interesting because it contains fossils of vestimentiferan worms, gastropods and brachiopods, but no clam or mussel fossils. In contrast, modern and Paleozoic faunal assemblages described thus far include clams, mussels and gastropods, but no brachiopods. Does this mean that brachiopods have competed with molluscs for ecological niches at vents, and have moved in and out of the hydrothermal vent environment over time? Fossilization of organisms is a selective process that does not preserve all the fauna that are present at vents. Identification of fossils at the species level is often difficult, especially where microbes are concerned. Notwithstanding, it is important to search for more examples of ancient fossil assemblages and to trace the fossil record of life at hydrothermal vents back as far as possible to shed light on how vent communities have evolved, and whether life on earth might have originated at submarine hydrothermal vents.

Summary

Formation of hydrothermal deposits is an integral aspect of seafloor accretion at mid-ocean ridges. These deposits are valuable for their metals, for the role that they play in fostering hydrothermal vent ecosystems, for the clues that they hold to understanding spatial–temporal variability in hydrothermal vent systems, and as geologic records of how life at hydrothermal vents has evolved. From these deposits we may gain insights about biogeochemical processes at high temperatures and pressures that can be applied to understanding life in inaccessible realms within the earth's crust or on other planetary bodies. We are only beginning to unravel the complexities of ridge hydrothermal vent deposits. Much exploration and interdisciplinary study remains to be done to obtain the valuable information that they contain.

See also

Deep-sea Ridges, Microbiology. Hydrothermal Vent Fluids, Chemistry of. Hydrothermal Vent Biota. Hydrothermal Vent Fauna, Physiology of. Mid-ocean Ridge Geochemistry and Petrology. Mid-ocean Ridge Seismic Structure. Propagating Rifts and Microplates. Seamounts and Off-ridge Volcanism.

Further Reading

Dilek Y, Moores E, Elthon D and Nicolas A (eds) (2000) *Ophiolites and Oceanic Crust: New Insights from Field Studies and the Ocean Drilling Program. Geological Society of America Memoir*. Boulder: Geological Society of America.

Haymon RM (1989) Hydrothermal processes and products on the Galapagos Rift and East Pacific Rise, 1989. In: Winterer EL, Hussong DM and Decker RW (eds) *The Geology of North America: The Eastern Pacific Ocean and Hawaii*, vol. N, pp. 125–144. Boulder: Geological Society of America.

Haymon RM (1996) The response of ridge crest hydrothermal systems to segmented, episodic magma supply. In: MacLeod CJ, Tyler P and Walker CL (eds) *Tectonic, Magmatic, Hydrothermal, and Biological Segmentation of Mid-Ocean Ridges*, Special Publication 118, pp. 157–168. London: Geological Society.

Humphris SE, Zierenberg RA, Mullineaux LS and Thomson RE (eds) (1995) *Seafloor Hydrothermal Systems: Physical, Chemical, Biological, and Geological Interactions, Geophysical Monograph* 91. Washington, DC: American Geophysical Union.

Little CTS, Herrington RJ, Haymon RM and Danelian T (1999) Early Jurassic hydrothermal vent community from the Franciscan Complex, San Rafael Mountains, California. *Geology* 27: 167–170.

Tivey MK, Stakes DS, Cook TL, Hannington MD and 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 petrological and geochemical study. *Journal of Geophysical Research* 104: 22 859–22 883.

HYDROTHERMAL VENT ECOLOGY

C. L. Van Dover, The College of William and Mary, Williamsburg, Virginia, USA

doi:10.1006/rwos.2001.0104

Introduction

Most of the ocean floor is covered with a thick layer of sediment and is populated by sparse and minute, mud-dwelling and mud-consuming invertebrates. In striking contrast, the volcanic basalt pavement of mid-ocean ridges hosts hydrothermal vents and their attendant lush communities of large invertebrates that ultimately rely on inorganic chemicals for their nutrition. Vents themselves are sustained by tectonic forces that fracture the basalt and allow sea water to penetrate deep within the ocean crust, and by volcanism, which generates the hot rock at depth that strips sea water of oxygen and magnesium. The hot rock gives up to the nascent vent fluid a variety of metals, especially copper, iron, and zinc, as well as reduced compounds such as hydrogen sulfide and methane. The vent fluid, thermally buoyant, rises to exit as hot springs on the seafloor.

Discovered first by geologists in 1977 along a stretch of mountain range known as the Galapagos Rift, near the equator in the eastern Pacific Ocean, hydrothermal vents are now known to occur along every major ridge system on the planet. Several of these ridge systems – in the Arctic and Antarctic, in the Indian Ocean, in the southern Atlantic – are only just beginning to be explored. Regional species composition of the vent fauna differs between ocean basins and, sometimes, even within a basin. Most of the species that occur at vents have never been found in the adjacent, nonvent deep sea and are considered to be endemic, adapted to the chemical milieu of the vent environment. Reduced compounds carried in hydrothermal fluids, together with oxygen from the surrounding sea water, fuel the microbial fixation of inorganic carbon into organic carbon that forms the chemosynthetic base of the vent food web.

Hydrothermal vents on midocean ridges are thus globally distributed, insular ecosystems that support endemic faunas through chemosynthetic processes rather than through photosynthesis. They are effectively decoupled by depth (typically $> 1000\,\mathrm{m}$) from climatic variations and anthropogenic activities, but are tightly coupled to geophysical processes of tectonism and volcanism. Vents thus offer unique opportunities for biologists to study adaptations that allow life to persist in this extreme environment and to explore planetary controls on biodiversity and biogeography along submarine, hydrothermal 'archipelagoes', where propagules are water-borne and subject to dispersal in an open system. Further, because vents are thought to have been a primordial component of the oceans and because there is increasing speculation that early life on this planet may have thrived in hot environments and on chemicals rather than on an organic soup for nourishment, extant hydrothermal systems are thought by many to be analogues for sites where early life may have evolved on this and other planets or planetary bodies in our solar system.

Microorganisms and the Chemosynthetic Basis for Life at Vents

The terms 'chemosynthesis' and 'photosynthesis' are imprecise. While a voluminous nomenclature is available to differentiate among variations in these processes, for simplicity, chemosynthesis and photosynthesis are used here.

In photosynthesis, sunlight captured by proteins provides energy for the conversion of inorganic carbon (carbon dioxide, CO_2) and water (H_2O) into organic carbon (carbohydrates, $[CH_2O]$ and oxygen (O_2) (eqn [1]).

$$CO_2 + H_2O \xrightarrow{\text{light}} [CH_2O] + O_2 \qquad [1]$$

Photosynthesis by plants is the basis for consumer and degradative food webs both on land and, as a rain of organic detritus derived from surface phytoplankton productivity, on the seabed. In the deep sea, detrital inputs of organic carbon are exceedingly small, accounting for the paucity of consumer biomass in abyssal muds. At hydrothermal vents, the supply of surface-derived organic material is overwhelmed by the supply of new organic carbon generated through chemical oxidation of hydrogen sulfide (H_2S) (eqn [2]).

$$CO_2 + H_2O + H_2S + O_2 \rightarrow [CH_2O] + H_2SO_4 \qquad [2]$$

Metabolic fixation pathways for carbon can be identical in photosynthetic plants and chemosynthetic microorganisms, namely the Calvin–Benson cycle, but the energy-yielding processes that fuel the Calvin–Benson cycle (photon capture versus chemical oxidation) are distinctive. High biomass at hydrothermal vents is in part a consequence of the aerobic nature of the process described in eqn [2]. Oxygen is used to oxidize the hydrogen sulfide, generating a large energy yield that in turn can fuel the production of large amounts of organic carbon (**Figure 1**). Nonaerobic chemical reactions, such as oxidation of vent-supplied hydrogen (H_2) by carbon dioxide (CO_2), can also support chemosynthesis at vents, but energy yields under such anaerobic conditions are much lower than from aerobic oxidation. Microorganisms using these anaerobic reactions cannot by themselves support complex food webs and large invertebrates.

Symbiosis and the Host–Symbiont Relationship

One of the hallmarks of many hydrothermal vent communities is the dominance of the biomass by invertebrate species that host chemosynthetic microorganisms within their tissues. Giant, red-plumed, vestimentiferan tubeworms (*Riftia pachyptila*; **Figure 2**) so far provide the ultimate in host accommo-

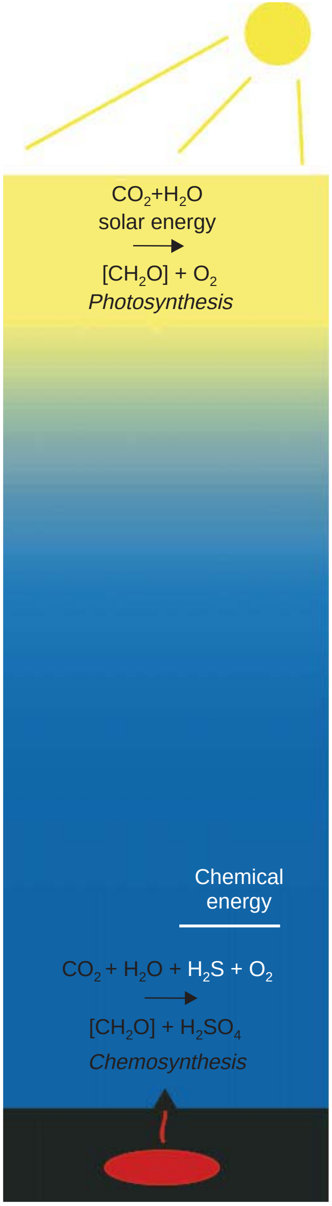

Figure 1 Photosynthetic and chemosynthetic processes in the ocean. Sunlight fuels the generation of organic material (CH_2O) from inorganic carbon dioxide (CO_2) and water (H_2O) by phytoplankton in surface, illuminated waters. At depths where hydrothermal vents exist (typically > 2000 m), no sunlight penetrates. In place of sunlight, the chemical oxidation of sulfide (H_2S) by oxygen (O_2) fuels the conversion of carbon dioxide to organic carbon by chemosynthetic bacteria.

dation of endosymbiotic bacteria. These worms live in white, chitinous tubes, with their plumes extended into the zone of turbulent mixing of warm (~ 20°C), sulfide-rich, hydrothermal fluid and cold (2°C), oxygenated sea water. When discovered in 1977, vestimentiferan tubeworms were remarkable for their size (up to several meters in length) and the complete absence of a digestive system in adults. In fact, the digestive system has been replaced by the trophosome, which is a specialized, paired organ derived from the larval gut. The trophosome is richly infiltrated with blood capillaries and each of its lobes lies within a blood-filled body cavity. The blood itself is rich in hemoglobin. Host bacteriocyte cells in the trophosome house chemosynthetic bacteria that use hydrogen sulfide and oxygen to fuel the production of organic carbon, as described above.

The metabolic requirements of the tubeworm endosymbiotic bacteria place some remarkable burdens on the host. First, there is a novel requirement for delivery of sulfide to the bacteria, which reside at a location remote from the site of gas exchange (the plume). Sulfide is normally a potent toxin to animals, poisoning the cellular enzyme system that generates ATP (adenosine triphosphate), the currency of metabolism. Sulfide also competes with oxygen for binding sites on hemoglobin. Tubeworm hemoglobin has separate binding sites for oxygen and sulfide, so that both can be transported throughout the worm in the circulatory system without competition. When bound to hemoglobin, the

Figure 2 The giant tubeworm *Riftia pachyptila*. The red plume of the tubeworm acts as a gill for uptake of dissolved gases. The trunk of the worm is found inside the white, chitinous tube. (Photograph by Dudley Foster, Woods Hole Oceanographic Institution.)

Figure 3 Swarming shrimp (*Rimicaris exoculata*) at a hydrothermal vent on the Mid-Atlantic Ridge. (Photograph by C.L. Van Dover.)

sulfide is not reactive and so enzyme systems remain unchallenged. Once delivered to the bacteria in the trophosome, the sulfide is quickly oxidized and loses its toxic potential.

Novel requirements for carbon dioxide are also found in tubeworms. The usual flow of CO_2 is out of an animal, as the end-product of metabolism, but the resident bacteria of the trophosome require a net uptake of CO_2. Maintenance of high concentrations of inorganic carbon in the blood of the tubeworm is facilitated by the high partial pressure of CO_2 in the water surrounding the site of uptake (the plume) and by the alkaline internal pH of the blood (7.3–7.4), which favors the bicarbonate form (HCO_3^-) of carbon dioxide and thus maintains a steep concentration gradient for diffusion of CO_2 from the environment into the blood.

As described above, the anatomy of the tubeworm is well adapted for life in sulfide- and CO_2-rich vent fluids and for supporting its endosymbiotic, chemosynthetic bacteria. The bacteria provide nearly all of the nutrition for the host, with the exception, perhaps, of small amounts of dissolved organic materials taken up across the tissues of the plume. In turn, the bacteria are provided with a chemically rich and stable environment for growth.

Other large invertebrates at vents also derive much of their nutrition from endosymbiotic, chemosynthetic bacteria, including the 20 to 30-cm long vesicomyid clams and bathymodiolid mussels. While vent mussels have a fairly normal digestive system and are capable of filter-feeding just as shallow-water mussels do, vent clams lack a functional digestive system. Both types of bivalves have enlarged gills and it is within these gills that the endosymbiotic bacteria are found. Clams are thought to take up hydrogen sulfide via their highly vascularized foot, with which they probe cracks in the basalt where vent fluids emanate.

Not all chemosynthetic bacteria that nourish vent invertebrates are endosymbiotic. Shrimp that dominate vents in the Atlantic (**Figure 3**) host chemosynthetic bacteria on their carapace (i.e., the bacteria are episymbiotic) and seem to depend on these bacteria for a significant portion of their diet. Other chemosynthetic bacteria are free-living, suspended in the water column, providing nourishment to suspension-feeding invertebrates such as barnacles, or grow as mats or films on surfaces, where grazers such as limpets and polychaetes forage. Heterotrophic bacteria (using organic rather than inorganic compounds) may also be important for consumers within the vent invertebrate food web, but this has yet to be examined carefully.

Thermal Adaptations

While hydrothermal vent communities live at temperatures slightly elevated above ambient sea water temperature, the existence of highly productive communities at vents is a consequence of fluid chemistry rather than thermal input. Nevertheless, there are some invertebrates, notably the large, thumb-sized polychaetes in the family Alvinellidae (**Figure 4**), that are especially tolerant of high tem-

Figure 4 The alvinellid polychaete *Alvinella caudata*, beside its fragile tube. (Photograph by J. Porteous, Woods Hole Oceanographic Institution.)

peratures and that compete with desert ants for the *Guinness Book of World Records* in the category of multicellular animal living at a thermal extreme. Alvinellids live on the sides of black smoker sulfide chimneys, and are reported to survive brief exposures to temperatures as high as 105°C. They routinely experience a thermal gradient of 50–60°C over the length of their bodies. Temperature tolerance in these worms is not completely understood, but thermal stability of enzymes has been shown to increase in alvinellid species that occupy increasingly warmer habitats. Membranes may also be adapted for thermal stability through an increase in the degree of double bonding in fatty acids in species living in warmer portions of the vent habitat.

Shrimp (*Rimicaris exoculata*) that swarm on black smoker chimneys in close proximity to extremely high temperature (350°C) fluids are not bathed in excessively hot water, but they do have paired photoreceptive organs that may function to detect the glow emitted by the hot water. The organs are derived from ordinary shrimp eyes, but the photoreceptive surfaces are hypertrophied and rich in visual pigment (rhodopsin). The eyestalks are lost and the derived eyes extend back along the dorsal surface of the shrimp, beneath the transparent carapace. These 'eyes' have also lost their optic (lens) systems, so they cannot form an image, but they are optimized to detect gradients of dim light. While light from black smokers has now been well documented, the behavioral response of the shrimp to this light has not been studied.

Community Dynamics

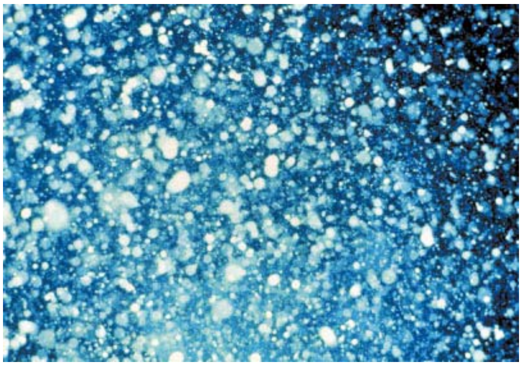

Figure 5 Flocculent material suspended in the water column 1 m above new ocean crust. The floc is a mineral by-product of microbial production and emanated from cracks in the seafloor. (Photograph by Alvin, Woods Hole Oceanographic Institution.)

There could hardly be a greater dynamic contrast than that found between the cold, food-limited, relentlessly stable and vast deep sea environment, and the thermally complex, trophically rich, ephemeral, and insular deep-sea hydrothermal vent fields. Since the discovery of vents, ecologists have attempted to predict the cycle of community development over the life span of a vent field by interpolation and extrapolation from snapshot observations. The 1991 seafloor volcanic eruption at the Venture Hydrothermal Field on the East Pacific Rise was witnessed within days to weeks of the event, providing biologists with the first submarine equivalent of Krakatau. At the time of the Venture eruption, existing vent communities were obliterated by fresh lava flows, pervasive warm-water venting was observed along ~1.5 km of ridge axis, and a dense 'bloom' of flocculent material poured from cracks between lobes of lava, obscuring visual navigation (**Figure 5**). The flocs were determined to be the mineral by-product of microbial production. Within one year, venting became focused at numerous sites along the ridge axis and the first colonists had arrived, including a small tubeworm species (*Tevnia jerichonana*) and dense aggregations of several species of limpets. Mobile vent organisms, including vent crabs and squat lobsters, zoarcid fish, and swarming amphipods were also well represented. After 2.5 years, some vents had shut off but, where venting persisted, mature colonies of the giant tubeworm (*Riftia pachyptila*) were established, along with a variety of smaller invertebrates that live among the tubeworm tubes, including shrimp, limpets, amphipods, and polychaetes. Growth rates of *R. pachyptila* were measured to be among the most rapid of any aquatic invertebrate. Within 5 years, 75% of the regional species pool could be found at the new vents and mussel beds were well-established and beginning to overwhelm the *R. pachyptila* thickets. In this example, vesicoymid clams were the last of the big megafaunal species to arrive at the site, despite the presence of adult populations within several kilometers of the area overrun by fresh lava. Mussels appear to have a competitive edge among the larger taxa at vents, in part because they are mobile and can relocate as necessary to cope with changing flow patterns of vent fluids, while tubeworms are stationary and have few options for tracking vent flow. In addition, because mussels can filter-feed as well as derive nutrition from their endosymbiotic bacteria, they are among the last species to disappear as a vent shuts down. Ultimately, it is the mobile scavengers – the crabs and fish and octopus – that witness the final demise of a vent field.

The eruption at the Venture Hydrothermal Field was not entirely unexpected – geologists were studying this region of the ridge axis because it was so inflated and appeared to be ripe for an eruptive event. Localization of seafloor eruptions on the Juan de Fuca Ridge in the northeast Pacific (off the coast of Vancouver Island) now takes place in real-time, facilitated by a legacy of the cold war era, namely through acoustic signals received by underwater sound-surveillance systems originally designed to track enemy submarines. As eruptions take place, T-waves (low-frequency, tertiary waves characteristic of lava in motion) are transmitted into the water column. Navy hydrophone networks allow the T-waves to be placed in a geographical context and traced from start to finish. One migration of lava in June 1993 was traced for about 40 km below the ocean crust over a two-day period before it finally erupted onto the seafloor. As at the Venture Field, fresh lava on the seafloor was observed, along with venting of flocculent material derived from microbial production. Sites of persistent venting were colonized by populations of vent invertebrates within one year, some of which were reproductively mature.

The two examples of community dynamics cited here suggest that the species composition of all vent communities is constantly changing. But some vent sites are long-lived, and repeat visits to these long-lived sites over a 15-year period document essentially no change in the nature of the fauna. The best example of this to date is the TAG site on the Mid-Atlantic Ridge. TAG is a large sulfide mound (100 m diameter) that has occupied the junction of cross-cutting faults and fissures for more than 100 000 years. Swarming shrimp (*Rimicaris exoculata*) and anemones (*Maractis rimicarivora*) dominated the site when it was first discovered in 1985 and continued to dominate through the most recent set of observations in 1998, despite massive disruptions of hydrothermal flow caused by drilling in 1994. There have been shifts in the precise location of the primary masses of shrimp as they track local natural and anthropogenic changes in vent flow on the mound, and we assume that there has been replacement of generations by recruitment. But there has been no succession observed, no invasion by other taxa. The absence of change does little to attract ecologists, who thrive on dynamic systems, but the stability of the species composition at TAG and other sites has profound implications regarding the selective pressures encountered by the species that inhabit these sites compared to sites that are constantly threatened by lava overruns or tectonic shifts in plumbing.

Figure 6 The ancient barnacle *Neolepas zevinae*. (Photograph by C.L. Van Dover.)

Origins of Vent Faunas, Biogeography, and Biodiversity

Evolutionary paths that brought invertebrate taxa to vents are varied. Several major taxa, including the galatheid squat lobsters, pycnogonid sea spiders, and echinoderms are likely to be immigrants from the surrounding deep sea. Some species are closely related to (and presumably derived from) shallow-water genera. Many of the most familiar vent taxa – the vesicomyid clams, bathymodiolid mussels, vestimentiferan tubeworms, alvinocarid shrimp – are allied to genera and families found in a variety of deep-sea chemosynthetic ecosystems (i.e., seeps and whale-falls as well as vents). The direction of invasion (seep-to-vent or vice versa) can be inferred using molecular techniques. For example, molecular phylogenetics suggests that the bathymodiolid mussel group invaded vents from seeps, with several seep species resulting from reinvasion of the seep habitat by vent ancestors.

There are also specialized taxa so far known only from hydrothermal vents. The most conspicuous of these is the alvinellid polychaete family, whose members often occupy the warmest habitable waters of a vent site. Still other taxa appear to be relicts of ancient lineages that have found refuge in the vent environment. These relict taxa include the stalked barnacle, *Neolepas zevinae* (**Figure 6**) and the archaeogastropod limpet, *Neomphalus fretterae*.

Fossil vent communities found on land provide a glimpse of Silurian vent assemblages. Vestimentiferans are reported from some of the oldest vent deposits known, accompanied by brachiopods and monoplacophorans. Brachiopods and monoplacophorans are so far poorly represented in modern vent communities, if at all.

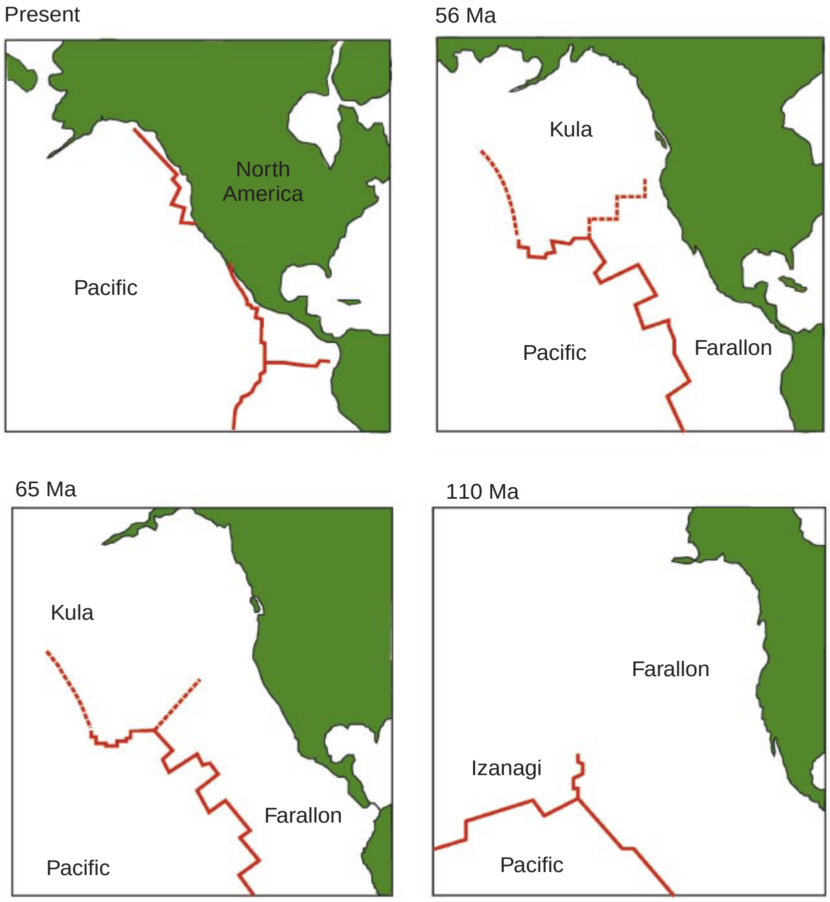

Figure 7 Bisection of a mid-ocean ridge by the North American Plate. At one time (56 Ma), there was a continuous mid-ocean ridge in the eastern Pacific basin but, as the North American Plate overrode the ridge system, it was bisected to form the northeast Pacific ridge system (Juan de Fuca, Explorer, Endeavour, and Gorda Ridges) and the East Pacific Rise (emerging in the Gulf of California and running south toward Antarctica). (Reproduced from Tunnicliffe *et al.* 1996.)

When vents were first discovered, some biologists hypothesized that the vent fauna would be globally cosmopolitan. Subsequent explorations have shown this hypothesis to be false, and mechanisms that allow isolation and differentiation of faunas have been postulated. One of the best examples comes from a comparison of faunas from the Juan de Fuca Ridge and East Pacific Rise. At one time (56 Ma), these ridges were one continuous ridge system, but around 37 Ma the North American Plate began to override this ridge (**Figure** 7), splitting the parent faunal assemblage into two daughter assemblages that are distinct yet closely allied at the generic level.

Similarities among faunas at the species level may be reduced to nearly zero at vent sites that are in separate ocean basins. This observation suggests that major additions to the global vent faunal inventory await us in the unexplored ocean basins; the potential for discovery of novel adaptations to the vent ecosystem is extremely high.

Vent biologists are just beginning to examine global patterns in biodiversity. Preliminary measures show a strong correlation between spreading rate and species richness, raising the hypothesis that patterns of volcanism may be an ultimate control on species diversity in hydrothermal vent ecosystems. Where ridges are fast-spreading, the magma budget is high and the temporal and spatial frequency of vents along the ridge axis is high. In contrast, on slow-spreading ridges, the magma budget is low and vents are far apart. Because distances between vents are short on fast-spreading ridges, species are less likely to go extinct. At slow-spreading ridges, allopatric speciation by isolation may be favored, but species are more likely to go extinct because of the distance between vents. Many of the species that dominate vents on slow-spreading systems have mobile rather than sessile adults, suggesting that distance may act as a selective filter for dispersal capability in these systems.

Vent Systems and the Origin of Life

Without doubt, the most provocative consequence of the discovery of seafloor hydrothermal vents is the suggestion that vents may have been the site where life originated on Earth. In contrast to the heterotrophic hypothesis of the origin of life, with its nourishing 'organic soup', the vent theory suggests that the earliest life was chemosynthetic, taking biochemical advantage of the large degree of chemical disequilibrium associated with mixing zones of low- and high-temperature portions of hydrothermal systems. A case has been made that the thermophilic nature of the most ancient known lineages of life is indicative of an origin of life at hot springs, but this argument finds limited support, since these most ancient cell types are still very complex and far removed from the progenitors of life.

One model for the origin of life at vents suggests the following acellular precursor: a monomolecular, negatively-charged organic layer bonded to positively charged mineral surfaces at the interface of hot water. In this model, pyrite, which forms exergonically from iron monosulfide and hydrogen sulfide (both components of vent fluids), serves as the mineral surface. The pyrite-forming reaction yields two free electrons that can be used for building biochemical constituents; simple organic molecules interacting with the pyrite could be reduced to more complex organic molecules. The simple organics also derive from the vent fluids, through abiogenic synthesis. In a secondary stage of development, the precursor evolves to being semicellular, still supported by minerals, but with a lipid membrane and internal broth, with increasing metabolic capabilities. In the final stage of origin, the pyrite support is abandoned and true cellular organisms arise. The elegance of this model is that it uses an energetically realistic inorganic chemical reaction to create a cationic substrate that can bind with organic compounds, all within a single setting.

Discovery of vent ecosystems and the appreciation of their chemosynthetic basis has influenced the search for life elsewhere in the solar system. When the Viking Mission to Mars took place, the emphasis was on a search for photoautotrophic processes, but now the search for evidence of past or extant life on other planets highlights environments where chemosynthetic processes may take place, including hydrothermal areas.

Closing Remarks

Hydrothermal vent ecology remains a field ripe for discovery of novel faunas and adaptations, as vents in new ocean basins are explored. Because access to deep-sea ecosystems is continually improving, biologists can now undertake quantitative sampling and time-series investigations that are certain to reshape our understanding of the physiological ecology, population biology, community dynamics, and biogeography of vent faunas in the near future.

See also

Hydrothermal Vent Biota. Hydrothermal Vent Fluids, Chemistry of. Hydrothermal Vent Deposits. Hydrothermal Vent Fauna, Physiology of. Mid-ocean Ridge Tectonics, Volcanism and Geomorphology.

Further Reading

Bock GR and Goode JA (eds) (1996) *Evolution of Hydrothermal Ecosystems on Earth (and Mars?).* New York: Ciba Foundation.

Childress JJ and Fisher CR (1992) The biology of hydrothermal vent animals: physiology, biochemistry, and autotrophic symbioses. *Oceanography and Marine Biology Annual Review* 30: 337–441.

Desbruyères D and Segonzac M (eds) (1997) *Handbook of Deep-Sea Hydrothermal Vent Fauna.* Brest: IFREMER.

Fisher CR (1990) Chemoautotrophic and methanotrophic symbioses in marine invertebrates. *Critical Reviews in Aquatic Science* 2: 399–436.

Humphris SE, Zierenberg RA, Mullineaux LS and Thomson RE (eds) (1995) *Seafloor Hydrothermal Systems: Physical, Chemical, Biological and Geological Interactions.* Washington, DC: American Geophysical Union.

Karl DM (ed.) (1995) *The Microbiology of Deep-Sea Hydrothermal Vents.* New York: CRC Press.

Shank TM, Fornari DJ, Von Damm KL *et al.* (1998) Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents (9°N, East Pacific Rise). *Deep-Sea Research* 45: 465–516.

Tunnicliffe V (1991) The biology of hydrothermal vents: ecology and evolution. *Ocenography and Marine Biology Annual Review* 29: 319–407.

Tunnicliffe V, Fowler CMR and McArthur AG (1996) Plate tectonic history and hot vent biogeography. In: MacLeod CJ, Tyler PA and Walker CL (eds) *Tectonic, Magmatic, Hydrothermal and Biological Segmentation of Mid-Ocean Ridges*, Geological Society Special Publication 118, pp. 225–238.

Tyler PA and Young CM (1999) Reproduction and dispersal at vents and cold seeps: a review. *Journal of the Marine Biology Association of the UK* 79: 193–208.

Van Dover CL (2000) *The Ecology of Deep-Sea Hydrothermal Vents.* Princeton: Princeton University Press.