in the oceanic crust. *J. Geophys. Res.* 101:2943–62

Kelley DS. 1997. Fluid evolution in slow-spreading environments. *Proc. Ocean Drill. Program Sci. Results* 153:399–415

Kelley DS, Delaney JR. 1987. Two-phase separation and fracturing in mid-ocean ridge gabbros at temperatures greater than 700°C. *Earth Planet. Sci. Lett.* 83:53–66

Kelley DS, Delaney JR, Schrenk MO, Baross JA. 1999. Sulfide-microbial habitats in a submarine hydrothermal field. *Eos Trans. Am. Geophys. Union* 80:86

Kelley DS, Delaney JR, Yoerger DA. 2001b. Geology and venting characteristics of the Mothra Hydrothermal Field, Endeavour Segment, Juan de Fuca Ridge. *Geology* 29:959–62

Kelley DS, Delaney JR, Yoerger DA, Mathez E. 1998a. Multiscalar investigation of the Mothra Hydrothermal Field, Endeavour Segment of the Juan de Fuca Ridge. *Eos Trans. Am. Geophys. Union* 79:810

Kelley DS, Früh-Green GL. 1999. Abiogenic methane in deep-seated mid-ocean ridge environments: insights from stable isotope analyses. *J. Geophys. Res.* 104:10439–60

Kelley DS, Früh-Green GL. 2000. Volatiles in mid-ocean ridge environments. In *Ophiolites and Oceanic Crust: New Insights from Field Studies and the Ocean Drilling Program*, ed. Y Dilek, E Moores, D Elthon, A Nicolas, pp. 237–72. Geol. Soc. Am. Spec. Pap. 349. Boulder, CO: Geol. Soc. Am. 552 pp.

Kelley DS, Früh-Green GL. 2001. Volatile lines of descent in submarine plutonic environments: insights from stable isotope and fluid inclusion analyses. *Geochim. Cosmochim. Acta* 19:3325–46

Kelley DS, Gillis KM, Thompson G. 1993. Fluid evolution in submarine magma-hydrothermal systems at the Mid-Atlantic Ridge. *J. Geophys. Res.* 98:19579–96

Kelley DS, Karson JA, Blackman DK, Früh-Green GL, Butterfield DA, et al. 2001a. An off-axis hydrothermal vent field near the Mid-Atlantic Ridge at 30°N. *Nature* 412: 145–49

Kelley DS, Karson JA, Blackman DK, Früh-Green GL, Butterfield DA, et al. 2001c. An overview of the Lost City Vent Field: an extensive off-axis serpentinite-hosted hydrothermal field, 30°N, Mid-Atlantic Ridge. *Eos Trans. Am. Geopys. Union* 82:1100

Kelley DS, Lilley MD, Lupton JE, Olson EJ. 1998b. Enriched H_2, CH_4 and ^3He concentrations in hydrothermal plumes associated with the 1996 Gorda Ridge eruptive event. *Deep-Sea Res. II* 45:2665–82

Kelley DS, Malpas J. 1996. Melt-fluid evolution in gabbroic rocks from the Hess Deep, Ocean Drilling Leg 147. In *Proceeding of the Ocean Drilling Program, Scienticfic Results*, ed. J Allan, K Gillis, C Mevel, 147:213–26. College Station, TX: Ocean Drill. Program. 544 pp.

Kelley DS, Robinson PT, Malpas JG. 1992. Processes of brine generation and circulation in the oceanic crust: fluid inclusion evidence from the Troodos ophiolite, Cyprus. *J. Geophys. Res.* 97:9307–22

Kelly RM, Adams MWW. 1994. Metabolism in hyperthermophilic microorganisms. *Antonie van Leeuwenhoek.* 66:247–70

Kidd RGW. 1977. A model for the formation of the upper oceanic crust. *Geophys. J. R. Astron. Soc.* 50:149–83

Klein FW, Koyanagi RY, Nakata JS, Tanigawa WR. 1987. The seismicity of Kilauea's magma system. In *Volcanism in Hawaii*, ed. RW Decker, TL Wright, PH Stauffer, pp. 1019–185. US Geol. Surv. Prof. Pap. No. 1350

Kleinrock MC, Humphris SE. 1996. Structural control on sea-floor hydrothermal activity at the TAG active mound. *Nature* 382:149–53

Kletzen A, Adams MWW. 1996. Tungsten in biology. *FEMS Microbiol. Rev.* 18:5–64

Klinkhammer GP, Chin CS, Keller RA, Dählmann A, Sahling H, et al. 2001. Discovery of new hydrothermal vent sites in Bransfield Strait, Antactica. *Earth Planet. Sci. Lett.* 193:395–407

Knapp RB, Knight JE. 1977. Differential thermal expansion of pore fluids: fracture propagation and microearthquake production in hot pluton environments. *J. Geophys. Res.* 81:2515–22

Kulm LD, Suess E. 1990. Relationship between carbonate deposits and fluid venting: Oregon accretionary prism. *J. Geophys. Res.* 95: 8899–915

Kushiro I. 2001. Partial melting experiments on peridotite and origin of mid-ocean ridge basalt. *Annu. Rev. Earth Planet. Sci.* 29:71–107

Lagabrielle Y, Bideau D, Cannat M, Karson JA, Mevel C. 1998. Ultramafic-mafic plutonic rock suites exposed along the Mid-Atlantic Ridge (10°N–30°N). Symmetrical-asymetrical distribution and implications for seafloor spreading processes. See Buck et al. 1998, pp. 153–76

Lagabrielle Y, Cormier MH. 1999. Formation of large summit troughs along the East Pacific Rise as collapse calderas: an evolutionary model. *J. Geophys. Res.* 104:12971–88

Lalou C, Reyss J-L, Brichet E. 1998. Age of sub-bottom sulfide samples at the TAG active mound. *Proc. Ocean Drill. Program Sci. Results* 158:111–17

Lalou C, Reyss J-L, Brichet E, Rona PA, Thompson G. 1995. Hydrothermal activity on a 10^5-year scale at a slow-spreading ridge, TAG hydrothermal field, Mid-Atlantic Ridge 26°N. *J. Geophys. Res.* 100:17855–62

Langseth MX, Gill CJ, Williams Q, Perfit MR. 1966. Crustal structure of mid-ocean ridges, 5. Heat flow through the Atlantic Ocean floor and convection currents. *J. Geophys. Res.* 71: 5321–55

Lavelle JW. 1995. The initial rise of a hydrothermal plume from a line source—results from a three-dimensional numerical model. *Geophys. Res. Lett.* 22:159–62

Lawerence RM, Karson JA, Hurst SD. 1998. Dike orientations and fault-block rotations in slow-spread oceanic crust at the SMARK Area, Mid-Atlantic Ridge at 22°40′N. *J. Geophys. Res.* 103:663–76

Legin E, Copinet A, Duchiron F. 1998. Production of thermostable amylotic enzymes by *Thermococcus hydrothermalis*. *Biotechnol. Lett.* 20:364–67

L'Haridon SL, Reysenbach A-L, Glenat P, Prieru D, Jeanthon C. 1995. Hot subterranean biosphere in continental reservoir. *Nature* 337:223–24

Lilley MD, Baross JA, Gordon LI. 1983. Reduced gases and bacteria in hydrothermal fluids: the Galapagos spreading center and 21°N East Pacific Rise. See Rona et al. 1983, pp. 411–47

Lilley MD, Butterfield DA, Kelley DS, Tivey NK, Delaney JR, et al. 2000. Long- and short-term variability in hydrothermal activity at the Endeavour RIDGE Observatory site. *Eos Trans. Am. Geophys. Union* 81:628

Lilley MD, Butterfield DA, Olson EJ, Lupton JE, Mackos S, et al. 1993. Anomalous CH_4 and NH_4^+ concentrations at an unsedimented mid-ocean-ridge hydrothermal system. *Nature* 364:45–47

Lilley MD, Landsteiner MC, McLaughlin EA, Parker CB, Cherkaoui ASM, et al. 1995. Real-time mapping of hydrothermal plumes on the Endeavour Segment of the Juan de Fuca. *Eos Trans. Am. Geophys. Union* 76:420

Lilley MD, Lupton JE, Von Damm KL. 1992. Volatiles in the 9°N hydrothermal system: a comparison of 1991 and 1992 data. *Eos Trans. Am. Geophys. Union, Fall Meet. Suppl.* 73(43):524

Lilley MD, Olson EJ. 2001. Methane and hydrogen in active hydrothermal systems. *Annu. Gold. Conf., 11th*, 3682

Lister CRB. 1974. On the penetration of water into hot rock. *Geophys. J. R. Astron. Soc.* 39:465–509

Lister CRB. 1983. The basic physics of water penetration into hot rock. See Rona et al. 1983, pp. 141–76

Longnecker K, Reysenbach A-L. 2001. Expansion of the geographic distrobution of a novel lineage of ε-Proteobacteria to a hydrothermal vent site on the Southern East Pacific Rise. *FEMS Microbiol. Ecol.* 35:287–93

Lowell RP, Germanovich LN. 1995. Dike injection and the formation of megaplumes at ocean ridges. *Science* 267:1804–7

Lowell RP, Rona PA, Von Herzen RP. 1995. Seafloor hydrothermal systems. *J. Geophys. Res.* 100:327–52

Lowell RP, Xu W. 2000. Subcritical two-phase seawater convection near a dike. *Earth Planet. Sci. Lett.* 147:385–96

Lupton JE. 1995. Hydrothermal plumes: near and far field. See Humphris et al. 1995, pp. 317–46

Lupton JE, Baker E, Massoth G. 1989. Variable ^{3}He/heat ratios in submarine hydrothermal systems: evidence from two plumes over the Juan de Fuca Ridge. *Nature* 337:161–64

Lupton JE, Baker ET, Massoth GJ. 1999. Helium, heat, and the generation of hydrothermal event plumes at mid-ocean ridges. *Earth Planet. Sci. Lett.* 171:343–50

Lupton JE, Baker ET, Massoth GJ. 2000. Reply to comment by MR Palmer and GGJ Ernst on "Helium, heat, and the generation of hydrothermal event plumes at mid-ocean ridges" by JE Lupton, ET Baker, and GJ Massoth. *Earth Planet. Sci. Lett.* 180:219–22

Lutz RA, Shank TM, Fornari DJ, Haymon RM, Lilley MD, et al. 1994. Rapid growth at deep-sea vents. *Nature* 371:663–64

Macdonald KC. 1998. Linkages between faulting, volcanism, and hydrothermal activity and segmentation on fast-spreading centers. See Buck et al. 1998, pp. 27–58

Macdonald KC, Fox PJ. 1988. The axial summit graben and cross-sectinal shape of the East Pacific Rise as indicators of axial magma chambers and recent volcanic eruptions. *Earth Planet. Sci. Lett.* 88:119–31

MacLeod CJ, Yaouancq G. 2000. A fossil melt lens in the Oman ophiolite: implications for magma chamber processes at fast-spreading ridges. *Earth Planet. Sci. Lett.* 176:357–73

Magde LS, Barclay AH, Toomey DR, Detrick RS, Collins JA. 2000. Crustal magma plumbing within a segment of the Mid-Atlantic Ridge, 35°N. *Earth Planet. Sci. Lett.* 175:55–67

Manning CE, MacLeod CJ, Weston PE. 2000. Lower-crustal cracking front at fast-spreading ridges: evidence from the East Pacific Rise and Oman ophiolites. In *Ophiolites and Oceanic Crust: New Insights from Field Studies and the Ocean Drilling Program*, ed. Y Dilek, E Moores, D Elthos, A Nicoals, pp. 261–72, Geol. Soc. Am. Spec. Pap. 349. Boulder, CO: Geol. Soc. Am. 552 pp.

Manning C, Weston PE, Mahon KI. 1996. Rapid high temperature metamorphism of the East Pacific Rise gabbros from Hess Deep. *Earth Planet. Sci. Lett.* 144:123–32

Marsh AG, Mullineaux LS, Young CM, Manahan DT. 2001. Larval dispersal potential of the tubeworm *Riftia pachyptila* at deep-sea hydrothermal vents. *Nature* 411:77–80

Marshall WL. 1994. Hydrothermal synthesis of amino acids. *Geochim. Cosmochim. Acta* 58:2099–106

Massoth GJ, Baker ET, Feely RA, Lupton JE, Collier RW, et al. 1998. Manganese and iron in hydrothermal plumes resulting from the 1996 Gorda Ridge Event. *Deep-Sea Res. II* 45:2683–712

Mathez EA. 1984. Influence of degassing on oxidation states of basaltic magmas. *Nature* 310:371–75

Mathez EA, Dietrich VJ, Holloway JR, Boudreau AE. 1989. Carbon distribution in the Stillwater Complex and evolution of vapor during crystallization of Stillwater and Bushveld magmas. *J. Petrol.* 30:153–73

McCollom TM. 2000. Geochemical constraints on primary productivity in submarine hydrothermal vent plumes. *Deep-Sea Res. I* 47:85–101

McCollom TM, Seewald JS. 2001. A reassessment of the potential for reduction of dissolved CO_2 to hydrocarbons during serpentinization of olivine. *Geochim. Cosmochim. Acta* 21:3769–78

McCollom TM, Shock EL. 1997. Geochemical constraints on chemolithoautotrophic metabolism by microorganisms in seafloor hydrothermal systems. *Geochim. Cosmochim. Acta* 61:4375–91

McDuff RE, Delaney JR, Lilley MD, Butterfield DA. 1994. Are up flow zones boundaries between adjacent hydrothermal systems? *Eos Trans. Am. Geophys. Union* 75:618

McKenzie D, Bickle MJ. 1988. The volume and composition of melt generated by extension of the lithosphere. *J. Petrol.* 29:625–79

McLaughlin EA. 1998. *Microbial hydrogen oxidation in hydrothermal systems*. PhD thesis. Univ. Washington. 125 pp.

McLaughlin EA, Lilley MD, Olson EJ, Rust T. 1996. Microbial hydrogen oxidation in the Loihi event plumes: microbial rapid response. *Eos Trans. Am. Geophys. Union* 46:398

Mehta M, Baross JA. 2000. Investigating the role of nitrogen fixation at hydrothermal vents. *NSF Hyperthermophile Symp.*, Oct. 25–27. NC Univ., Raleigh

Mével C, Cannat M, Gente P, Marion E, Auzende JM, et al. 1991. Emplacement of deep crustal and mantle rocks on the west median valley wall of the MARK area (MAR 23°N). *Tectonophysics* 190:31–53

Meyer PS, Sapp K. 1994. Crystal size distribution, mineral chemistry, and crystallization history of ODP Site 735B gabbros. *Eos Trans. Am. Geophys. Union* 75:627

Michael PJ. 1988. The concentration, behavior and storage of H_2O in the suboceanic upper mantle: implications for mantle metasomatism. *Geochim. Cosmochim. Acta* 52:555–66

Michels PC, Hei D, Clark DS. 1996. Pressure effects on enzyme activity and stability at high temperatures. *Adv. Protein Chem.* 48: 341–76

Miller SL, Bada JL. 1988. Submarine hot springs and the origin of life. *Nature* 334: 609–11

Moore JG. 1977. Water content of basalt erupted on the ocean floor. *Contrib. Mineral. Petrol.* 28:272–79

Morgan JP, Chen YJ. 1993a. Dependence of ridge-axis morphology on magma supply and spreading rate. *Nature* 364:706–8

Morgan JP, Chen YJ. 1993b. The genesis of oceanic crust: magma injection, hydrothermal circulation, and crustal flow. *J. Geophys. Res.* 98:6283–97

Mottl MJ. 1983. Metabasalts, axial hot springs, and the structure of hydrothermal systems at mid-ocean ridges. *Geol. Soc. Am. Bull.* 94: 161–80

Mottl MJ, Haggerty JA. 1989. Upwelling of Cl-poor, S- and C-rich waters through a serpentinite seamount, Mariana Forearc, ODP Leg 125. *Eos Trans. Am. Geophys. Union* 70: 1382

Mottl MJ, Wheat CG. 1994. Hydrothermal circuation through mid-ocean ridge flanks: fluxes of heat and magnesium. *Geochim. Cosmochim. Acta* 58:2225–37

Moyer CL, Dobbs FC, Karl DM. 1995. Phylogenetic diversity of the bacterial community from a microbial mat at an active, hydrothermal vent system, Loihi seamount, Hawaii. *Appl. Environ. Microbiol.* 61:1555–62

Moyer CL, Tiedje JM, Dobbs FC, Karl DM. 1998. Diversity of deep-sea hydrothermal vent *Archaea* from Loihi Seamount, Hawaii. *Deep-Sea Res. II* 45:303–17

Muehlenbachs K, Clayton RN. 1972. Oxygen isotope studies of fresh and weathered submarine basalts. *Can. J. Earth Sci.* 9:172–84

Mukund S, Adams MWW. 1995. Glyceraldehyde-3-phosphate ferrdoxin oxidoreductase, a novel tungsten-containing enzyme with a potential glycolytic role in the hyperthermophilic archaeon *Pyrococcus furiosus*. *J. Biol. Chem.* 270:8389

Mullineaux LS, France SC. 1995. Dispersal mechanisms of deep-sea hydrothermal vent fauna. See Humprhis et al. 1995, pp. 408–424

Mutter JC, Barth GA, Buhl P, Detrick RS, Orcutt J, Harding A. 1988. Magma distribution across ridge-axis discontinuities on the East Pacific Rise from multichannel seismic images. *Nature* 336:156–58

Mysen BO, ed. 1987. *Magmatic Processes: Physicochemical Principles*, Vol. 1. Spec. Publ. Geochem. Soc. Lancaster Press. 500 pp.

Nehlig P. 1991. Salinity of oceanic hydrothermal fluids: a fluid inclusion study. *Earth Planet. Sci. Lett.* 102:310–25

Nehlig P, Juteau T. 1988. Flow porosities, permeabilities, and preliminary data on fluid inclusions and fossil geothermal gradients in the crustal sequence of the Sumail ophiolite, Oman. *Tectonophysics* 151:199–21

Nehlig P, Juteau T, Bendel V, Cotten J. 1994. The root zones of oceanic hydrothermal systems: constraints from the Samail ophiolites (Oman). *J. Geophys. Res.* 99:4703–13

Nelson DC, Fisher CR. 1995. Chemoautotrophic and methanogenic endosymbiotic bacteria at deep-sea vents and seeps. In *The Microbiology of Deep-Sea Hydrothermal Vents*, ed. DM Karl, pp. 125–67. Boca Raton, FL: CRC Press. 299 pp.

Nelson D, Haymon RM, Lilley M. 1991. Rapid growth of unusual hydrothermal bacteria observed at new vents during AdVenture dive program to the EPR at 9°45–52′N. *Eos Trans. Am. Geophys. Union* 72:481

Nelson DC, Wirsen CO, Jannasch HW. 1989. Characterization of large autotrophic *Beggiatoa* abundant at hydrothermal vents of the Guaymas Basin. *Appl. Environ. Microbiol.* 55:2909–917

Nicolas A, Rabinowicz M. 1984. Mantle flow patterns of oceanic spreading centres: relation with ophiolitic and oceanic structures. In *Ophiolites and Oceanic Lithosphere*. *Geol. Soc. London Spec. Publ.* 13:147–51

Niida K. 1997. Mineralogy of MARK

peridotites: replacement through magma channeling examined from Hole 920D, MARK area. *Proc. Ocean Drill. Program Sci. Results* 153:265–75

Nishihara H, Igarashi Y, Kodama T. 1990. A new isolate of *Hydrogenobacter*, an obligately chemolithoautotrophic, thermophilic, halophilic and aerobic hydrogen-oxidizing bacteium from seaside saline hot spring. *Arch. Microbiol.* 153:294–98

Nishihara H, Yaguchi T, Chung SY, Suzuki K, Yanagi M, et al. 1998. Phylogenetic position of an obligately chemoautotrophic, marine hydrogen-oxidizing bacterium, *Hydrogenovibriio marinus*, on the basis of 16S rRNA gene sequences and two from I RuBisCO gene sequences. *Arch. Microbiol.* 169:364–68

Niu Y. 1997. Mantle melting and melt extraction processes beneath ocean ridges: evidence from abysall peridotites. *J. Petrol.* 38:1047–74

Niu Y, Bideau D, Hekinian R, Batiza R. 2001. Mantle compositional control on the extent of mantle melting, crust production, gravity anomaly, ridge morphology, and ridge segmentation: a case study at the Mid-Atlantic Ridge 33–35°N. *Earth Planet. Sci. Lett.* 186: 383–99

Nojiri Y, Ishibashi J, Kawai T, Otsuki A, Sakai H. 1989. Hydrothermal plumes along the North Fiji Basin spreading axis. *Nature* 342: 667–70

Norton D. 1984. Theory of hydrothermal systems. *Annu. Rev. Earth Planet. Sci.* 12:155–77

Oberbeck VR, Fogelman G. 1990. Impact constraints on the environment for chemical evolution and the continuity of life. *Orig. Life Evol. Biosph.* 20:181–95

Oberbeck VR, Mancinelli RL. 1994. Asteroid impacts, microbes, and cooling of the atmosphere. *BioScience* 44:173–77

Orphan VJ, House CH, Hinrichs K-U, McKeegan KD, Delong EF. 2001. Methane-consuming archaea revealed by directly coupled isotopic and phylogenetic analysis. *Science* 293:484–87

Pace NR. 1997. A molecular view of microbial diversity and the biosphere. *Science* 276: 734–40

Palmer MR, Ernst GGJ. 1998. Generation of hydrothermal megaplumes by cooling of pillow basalts at mid-ocean ridges. *Nature* 393:643–47

Palmer MR, Ernst GGJ. 2000. Comment on "Helium, heat and the generation of hydrothermal event plumes at mid-ocean ridges", by JE Lupton, ET Baker, and GJ Massoth. *Earth Planet. Sci. Lett.* 180:215–18

Parkes RJ, Cragg BA, Bale SJ, Getliff JM, Goodman K, et al. 1994. Deep bacterial biosphere in Pacific Ocean sediments. *Nature* 371:410–13

Pedersen K. 1997. Microbial life in deep granitic rock. *FEMS Microbiol. Rev.* 20:399–414

Pedersen K. 2000. The hydrogen-driven intraterrestrial biosphere and its influence on the hydrochemical conditions in crystalline bedrock aquifers. In *Hydrogeology of Crystalline Rocks*, ed. I Stober, K Bucher, 34:249–59. Water Sci. Technol. Libr. Dordrecht, Netherlands: Kluwer Acad.

Perfit MR, Chadwick WW Jr. 1998. Magmatism at mid-ocean ridges: constraints from volcanological and geochemical investigations. See Buck et al. 1998, pp. 59–115

Perfit MR, Fornari DJ, Malahoff A, Embley RW. 1994. Small-scale spatial and temporal variations in mid-ocean ridge crest magmatic processes. *Geology* 22:375–79

Pineau F, Javoy M. 1983. Carbon isotopes and concentrations in mid-oceanic ridge basalts. *Earth Planet. Sci. Lett.* 62:239–57

Pledger RJ, Baross JA. 1989. Characterization of an extremely thermophilic archaebacterium isolated from a black smoker polychaete (*Paralvinella sp.*) at the Juan de Fuca Ridge. *Syst. Appl. Microbiol.* 12:249–56

Pledger RJ, Baross JA. 1991. Preliminary description and nutritional characterization of chemoorganotrophic archaeobacterium growing at temperatures of up to 110°C isolated from a submarine hydrothermal vent environment. *J. Gen. Microbiol.* 137:203–13

Pledger RJ, Crump B, Baross JA. 1994. A

barophilic response by two hyperthermophilic hydrothermal vent Archaea: acceleration of growth rate by supra-optimal temperature by elevated pressure. *FEMS Microbiol. Ecol.* 14:233–42

Pockalny RA, Detrick RS, Fox PJ. 1988. Morphology and tectonics of the Kane Transform from Sea Beam bathymetric data. *J. Geophys. Res.* 93:3179–94

Presnall DC, Dixon SA, Dixon JR, O'Donnell TH, Brebber NL, et al. 1978. Liquidus phase relations on the join diopside-forsterite-anorthite from 1 atm to 20 kbar: their bearing on the generation and crystallization of basaltic magmas. *Contrib. Mineral. Petrol.* 66:203–20

Pruis MJ, Johnson HP. 1996. Time-dependent porosity of very young upper oceanic crust from ocean bottom gravity measurements. *Eos Trans. Am. Geophys. Union* 77:706

Pruis MJ, Johnson HP. 1998. Porosity of very young oceanic crust from sea floor gravity measurements. *Geophys. Res. Lett.* 25:1959–62

Qian Y, Engel MH, Macko SA, Carpenter SD, Demin JW. 1993. Kinetics of peptide hydrolysis and amino acid stability at high temperature. *Geochim. Cosmochim. Acta* 57:3281–93

Reynolds TJ, Beane RE. 1985. Evolution of hydrothermal fluid characteristics at the Santa Rita, New Mexico, porphyry copper deposit. *Econ. Geol.* 80:1328–47

Reysenbach A-L, Cady SL. 2001. Microbiology of ancient and modern hydrothermal systems. *Trends Microbiol.* 9:79–86

Reysenbach A-L, Ehringer M, Hershberger K. 2000. Microbial diversity at 83°C in Calcite Springs, Yellowstone National Park: another environment where the Aquificales and "Korarchaeota" coexist. *Extremophiles* 4:61–67

Reysenbach A-L, Longnecker K, Kirshtein J. 2000. Novel bacterial and archaeal lineages from an in situ growth chamber deployed at a Mid-Atlantic Ridge vent. *Appl. Environ. Microbiol.* 66:3798–806

Richards HG, Cann JR. 1989. Mineralogical zonation and metasomatism of the alteration pipes of Cyprus sulfide deposits. *Econ. Geol.* 84:91–115

Rieley G, Van Dover CL, Hedrick DB, Eglinton G. 1999. Trophic ecology of *Rimicaris exoculata*: a combined lipid abundance stable isotope approach. *Mar. Biol.* 133:495–99

Robigou V, Delaney JR, Parker CB. 1995. Rapid growth of sulfide deposits in hydrothermal vent fields of the Endeavour Segment, Juan de Fuca Ridge. *Eos Trans. Am. Geophys. Union* 76:420

Robigou V, Delaney JR, Stakes D. 1993. The High-Rise hydrothermal vent field, Endeavour Segment, Juan de Fuca Ridge. *Geophys. Res. Lett.* 20:1887–90

Rona PA, Bostrom K, Laubier L, Smith KL Jr, eds. 1983. *Hydrothermal Processes at Seafloor Spreading Centers*. New York: Plenum. 796 pp.

Rona PA, Bougault H, Charlou JL, Appriou P, Nelsen TA, et al. 1992. Hydrothermal circulation, serpentinization, and degassing at a rift valley–fracture zone intersection: Mid-Atlantic Ridge near 15°N, 45°W. *Geology* 20:783–86

Rona PA, Hannington MD, Raman CV, Thompson G, Tivey MK, et al. 1993. Active and relict sea-floor hydrothermal mineralization at the TAG hyrothermal field, Mid-Atlantic Ridge. *Econ. Geol.* 88:1989–2017

Rona PA, Klinkhammer G, Nelsen TA, Trefry JH, Elderfield H. 1986. Black smokers, massive sulfides, and vent biota at the Mid-Atlantic Ridge. *Nature* 321:33–37

Rona PA, Thomson G, Mottl MJ, Karson JA, Jenkins WJ, et al. 1984. Hydrothermal activity at the TAG hydrothermal field, Mid-Atlantic Ridge crest at 26°N. *J. Geophys. Res.* 89:11365–77

Rona PA, Trivet DA. 1992. Discrete and diffuse heat transfer at AHSES vent field, Axial Volcano, Juan de Fuca Ridge. *Earth Planet. Sci. Lett.* 109:57–71

Rona PA, Widenfalk L, Boträm K. 1987. Serpentinized ultramafics and hydrothermal activity at the Mid-Atlantic Ridge crest near 15°N. *J. Geophys. Res.* 92:1417–27

Roy R, Mukund S, Schut G, Dunn DM, Weiss

R, Adams MWW. 1999. Purification and molecular characterization of a tungsten-containing formaldehyde ferrodixin oxidoreductase from the hyperthermnophilic archaeon *Pyrococcus furiosus*: the third of a putative five member tungstoenzyme family. *J. Bacteriol.* 181:1171–80

Rubin AM. 1995. Propagation of magma-filled cracks. *Annu. Rev. Earth Planet. Sci.* 23:287–336

Rubin AM, Pollard DD. 1988. Dike-induced faulting in rift zones of Iceland and afar. *Geology* 16:413–17

Russell MJ, Daia DE, Hall AJ. 1998. The emergence of life from FeS bubbles at alkaline hot springs in an acid ocean. See Wiegel & Adams 1998, pp. 77–126

Russel MJ, Daniel RM, Hall AJ, Sherringham J. 1994. A hydrothermally precipitated catalytic iron sulphide membrane as a first step toward life. *J. Mol. Evol.* 39:231–43

Russell MJ, Hall JA. 1996. The emergence of life from iron monosulfide bubbles at a submarine hydrothermal redox and pH front. *J. Geol. Soc.* 153:1–26

Ryan MP. 1987. Neutral buoyancy and the mechanical evolution of magmatic systems. See Mysen 1987, pp. 259–87

Ryan MP. 1994. Neutral-buoyancy controlled magma transport and storage in mid-ocean ridge magma reservoirs and their sheeted dike complex: a summary of basic relationships. In *Magmatic Systems*, ed MP Ryan, pp. 97–138. London: Academic. 401 pp.

Saccocia PJ, Gillis KM. 1995. Hydrothermal upflow zones in the oceanic crust. *Earth Planet. Sci. Lett.* 136:1–16

Sansone FJ, Resing JA, Tribble GW, Sedwick PN, Kelley KM, Hon K. 1991. Lava-seawater interactions at shallow-water submarine lava flows. *Geophys. Res. Lett.* 18:1731–34

Sansone FJ, Wen X, Holmes ME, Resing JA, Rust TM, et al. 1996. Dissolved gases in Loihi hydrothermal plumes following the 1996 seismic event. *Eos Trans. Am. Geophys. Union* 77:398

Sarrazin J, Juniper SK. 1999. Biological characteristics of a hydrothermal edifice mosaic community. *Mar. Ecol.* 185:1–19

Sarrazin J, Robigou V, Juniper SK, Delaney JR. 1997. Biological and geological dynamics over four years on a high-temperature sulfide structure at the Juan de Fuca Ridge hydrothermal observatory. *Mar. Ecol. Prog. Ser.* 153:5–24

Schidlowski M. 1988. A 3,800-million-year isotopic record of life from carbon in sedimentary rocks. *Nature* 333:313–18

Schneider ME, Eggler DH. 1986. Fluids in equilibrium with peridotite minerals. *Geochim. Cosmochim. Acta* 50:711–24

Schopf JW, Klein C. 1992. *The Proterozoic Biosphere: A Multidisciplinary Study*, ed. JW Schopf, C Klein. Cambridge: Cambridge Univ. Press. 1187 pp.

Schreiner AE, Fox CG, Dziak RP. 1995. Spectra and magnitudes of T-waves from the 1993 earthquake swarm on the Juan de Fuca Ridge. *Geophys. Res. Lett.* 222:139–42

Schrenk MO, Kaye JZ, Baross JA, Kelley DS, Delaney JR. 1998. Microbe-mineral associations in intact hydrothermal vent chimneys recovered from the Juan de Fuca Ridge. *Eos Trans. Am. Geophys. Union* 79:59

Schrenk MO, Kelley DS, Baross JA. 1999a. Microbial diversity in a 300°C black smoker chimney; relationships with thermal and geochemical gradients. *ASM Conf. Microbiol. Biodivers.*, Aug. 5–8. Chicago, IL

Schrenk MO, Kelley DS, Baross JA. 1999b. Attachment of hyperthermophilic microorganisms to mineral substrata; in-situ observations and subseafloor analogs. *Proc. Geol. Soc. Am.* 31:7

Schultz A, Delaney JR, McDuff RE. 1992. On the partitioning of heat flux between diffuse and point source seafloor venting. *J. Geophys. Res.* 97:12299–314

Schultz A, Elderfield H. 1997. Controls on the physics and chemistry of seafloor hydrothermal circulation. *Phils. Trans. R. Soc. London Ser. A* 355:387–425

Schwartzman D, McMenamin M, Volk T. 1993. Did surface temperatures constrain microbial evolution? *BioScience* 43:390–91

Seaman PG. 1998. *The development of ikaite in a fjord environment with special reference to Ikka Fjord*. PhD thesis. Imperial Coll. Sci. Technol. Med., Univ. London. 263 pp. Unpublished

Seyfried WE. 1987. Experimental and theoretical constraints on hydrothermal alteration processes at mid-ocean ridges. *Annu. Rev. Earth Planet.* 15:317–35

Seyfried WE, Berndt ME, Seewald JS. 1988. Hydrothermal alteration of the oceanic crust: constraints from diabase alteration experiments, hot-spring fluids and composition of the oceanic crust. *Can. Mineral.* 26:787–804

Seyfried WE Jr, Ding K. 1995. Phase equilibria in subseafloor hydrothermal systems: a review of the role of redox, temperature, pH and dissolved Cl on the chemistry of hot spring fluids at mid-ocean ridges. See Humphris et al. 1995, pp. 248–72

Shank TM, Fornari DJ, Von Damm KL, Lilley MD, Haymon RM, Lutz RA. 1998. Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents (9°50′N, East Pacific Rise). *Deep-Sea Res. II* 45:465–515

Shaw HR. 1980. The fracture mechanisms of magma transport from the mantle to the surface. In *Physics of Magmatic Processes*, ed. RB Hargraves, pp. 201–323. Princeton, NJ: Princeton Univ. Press. 585 pp.

Shillito B, Ravaux J, Gaill F, Delachambre J, Thiebaut E. 1999. Preliminary data on carbon production of deep-sea vent tubeworms. *Mar. Ecol. Prog. Ser.* 183:275–79

Shock EL. 1990. Geochemical constraints on the origin of organic compounds in hydrothermal systems. *Orig. Life Evol. Biosph.* 20: 331–67

Shock EL. 1992. Chemical environments of submarine hydrothermal systems. *Orig. Life Evol. Biosph.* 22:67–107

Shock EL. 1993. Hydrothermal dehydration of aqueous organic compounds. *Geochim. Cosmochim. Acta* 57:3341–49

Shock EL. 1996. Hydrothermal systems as environments for the emergence of life. *Evol. Hydrotherm. Syst. Earth Mars* 202:40–60

Shock EL, Schulte MD. 1998. Organic synthesis during fluid mixing in hydrothermal systems. *J. Geophys. Res.* 103:28513–27

Silver S. 1994. Exploiting heavy metal resistance systems in bioremediation. *Res. Microbiol.* 14:61–67

Simoneit BRT. 1993. Aqueous high-temperature and high-pressure organic geochemistry of hydrothermal vent systems. *Geochim. Cosmochim. Acta* 57:3231–43

Sinha MC, Navin DA, MacGregor LM, Constable S, Peirce C, et al. 1997. Evidence for accumulated melt beneath the slow-spreading Mid-Atlantic Ridge. *Philos. Trans. R. Soc. London Ser. A* 355:233–53

Sinton JM, Detrick RS. 1992. Mid-ocean ridge magma chambers. *J. Geophys. Res.* 97:197–216

Sleep NH, Zahnle KJ, Kasting JF, Morowitz HJ. 1989. Annihilation of ecocystems by large asteroid impacts on the early Earth. *Nature* 342:139–42

Slobodkin AB, Campbell B, Cary SC, Bonch-Osmolovskaya E, Jeanthon C. 2001. Evdidence for the presence of thermophilic Fe(III)-reducing microorganisms in deep-sea hydrothermal vents at 13°N (East Pacific Rise). *FEMS Microbiol. Ecol.* 36:235–43

Slobodkin AB, Wiegel J. 1997. Fe(III) as an electron acceptor for H_2 oxidation in thermophilic anaerobic enrichment cultures from geothermal areas. *Extremophiles* 1:106–9

Smith DK, Cann JR. 1990. Hundreds of small volcanoes on the median valley floor of the Mid-Atlantic Ridge at 24°–30°N. *Nature* 348:427–31

Smith DK, Cann JR. 1992. The role of seamount volcanism in crustal construction at the Mid-Atlantic Ride (24°–30°N). *J. Geophys. Res.* 97:1645–58

Smith DK, Tivey MA, Schouten H, Cann JR. 1999. Locating the spreading axis along 80 km of the Mid-Atlantic Ridge south of the Atlantis Transform. *J. Geophys. Res.* 104: 7599–612

Sobolev AV, Chaussidon M. 1996. H_2O concentrations in primary melts from supra-subduction zones and mid-ocean ridges:

implications for H_2O storage and recycling in the mantle. *Earth Planet. Sci. Lett.* 137:45–55

Sohn RA, Fornari DJ, Von Damm KL, Hildebrand JA, Webb SC. 1998. Seismic evidence and hydrothermal evidence for a cracking event on the East Pacific Rise crest at 9°50′N. *Nature* 396:159–61

Sorokin DY, Tourova TP, Kuenen JG. 2000. A new facultatively autotrophic hydrogen- and sulfur-oxidizing bacterium from an alkaline environment. *Extremophiles* 4:237–45

Sparks RSJ, Barclay J, Jaupart C, Mader HM, Phillips JC. 1994. Physical aspects of magma degassing. I. Experimental and theoretical constrains on vesiculation. See Carroll & Holloway 1994, pp. 413–45

Sparks DW, Parmentier EM. 1994. The generation and migration of partial melt beneath oceanic spreading centers. See Ryan 1994, pp. 55–76

Sparks RSJ, Meyer P, Sigurdsson H. 1980. Density variation amongst mid-ocean ridge basalts: implications for magma mixing and the scarcity of primitive lavas. *Earth Planet. Sci. Lett.* 46:419–30

Stakes D, Mével C, Cannat M, Chaput T. 1991. Metamorphic stratigraphy of Hole 735B. *Proc. Ocean Drill. Program Sci. Results* 118: 153–80

Stakes DS, Shervais JW, Hopson CA. 1984. The volcano-tectonic cycle of the FAMOUS and AMAR valleys, Mid-Atlantic Ridge (36°N): evidence from basalt glass and phenocryst variations for a steady-state magma chamber beneath the valley mid-sections, AMAR 3. *J. Geophys. Res.* 89:6995–7028

Stetter KO. 1996. Hyperthermophilic procaryotes. *FEMS Microbiol. Rev.* 18:149–58

Stetter KO. 1999. Extremophiles and their adaptation to hot environments. *FEBS Lett.* 452:22–25

Stetter KO, Fiala G, Huber G, Huber R, Segerea A. 1990. Hyperthermophilic microorganisms. *FEMS Microbiol. Rev.* 75:117–24

Stevens TO, McKinley JP. 1995. Lithotrophic microbial ecosystems in deep basalt aquifers. *Science* 270:450–53

Stolper E, Holloway JR. 1988. Experimental determination of the solubility of carbon dioxide in molten basalt at low pressure. *Earth Planet. Sci. Lett.* 87:397–408

Streams ME, Fisher CR, Fiala-Mèdioni A. 1997. Methanotrophic symbiont location and fate of carbon incorporated from methane in a hydrocarbon seep mussel. *Mar. Biol.* 129:465–76

Summit M. 2000. *Ecology, physiology, and phylogeny of subseafloor thermophiles from mid-ocean edge environments*. pp. 1–95. PhD diss. Univ. Washington, Seattle

Summit M, Baross JA. 1998. Thermophilic subseafloor microorganisms from the 1996 North Gorda Ridge eruption. *Deep-Sea Res. II* 45:2751–66

Summit M, Baross JA. 2001. A novel microbial habitat in the mid-ocean ridge subsurface. *Proc. Natl. Acad. Sci. USA* 98:2158–63

Summit M, Peacock A, Ringelberg D, White DC, Baross JA. 2000. Phospholipid fatty acid-derived microbial biomass and community dynamics in hot, hydrothermally influenced sediments from Middle Valley, Juan de Fuca Ridge. *Proc. Ocean Drill. Program Sci. Results* 169:1–19. http://www.odp.tamu.edu/publications/169_SR/VOLUME/CHAPTERS/SR169_03.PDF

Summit M, Scott B, Nielson K, Mathur E, Baross J. 1998. Pressure enhances thermal stability of DNA polymerase from three thermophilic organisms. *Extremophiles* 2:339–45

Takai K, Horikoshi K. 1999. Genetic diversity of archaea in deep-sea hydrothermal vent environments. *Genetics* 152:1285–97

Takai K, Komatsu T, Inagaki F, Horikoshi K. 2001. Distribution of Archaea in a black smoker chimney structure. *Appl. Environ. Microbiol.* 67:3618–29

Takai K, Sako Y. 1999. A molecular view of archaeal diversity in marine and terrestrial hot water environments. *FEMS Microbiol. Ecol.* 28:177–88

Takai K, Sugai A, Itoh T, Horikoshi K. 2000. *Palaeococcus ferrophilus* gen. Nov., sp.

Nov., a barophilic, hyperthermophilic archaeon from a deep-sea hydrothermal vent chimney. *Int. J. Syst. Evol. Microbiol.* 50: 489–500

Taylor CD, Wirsen CO. 1997. Microbiology and ecology of filamentous sulfur formation. *Science* 277:1483–85

Taylor WR, Green DH. 1987. The petrogenetic role of methane: effect on liquidus phase relations and the solubility mechanism of reduced C-H volatiles. See Mysen 1987, pp. 121–54

Taylor WR, Green DH. 1988. Measurement of reduced peridotite C-O-H solidus and implications for redox melting of the mantle. *Nature* 332:349–52

Tebo BM. 1995. Metal precipitation by marine bacteria: potential for biotechnical applications. *Gen. Eng.* 17:231–63

Thompson G. 1983. Basalt-seawater interaction. See Rona et al. 1983, pp. 225–78

Thompson G, Humphris SE, Schroeder B, Sulanawska M, Rona PA. 1988. Active vents and massive sulfides at 26°N (TAG) and 23°N (Snakepit) on the Mid-Atlantic Ridge. *Can. Mineral.* 26:697–711

Thompson G, Mottl MJ, Rona PA. 1985. Morphology, mineralogy, and chemistry of hydrothermal deposits from the TAG area, 26°N Mid-Atlantic Ridge. *Chem. Geol.* 49:243–57

Tivey MA, Rona PA, Kleinrock MC. 1996. Reduced crustal magnetization beneath relict hydrothermal mounds: TAG hydrothermal field, Mid-Atlantic Ridge, 26°N. *Geophys. Res. Lett.* 23:3511–14

Tivey MK. 1995a. The influence of hydrothermal fluid composition and advection rates on black smoker chimney mineralogy: insights from modeling transport and reaction. *Geochim. Cosmochim. Acta* 59:1933–49

Tivey MK. 1995b. Modeling chimney growth and associated fluid flow at seafloor hydrothermal vent sites. See Humphris et al. 1995, pp. 158–77

Tivey MK, Delaney JR. 1986. Growth of large sulfide structures on the Endeavour Segment of the Juan de Fuca Ridge. *Earth Planet. Sci. Lett.* 77:303–17

Tivey MK, Humphris SE, Thompson G. 1995. Deducing patterns of fluid flow and mixing within the TAG active hydrothermal mound using mineralogical and geochemical data. *J. Geophys. Res.* 100:12527–55

Tivey MK, Mills RA, Teagle DAH. 1998. Temperature and salinity of fluid inclusions in anhydrite as indicators of seawater entrainment and heating in the TAG hydrothermal mound. *Proc. Ocean Drill. Program Sci. Results* 158:179–90

Tivey MK, Stakes DS, Cook TL, Hannington MD, Petersen S. 1999. A model for growth of steep-sided vent structures on the Endeavour Segment of the Juan de Fuca Ridge: results of a petrologic and geochemical study. *J. Geophys. Res.* 104:22859–83

Toomey DR, Purdy GM, Solomon S, Wilcock WSD. 1990. The three-dimensional seismic velocity structure of the East Pacific Rise near latitude 9°30N. *Nature* 347:639–44

Toomey DR, Solomon SC, Purdy GM. 1994. Tomographic imaging of the shallow crustal structure of the East Pacific Rise at 9°30′N. *J. Geophys. Res.* 99:24135–57

Torsvik T, Furnes H, Muehlenbachs K, Thorseth IH, Tumyr O. 1998. Evidence for microbial activity at the glass-alteration interface in oceanic basalts. *Earth Planet. Sci. Lett.* 162:165–76

Treves B, Harper GD. 1994. Exposure of serpentinites on the ocean floor: sequence of faulting and hydrofracturing in the northern Apennine ophicalcites. *Ofioliti* 19:435–66

Tunnicliffe V. 1988. Biogeography and evolution of hydrothermal vent fauna in the eastern Pacific Ocean. *Proc. R. Soc. London Ser. B* 233:347–66

Tunnicliffe V, Garrett F, Johnson HP. 1990. Physical and biological factors affecting the behavior and mortality of hydrothermal vent tubeworms (vestimentiferans). *Deep-Sea Res.* 37:103–25

Tunnicliffe V, Embley RW, Holden JF, Butterfield DA, Massoth GJ, et al. 1997. Biological colonization of new hydrothermal vents following an eruption on the Juan de Fuca Ridge. *Deep-Sea Res.* 44:1627–44

Tunnicliffe V, McArthur AG, McHugh D. 1998. A biogeographical perspective of the deep-sea hydrothermal vent fauna. *Adv. Mar. Biol.* 34:353–442

Turner RD, Lutz RA. 1984. Growth and distribution of mollusks at deep-sea vents and seeps. *Oceanus* 27:55–62

Tuttle JH. 1985. The role of sulfur-oxidizing bacteria at deep-sea hydrothermal vents. *Biol. Soc. Wash. Bull.* 6:335–43

Uhl AM, Daniel RM. 1999. The first description of an archaeal hemicellulase: the xylanase from *Thermocuccus zilligii* strain AN1. *Extremophile* 3:263–67

Van Dover CL. 2000. *The Ecology of Deep-Sea Hydrothermal Vents*. Princeton, NJ: Princeton Univ. Press. 424 pp.

Van Dover CL, Fry B. 1994. Microorganisms as food resources at deep sea hydrothermal vents. *Limnol. Oceanogr.* 39:51–7

Van Dover CL, Humphris SE, Fornari D, Cavanaugh CM, Collier R, et al. 2001. Biogeography and ecology setting of Indian Ocean hydrothermal vents. *Science.* 294:818–23

Van Dover CL, Szuts EZ, Chamberlain SC, Cann JR. 1989. A novel eye in "eyeless" shrimp from hydrothermal vents of the Mid-Atlantic Ridge. *Nature* 337:458–60

van Everdingen DA. 1995. Fracture characteristics of the sheeted dike complex, Troodos ophiolite, Cyprus: implications for permeability of oceanic crust. *J. Geophys. Res.* 100:19957–72

Vanko DA. 1988. Temperature, pressure, and composition of hydrothermal fluids, with their bearing on the magnitude of tectonic uplift at mid-ocean ridges, inferred from fluid inclusions in oceanic layer 3 rocks. *J. Geophys. Res.* 93:4595–611

Vanko DA, Griffith JD, Erickson CL. 1992. Calcium-rich brines and other hydrothermal fluids in fluid inclusions from plutonic rocks, Oceanographer Transform, Mid-Atlantic Ridge. *Geochim. Cosmochim. Acta* 56:35–47

Vanko DA, Stakes DS. 1991. Fluids in oceanic layer 3: evidence from veined rocks, Hole 735B, Southwest Indian Ridge Metamorphic stratigraphy of Hole 735B. *Proc. Ocean Drill. Program Sci. Results* 118:181–215

Veirs SR, McDuff RE, Lilley MD, Delaney JR. 1999. Locating hydrothermal vents by detecting buoyant, advected plumes. *J. Geophys. Res.* 104:29239–47

Voight JR. 2000. A review of predators and predation at deep-sea hydrothermal vents. *Cah. Biol. Mar.* 41:155–66

Völkl P, Huber R, Brobner E, Rachel R, Burggraf S, et al. 1993. *Pyrobaculum aerophilum* sp. nov., a novel nitrate-reducing hyperthermophilic archaeum. *Appl. Environ. Microbiol.* 59:2918–26

Von Damm KL. 1990. Seafloor hydrothermal activity: black smoker chemistry and chimneys. *Annu. Rev. Earth Planet. Sci.* 18:173–204

Von Damm KL. 1995. Controls on the chemistry and temporal variability of seafloor hydrothermal fluids. See Humphris et al. 1995, pp. 222–47

Von Damm KL. 2000. Chemistry of hydrothermal vent fluids from 9°–10°N, East Pacific Rise: "time zero," the immediate posteruptive period. *J. Geophys. Res.* 105:11203–22

Von Damm KL, Buttermore LG, Oosting SE, Bray AM, Fornari DJ, et al. 1997. Direct observation of the evolution of a seafloor "black smoker" from vapor to brine. *Earth Planet. Sci. Lett.* 149:101–11

Von Damm KL, Colodner DC, Edmonds J. 1992. Hydrothermal fluid chemistry at 9–10°N EPR: big changes and still changing. *Eos Trans. Am. Geophys. Union.* 73:524

Von Damm KL, Grebmeier JM, Edmond JM. 1991. Preliminary chemistry of hydrothermal vent fluids from 9–10°N East Pacific Rise. *Eos Trans. Am. Geophys. Union* 72:481

Wächtershäuser G. 1988. Before enzymes and templates: theory of surface metabolism. *Microbiol. Rev.* 52:452–84

Wächtershäuser G. 1998. The case for a hyperthermophilic, chemolithoautotrophic origin of life in an iron-sulfur world. See Wiegel & Adams 1998, pp. 47–58

Welhan JA. 1988. Origins of methane in hydrothermal systems. *Chem. Geol.* 71:183–98

Welhan JA, Craig H. 1983. Methane, hydrogen, and helium in hydrothermal fluids of 21°N on the East Pacific Rise. See Rona et al. 1983, pp. 391–409

Wetzel LR, Shock EL. 2000. Distinguishing ultramafic from basalt-hosted submarine hydrothermal systems by comparing calculated vent fluid compositions. *J. Geophys. Res.* 105:8319–40

Wheat CG, Mottl MJ. 1994. Hydrothermal cirulation, Juan de Fuca Ridge eastern flank: factors controlling basement water composition. *J. Geophys. Res.* 99:3067–80

Wheat CG, Mottl MJ. 2000. Composition of pore and spring waters from Baby Bare: global implications of geochemical fluxes from a ridge flank hydrothermal system. *Geochim. Cosmochim. Acta* 64:629–42

White SM, Macdonald KC, Haymon RM. 2000. Basaltic lava domes, lava lakes, and volcanic segmentation on the southern East Pacific Rise. *J. Geophys. Res.* 105:23519–36

Wiegel J, Adams MWW, eds. 1998. *Thermophiles: The Keys to Molecular Evolution and the Origin of Life*? London: Taylor & Francis

Wilcock WSD. 1997. A model for the formation of transient event plumes above mid-ocean ridge hydrothermal systems. *J. Geophys. Res.* 102:12109–21

Wilcock WSD, Archer SD, Purdy G. 2002. Microearthquakes on the Endeavour segment of the Juan de Fuca Ridge. *J. Geophys. Res.* In Press

Wilcock WSD, Delaney JR. 1996. Mid-ocean ridge sulfide deposits: evidence for heat extraction from magma chambers or cracking fronts? *Earth Planet. Sci. Lett.* 145:49–64

Winn CD, Cowen JP, Karl DM. 1995. Microbes in deep-sea hydrothermal plumes. See Karl 1995, pp. 255–73

Winn CD, Karl DM, Massoth GJ. 1986. Microorganisms in deep-sea hydrothermal plumes. *Nature* 320:744–46

Wirsen CO, Brinkhoff T, Kuever J, Muyzer G, Molyneaux S, et al. 1998. Comparison of a new *Thiomicrospira* strain from the Mid-Atlantic Ridge with known hydrothermal vent isolates. *Appl. Environ. Microbiol.* 64: 4057–59

Wirsen CO, Jannasch HW, Molyneaux SJ. 1993. Chemosynthetic microbial activity at Mid-Atlantic Ridge hydrothermal vent sites. *J. Geophy. Res.* 98:9693–703

Woese CR. 1998. The universal ancestor. *Proc. Natl. Acad. Sci. USA* 95:6854–59

Woese CR, Kandler O, Wheelis ML. 1990. Towards a natural system of organisms: proposals for the Domains Archaea, Bacteria, and Eukarya. *Proc. Natl. Acad. Sci. USA* 87: 4576–79

Wood BJ, Byrndzia T, Johnson KE. 1990. Mantle oxidation state and its relationship to tectonic environment and fluid speciation. *Science* 238:337–45

Woods AW, Delaney JR. 1992. The heat and fluid transfer associated with the flanges on hydrothermal venting structures. *Earth Planet. Sci. Lett.* 112:117–29

Wright DJ, Haymon RM, Fornari DJ. 1995. Crustal fissuring and its relationship to magmatic and hydrothermal processes on the East Pacific Rise crest (9°12′ to 54′N). *J. Geophys. Res.* 100:6097–120

Wyllie PJ, Ryabchikov ID. 2000. Volatile components, magmas, and critical fluids in upwelling mantle. *J. Petrol.* 41:1195–206

Yoder HS Jr. 1979. *The Evolution of the Igneous Rocks: Fiftieth Anniversary Perspectives*. Princeton, NJ: Princeton Univ. Press. 588 pp.

Yoder HS Jr, Tilley CE. 1962. Origin of basalt magmas: an experimental study of natural and synthetic rock systems. *J. Petrol.* 3:342–532

Zhang Y, Zindler A. 1993. Distribution and evolution of carbon and nitrogen in Earth. *Earth Planet. Sci. Lett.* 117:331–45

Zierenberg RA, Schiffman P. 1990. Microbial control of silver mineralization at a seafloor hydrothermal site on the northern Gorda Ridge. *Nature* 348:155–57

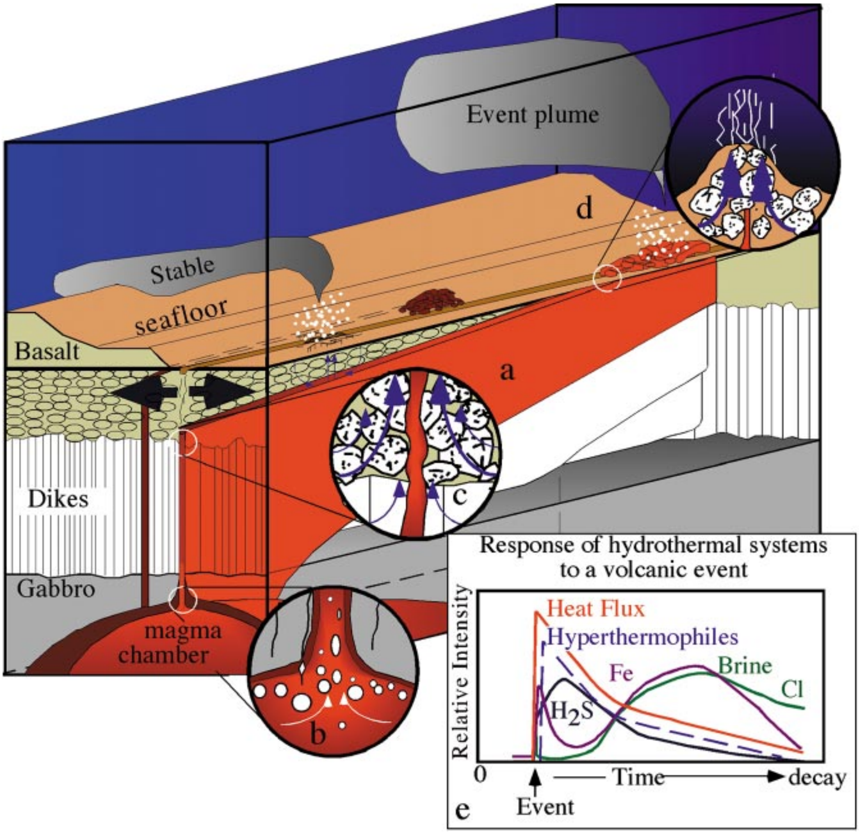

Figure 7 Schematic model for geological and geochemical processes impacted by a diking-eruptive event. (*a*) During a diking event, melt-filled fractures, commonly 1–1.5-m wide, propagate for several kilometers along axis. If the dike breaches the seafloor, a submarine eruption ensues. (*b*) All mid-ocean ridge magma chambers are saturated with carbon dioxide, which forms small bubbles near the top of the chamber. Expulsion of these gases helps to drive volcanic eruptions. (*c*) Injection of 1200°C melt may cause super heating of pore fluids in surrounding basaltic host rocks. Fluids are rapidly expelled into the overlying water column, entraining microbial material from beneath the seafloor. (*d*) Fluids rapidly circulate and cool the new flow. Volatiles dissolved in the fluids support microorganisms, resulting in microbial blooms for several months following an eruption. (*e*) The response of hydrothermal venting to a diking-eruptive event is shown (after Butterfield 1997).

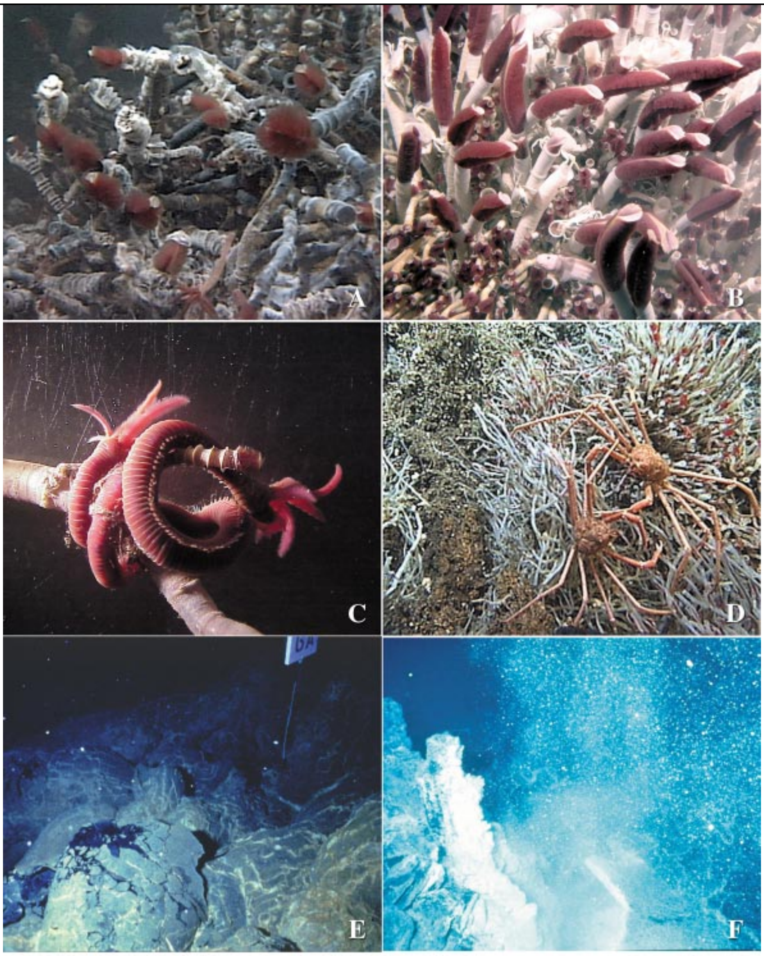

Figure 9 (*a*) Cluster of the vestimentiferan tube worm *Ridgeia piscesae* from the Mothra vent field on the Juan de Fuca Ridge, North East Pacific. These animals harbor sulfur oxidizing bacterial endosymbionts in a specialized organ. Tube diameters are typically less than 1 cm. (*b*) A dense cluster of the vestmentiferan tube worm *Riftia pachyptila* from the East Pacific Rise at 9°N. The diameter of the tubes are 2–3 cm. Also shown are small galetheid crabs (courtesy of T. Shank, Woods Hole Oceanographic Institution). (*c*) The palm worm, *Paralvinella palmiformis*, from Endeavour system on the Juan de Fuca Ridge, North East Pacific. The worms are wrapped around *Ridgeia piscesae*. *P. palmiformis* are typically 5–6 cm in length. (*d*) Deep-sea spider crabs, *Macroregonia macrochira*, basking on a bed of *Ridgeia piscesae* from Endeavour vent field on the Juan de Fuca Ridge, North East Pacific. (*e*) Microbial mats (*white material*) on fresh basalt from the CoAxial 1993 eruption, Juan de Fuca Ridge. (*f*) Microbial floc material, sometimes referred to as snow storms, emitted from the subsurface following a diking-eruption event at 9°N, East Pacific Rise (after Haymon et al. 1993). The floc material contains elemental sulfur, iron oxides and microorganisms.

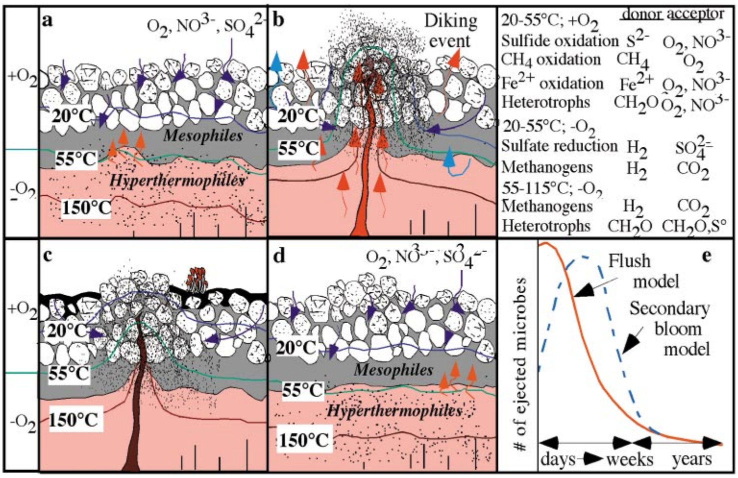

Figure 10 Model of microbial responses to submarine diking-eruptive events. (*a*) Hypothetical isotherms and the location of stable zones conducive to the growth of mesophiles and hyperthermophiles pre-eruption. (*b*) Dike injection induces very strong chemical and temperature gradients, resulting in transient high heat fluxes and intense periods of circulation. Deep fluids flushed out of the system carry microbes from all thermal zones into the water column. (*c*) As the system cools, volatiles and other sources of energy extracted from the fresh rock feed microbial populations in both shallow, aerobic habitats and deeper, anaerobic habitats. Possible reactions, metabolic processes, and electron donors and acceptors are shown in the far right panel. Organisms from all thermal zones are carried out of the system via fluid circulation. (*d*) Cooling of the dike removes the perturbation and the system returns to initial conditions. (*e*) The initial ejection of subseafloor microorganisms and subsequent bloom and decay versus time (after Delaney et al. 1998).

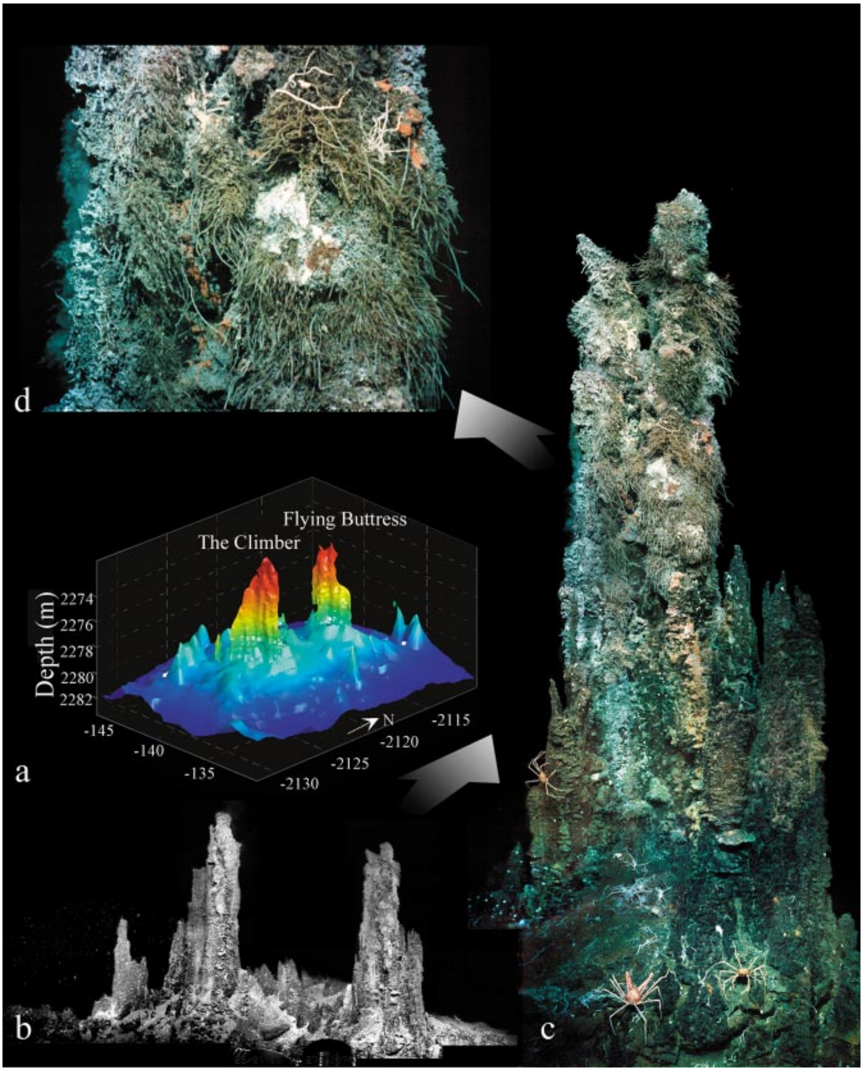

Figure 12 The Faulty Towers sulfide complex in the Mothra Hydrothermal Field, Endeavour Segment, Juan de Fuca Ridge. (*a*) Detailed bathymetry of the complex collected using a high-resolution sonar package on the remotely operated vehicle Jason. (*b*) The towers are actively venting ~200°C fluids, and are surrounded by smaller extinct pinnacles. Images for this photomosaic were collected with an electronic still camera that took digital still images very 15 seconds, coregistered with sonar data. (*c*) Close up of the actively venting sulfide edifice "Flying Buttress," which stands ~8 meters above the surrounding seafloor. (*d*) Close-up of dense clusters of *Ridgeia piscesae* on Flying Buttress and white mats composed of dense assemblages of microorganisms that oxidize H_2S.

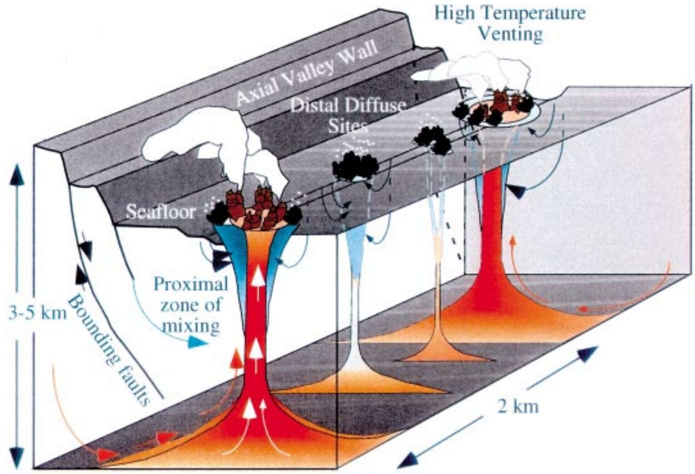

Figure 15 Schematic of high-temperature upflow zones, proximal low-temperature sites of diffuse venting, and distal low-temperature diffuse sites not associated with black smoker activity parallel to a spreading axis. A system such as this may be operative along the Endeavour Segment. A major question in submarine research is what the flow distribution is at depth, as this will govern chemical-thermal gradients and microbial habitats in subseafloor environments.

Annual Review of Earth and Planetary Sciences
Volume 30, 2002

CONTENTS

INDEXES

ERRATA

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