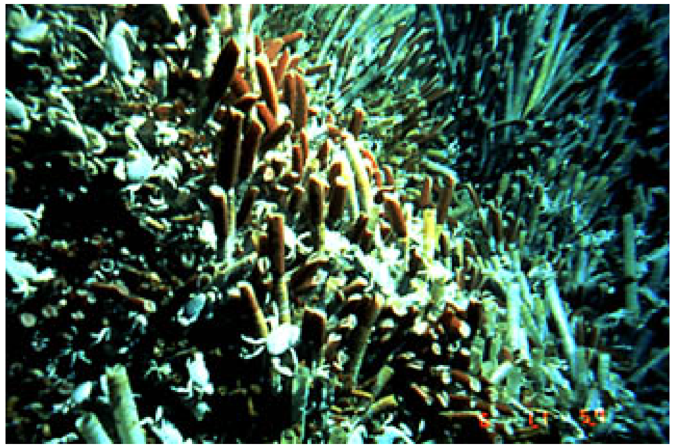
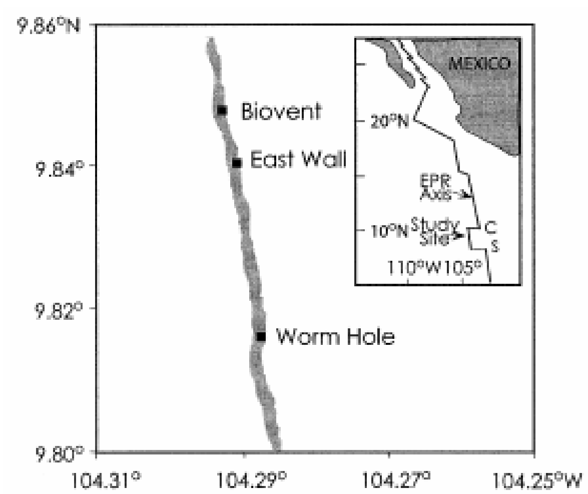
Hydrothermal Vent Communities

Carolyn Scearce

Early in the spring of 1991 a volcano erupted 2500 meters below the ocean's surface near hydrothermal venting sites at the northern portion of the East Pacific Rise. Prior to eruption, the sites, located over 4000 km SSW of Mexico's Pacific coast, hosted a thriving community. At hydrothermal vent sites, hot mineral rich water spews from the sea floor, and mixes with cold oceanic water. Vent chemistry provides the energy and raw materials with which microorganisms grow. These microorganisms form the basis of the food chain in which unexpectedly high organism densities and growth rates are observed. Unique communities are formed around vents, attracting unusual creatures such as red-plumed giant tube worms and massive clams, which cluster around the dark chimneys where vent fluids emerge.

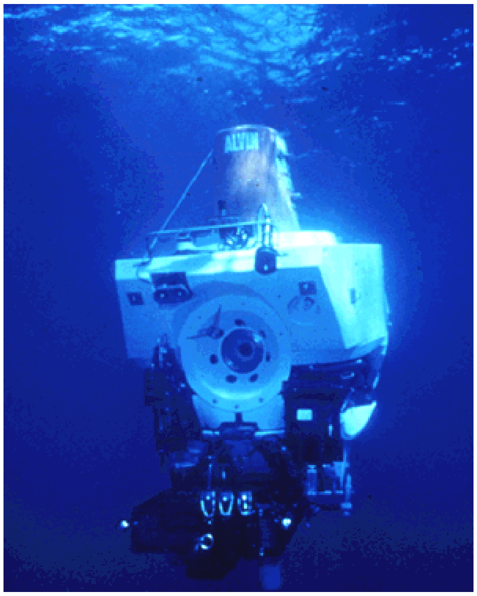


Vestimentiferan tube worms Riftia pachyptila from the East Pacific Rise
http://life.bio.sunysb.edu/marinebio/hotvent.html
Woods Hole Oceanographic Institution (Dept. of Ecology and Evolution, SUNY Stony Brook, 650 Life Sciences Building, Stony Brook. NY 11794-5245)



East Pacific Rise study site
http://micheli.stanford.edu/pdf/Mullineaux_EcolMon2003.pdf
Micheli Lab (Fiorenza Micheli, Marine Community Ecology, Stanford University, Stanford University, Stanford, CA 94305-2115)

In April of 1991, scientists conducting a site survey along the East Pacific Rise expected to find just such a community. Expedition members employed the services of *Alvin*, a submersible research vehicle with the capacity to carry a pilot and two passengers to a depth of 5 km. On April 4, members of the first dive found only fresh basalt and no signs of life. On a subsequent dive, conducted ten days later, a community was discovered that had been only partially covered by lava. Observers saw that some tubeworms were enveloped in obsidian, while others were cooked alive. Mussel shells were shattered and scattered all over the site (Lutz et al, 2001). Volcanic eruptions such as these not only kill off the organisms living in existing communities, but can alter the chemistry and reroute vent fluids (Mullineaux et al, 2003). In essence, an entirely new venting site replaces the previous one.



Photograph of the submersible *Alvin*
http://pubs.usgs.gov/gip/dynamic/exploring.html
United States Geological Survey (12201 Sunrise Valley Drive, Reston, VA 20192)

As disturbing as the devastation was after the 1991 eruption, still, it provided biologists with a unique opportunity to observe the process of ecological succession occurring at newly formed hydrothermal vents. Scientists have been monitoring the East Pacific Rise site frequently since the eruption, documenting the process by which organisms colonize a new vent. Microorganisms first moved in, filling the water near the vents and also forming microbial mats on nearby surfaces. These abundant microorganisms attracted mobile vent fauna such as amphipods, copepods, and crabs. Vestimiferan tube worms followed, replacing parts of the microbial mat. Later arrivals included crabs, mussels, and polychaete worms (Shank et al, 1998; Govenar et al, 2004). Associations between organisms are generally in flux during the initial 1-2 years of settlement, reaching maturity by approximately three years.

It can be a chancy life for organisms living at hydrothermal vents. Individual vent sites are extremely ephemeral on geological time scales, lasting only on the order of years to decades (Micheli et al, 2002). Volcanic eruptions can destroy whole communities, or vent fluids can cease to flow, slowly chilling and starving dependant communities. As vents wane, organismal associations can be observed slowly transitioning as they gain greater similarity to background communities (Tsurumi & Tunnicliffe, 2003). Mobile inhabitants may be able to escape from fading vent sites, but the large aggregations of sessile organisms die if fluids cease to flow. Organisms also face the standard biotic treats of predation and competition. Despite adversity, however, hydrothermal vent communities are among the most productive aquatic environments on earth, converting inorganic material into organic biomass at an unusually rapid rate.

The discovery of hydrothermal vents

Marine geologists studying ocean temperatures at the 2500 meter deep spreading center of the Galapagos Rift acquired their first definitive evidence for the existence of hydrothermal vents in May, 1976. A deep-tow vehicle deployed less than 40 meters above the volcanic ridge detected a buoyant plume of vent discharge. The vehicle, which originated from Scripps Institution of Oceanography's Marine Physical Laboratory, was equipped with a Conductivity Temperature Density device (CTD), sampling bottles, acoustic sensors, and cameras. Water samples and physical measurements helped identify the hydrothermal plume.

Black smoker
http://www.oceansonline.com/hydrothe.htm
Dr. C's Remarkable Ocean World (Dr. William Chamberlin, Fullerton College, North Orange County CC District, 1830 W. Romneya Dr., Anaheim, CA 92801-181)

While taking these samples, the vehicle also photographed the ocean floor. To everyone's surprise, these photographs revealed a dense, productive benthic community living in close proximity to the hydrothermal vent. Relying on this data, in 1977 Peter Lonsdale published the first scientific paper describing a hydrothermal vent life. The paper describes a community including mussels, anemones, and crabs, as well as evidence of burrowing activity. Lonsdale speculated that increased food resources near vent plumes allowed the animals to flourish, and suggested that searching for these unusual communities might serve as the simplest method of detecting hydrothermal vents.

In 1977 geologists returned to the Galapagos Rift, diving in *Alvin*, and had the first chance to see hydrothermal vent communities with their own eyes. Two years later a group of biologists, chemists, and geologists came back to the rift with a film crew from National Geographic in tow. A National Geographic documentary and an article by Robert Ballard and Fredrick Grassle (1979) resulted from the 1979 expedition, introducing the general public to the exotic world found at hydrothermal vents. *Alvin* brought back pictures of giant tube worms, foot-long clams, galatheid crabs, and other unusual creatures.

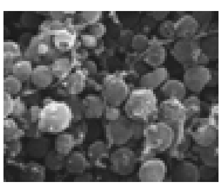
Though the discovery of vent communities came as a total surprise, the discovery of hydrothermal vents was not unanticipated. Based on measurements of heat flux, marine geologists had hypothesized about the existence of vents years before any were directly located (Lonsdale, 1977). Additionally, the composition of seawater itself indicated that unexplained chemical processes were taking place in the world's oceans. Seawater manganese concentrations were too high, while magnesium concentrations were too low to be accounted for by mineral contributions from river runoff alone. Chemical analysis of vent waters demonstrated that the circulation of water through the ocean crust decreased magnesium levels and increased manganese concentrations in ocean water.

Hydrothermal vents occur at ocean spreading centers, that is, at locations where tectonic plates are pulling apart, creating new ocean floor as volcanic material rises to fill in the space between the plates. At spreading centers ocean water infiltrates the ocean floor and mixes with molten crust, after which hydrothermal fluids rise back to the surface of the sea floor. As hydrothermal fluids return to the ocean floor, they exit through narrow chimneys known as white or black smokers (Metaxas, 2003). Exiting fluids range in temperatures between 300-400 degrees C and are rich in hydrogen sulfide, heavy metals, and other elements. The high temperatures of vent fluids cause them to be more buoyant than ocean water. As hydrothermal fluids escape into ocean waters, they form buoyant plumes that rapidly mix with ambient seawater. The plume rises until the fluids mix sufficiently to reach a state of neutral buoyancy. At this point the plume spreads out horizontally: ocean currents then dictate further mixing and movement (Van Dover, 2000).

The benthic zone surrounding hydrothermal vents is an extremely variable environment. Within this area, vent fluids and oceanic waters mix. These two water types possess very different physical and chemical properties. Consequently, temperature and chemical gradients form within vent environments. Small distances can make a big difference in the characteristics of the water experienced by organisms that live near vents. As currents shift, water properties can change dramatically in a matter of minutes or seconds. Toxic substances precipitate from vent fluids. Living in such a unique physical and chemical environment can require a considerable amount of adaptability.

Chemosynthesis

The extremely productive nature of hydrothermal vent communities puzzled scientists at first. Only certain organisms, known as primary producers, can process energy from strictly inorganic sources. These primary producers provide the organic compounds that other organisms need for growth and energy. Sunlight usually provides the energy for the production of organic compounds from inorganic compounds. Before hydrothermal vents were discovered, prevailing opinion held that deep-sea communities relied on the slow fallout of organic mater from the ocean's surface. At the surface sufficient sunlight penetrates to allow photosynthesis to occur, but even in the clearest waters there is not enough light to fuel photosynthesis much below 100-200 meters deep.



Tube worm symbionts
http://commtechlab.msu.edu/sites/dlc-me/zoo/microbes/riftiasym.html
Microbe Zoo (Comm Tech Lab, 253 Communication Arts & Sciences, Michigan State University, East Lansing, MI 48824)

Ecologists looked to photosynthetic processes as the ultimate source of energy that fueled aquatic food webs. However, most of the organic compounds from surface waters are consumed before they can penetrate to deep ocean waters. Consequently, photosynthetic fallout could not account for the level of biomass observed at venting sites. An alternative explanation was needed to account for hydrothermal community productivity. Instead of relying on photosynthesis, the vent food chain is built on the basis of chemosynthesis.

Hydrothermal vents have taught us that chemosynthetic microorganisms can serve as primary producers without the aid of sunlight. At vents and methane seeps, high concentrations of hydrogen sulfide or methane can provide microorganisms with the chemical energy to synthesize organic compounds (Childress & Fisher, 1992). While scientists had recorded chemosynthetic processes as early as 1887 (Jannasch, 1997), it took the discovery of hydrothermal vents to highlight how important this process could be.

A particularly intriguing aspect of chemosynthesis at hydrothermal vents is the symbiosis that exists between bacteria and some vent organisms. A range of vent organisms, including tubeworms, mussels, and clams, host symbiotic bacteria inside their bodies. Symbiotic bacteria living within an organism are known as endosymbionts. Episymbionts, or symbiotic bacteria living on the exterior of animals, are found on hydrothermal polychaete worms and shrimp.

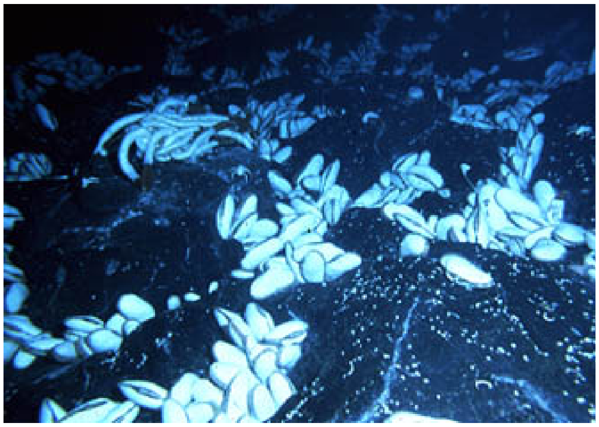
Organism adaptations to vent environments

For the mussels or giant tubeworms living on an actively venting chimney, environmental conditions vary dramatically from those experienced by organisms just outside the range of the vent's influence. Precipitating heavy metals and other toxic substances can literally rain down on nearby animals. Hydrogen sulfide, an essential component for the chemosynthetic processes that provide energy for vent communities, can have effects similar to cyanide on organisms not adapted to functioning at the high concentrations found at vent sites. Thermally adapted bacteria and archaea may live at temperatures in excess of 100 degrees C. It can take a great deal of adaptation to live in close proximity to hydrothermal vents. Many of the 500 + animals that have so far been discovered at vent sites seem to live exclusively in vent communities (Van Dover, 2000). To gain a better understanding of what it takes to live in a hydrothermal system, the physiology of some of the best studied vent organisms will be discussed.

The giant tubeworm *Riftia patchyptila*, which can grow up to 2 meters long, offers one of the most extreme examples of specialization for hydrothermal vent environments. *R. pachyptila* colonies, which can be found at sites within the Galapagos Rift and the East Pacific Rise, prefer locations with high flow vents (Childress & Fisher, 1992). Vestimiferans such as *R. pachyptila* live inside long narrow chitinous tubes that are permanently attached to the substratum. A retractable plume takes up nutrients from the external environment, but the worm possesses no digestive system (Van Dover, 2000). Its growth and metabolism depends on symbiotic bacteria housed in a specialized organ know as the throphosome. *R. pachyptilla* provides a stable environment and a steady supply of nutrients to the endosymbionts, while the endosymbionts supply abundant organic carbon to their host. The hemoglobin of *R. pachyptilla* not only binds to oxygen, but is adapted to reversibly bind to sulfide. Unbound sulfide would prove toxic to the tube

Riftia patchyptila
http://life.bio.sunysb.edu/marinebio/hotvent.html
Woods Hole Oceanographic Institution
(Dept. of Ecology and Evolution, SUNY Stony Brook, 650 Life Sciences Building, Stony Brook, NY 11794-5245)

worm but is essential to the metabolism of the resident symbiotic bacteria (Flores et al, 2005).



Calyptogena magnifica
http://life.bio.sunysb.edu/marinebio/hotvent.html
Woods Hole Oceanographic Institution (Dept. of Ecology and Evolution, SUNY Stony Brook, 650 Life Sciences Building, Stony Brook, NY 11794-5245)

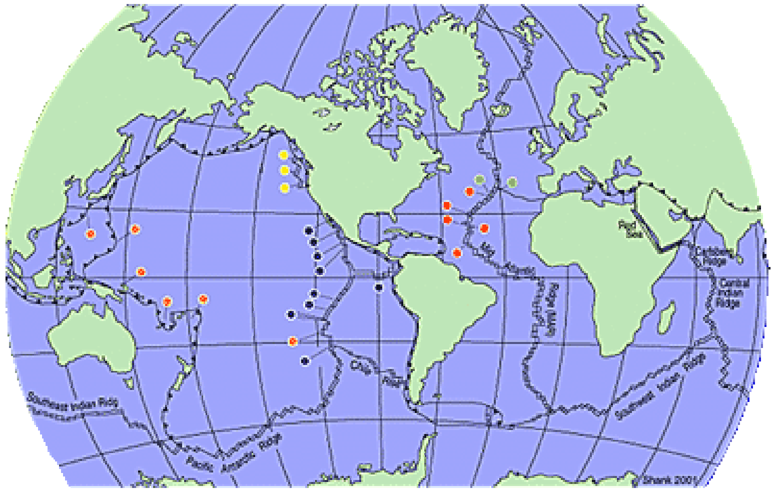
The vesticomid bivalves, mollusks with hinged shells, host symbiotic bacteria within vacuoles of their gills. The vesticomid *Calyptogena magnifica*, also found at vent sites of the East Pacific Rise and Galapagos Rift, prefer slower venting sites to those chosen by *R. pachyptilla*. *C. magnifica* possesses a functional, though highly reduced, mouth and gut, suggesting that these organisms acquire nutrition both through the symbiotic relationship and through feeding (Childress & Fisher, 1992). Studies of endosymbiont and host genomes suggest that *C. magnifica* clams can pass on bacterial symbionts from one generation to the next in the eggs of their young (Hurtado et al, 2003).

Though polychaete worms are small and are frequently difficult to detect, they form a large component of hydrothermal vent faunas (Ward et al, 2003). The polychaete *Alvinella pompejana*, found at the East Pacific Rise, lives in tubes along the sides of black smokers. The worm, which is adapted to deal with varied water temperatures, draws in 20 degree C water at the anterior end but the water temperature at the posterior end of the tube ranges from 30-60 degrees C. *A. pompejana* possesses a fully functional digestive track and is a deposit feeder (Van Dover, 2000). Mats of filamentous ectosymbionts colonize the epidermis of *Alvinella* spp. and possibly exchange metabolites with their symbionts.

Alvinella spp.
http://www.fathom.com/feature/122185/
Fathom Knowledge Network (Columbia University, 2960 Broadway, New York, NY 10027-6902)

The vent shrimp *Rimicaris exoculata* is found swarming over the chimneys of the Mid-Atlantic Ridge and has also recently been discovered at Indian Ocean vent sites (Van Dover, 2001). These shrimp do not have the eyes or eyestocks typical of non-vent shrimp. Instead, they possess a pair of fused eye organs that contain high concentrations of visual pigments (Van Dover, 2000). These photoreceptors are believed to be adapted for the detection of radiation associated with hydrothermal vent activity, and they see in infrared instead of the visible light spectrum. Like *A. pompejana, R. exoculata* host episymbiotic bacteria.

Vent communities and biogeography



Biogeography of hydrothermal vents
http://www.divediscover.whoi.edu/hottopics/biogeo.html
Woods Hole Oceanographic Institution (Information Office, MS#16, 266 Woods Hole Road, Woods Hole, MA 02543)

More than 200 vent fields have been documented since the late 1970's (Kelly et al, 2005). Hydrothermal vent sites are far from uniform. Factors affecting the structure of vent communities include vent field size, habitat stability, water depth, venting fluid temperature, habitat diversity, ecological succession stage, and larval exchange barriers (Tsurumi & Tunnicliffe, 2003). Compared to other deep-sea communities, hydrothermal vents show much higher productivity but much lower species diversity (Van Dover, 2000). Within individual communities, the distributions of organisms are affected by the environmental gradient created by the mixing of vent fluids with ambient sea water. Animals and microorganisms with greater tolerances for high temperatures and vent chemistry can be found at locations in closest proximity to vents, while organisms with lower tolerances are spaced farther away. Mobile animals not specialized for vent environments may make brief excursions into vent communities to grab a quick bite.

The first vent fields discovered were located in the Pacific Ocean. By the mid 1980's two deep-sea hydrothermal sites were identified along the Mid Atlantic Ridge, and three additional sites were discovered between 1993-1997 (Desbruyeres, 2003). In 2000 the Kiarei vent site was discovered in the Indian Ocean (Hashimoto, 2001). Because many of the longest known and most extensively studied sites are located in the Pacific Ocean, these tend to be the best-known communities. The most well studied sites of hydrothermal venting in the Pacific include those of the Galapagos Rift, the East Pacific Rise, and Juan de Fuca.

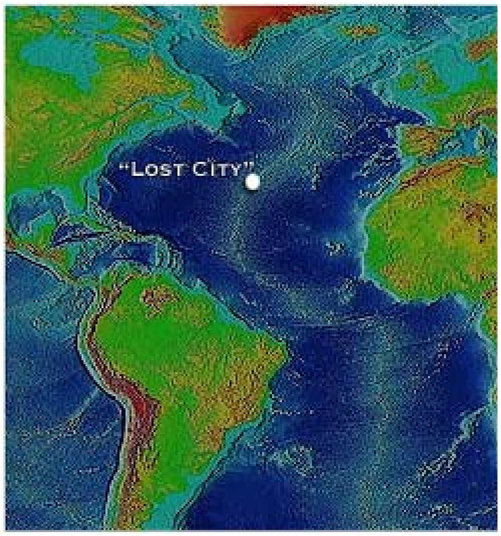
Factors associated with geographic location and the degree of isolation from other venting sites exerts a substantial influence on the organisms most likely to be found at a given hydrothermal vent. In the Pacific Ocean, similar communities are found at the Galapagos Rift and the East Pacific Rise, but the biogeography of Juan de Fuca is considerably different. As the community composition of the first two sites has already been discussed, here I will focus on the vent fields found around the Juan de Fuca Ridge. The majority of these fields are colonized by a single species of tube worm, *Ridgea piscesae*, which colonizes in closely associated groups of interwoven tubes, creating 'tubeworm bushes.' The bushy forms then serve as substrate for other invertebrates (Tsurumi & Tunnicliffe, 2001; Tsurumi & Tunnicliffe, 2003). The number of organisms and species colonizing an individual bush depends on the size and complexity of the aggregation. Although dozens of species can be found associated with these tubeworm clumps, only a few account for most of the biomass.

The Atlantic hydrothermal communities are substantially different from those found in the Pacific. Instead of being dominated by tube worms, the communities at deep water sites along the Mid Atlantic Ridge have swarms of shrimps that cluster around vent chimneys. Shallower vent sites are generally dominated by mussel beds. Studies of trophic structure in Atlantic vent systems show short food chains, with free-living and symbiotic bacteria composing the base. Mussels host symbiotic bacteria, while shrimp feed on free-living bacteria and small invertebrates feed on bacteria or detritus. Crabs can be found at intermediate and top levels of the food chain along with fish (Colaco et al, 2002).

An interdisciplinary team of scientists studied the biogeography of Kairei and Edmond vent fields in the Indian Ocean in 2001 (Van Dover, 2001). Shrimp swarm the centrally located black smokers in the Kairei Field, while anemones become more dominant in peripheral locations. Other common organisms include gastropods, crabs, flatworms, polychaetes and barnacles. The community found at Edmond Field is similar to that of Kairei, although with a lower degree of diversity. Thirty-six invertebrate taxa found in the Indian Ocean sites overlap with taxa previously known only to live in the Pacific. Only one exclusively Atlantic species was found, the shrimp *Rimicaris exoculata*. Some taxa can be found at vent sites in all three oceans, but molecular comparisons also confirm the closer genetic association between Pacific and Indian Ocean taxa. However, Indian Ocean communities are different enough to constitute a separate biogeographic province from either the Atlantic or the Pacific.

How organisms move from one site to another is important in regulating the composition of vent communities, both on biogeographic and local spatial scales. Many benthic invertebrates, such as tubeworms, polychaetes, and bivalve mollusks that populate hydrothermal vents have non-motile adult forms. Consequently, behavioral and transport processes effecting mobile larval stages strongly influence the distribution of these organisms. Some larvae must remain within their natal habitats to maintain local populations, but new sites cannot be colonized if some organisms are not either passively or actively transported to new locations (Metaxas, 2004). Larvae of *R. pachyptila*, known to rapidly colonize new vent sites, have the metabolic capacity to stay active for over a month without feeding and are thought to take advantage of ocean currents that flow along the East Pacific Rise (Marsh et al, 2001). The questions associated with organismal dispersal are fascinating, but can be difficult to study, due to remote locations, complex physical processes, and large quantities of very small organisms with high mortality rates. The Larvae At Ridge Vents (LARVAE) project participated in field expeditions in the late 1990's in order to study such questions (Mullineaux, 1998). Still, there is much to be learned.

Finding Lost City



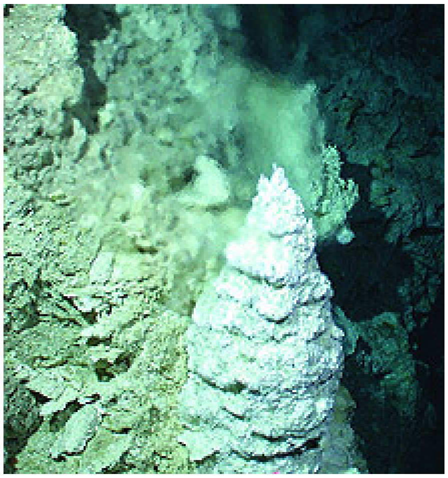
Map showing location of Lost City
http://whyfiles.org/shorties/172ocean_floor/
whyfiles.org (University of Wisconsin, Board of Regents)

Scientists discovered a new class of hydrothermal vents in the Atlantic as recently as December of 2000. Geologists performing a deep-water camera survey of the terrain near the under-sea mountain known as Atlantis Massif serendipitously recorded the Lost City site (Kelly et al, 2005a). The geological processes that drive venting at Lost City are different from those at other known sites. Consequently, the physical and chemical characteristics are also different. Generally, when searching for hydrothermal sites, scientists concentrate on the margins within 1-5 km of spreading centers. The Lost City hydrothermal field is located 15 km from the Mid Atlantic Ridge spreading center at the latitude of 30 degrees N. Instead of the black smoker formations built up by the precipitating fluids exposed to basalt, Lost City's formations are composed of large white carbonate chimneys. Here vent fluids are exposed to uplifted peridotites and are serpentinized. The pH is higher—basic rather that acidic—carbon dioxide levels are extremely low, and the temperature of vent fluids ranges only between 40-90 degrees C rather then in excess of 300 degrees C. Microorganisms acquire their energy from methane and pure hydrogen instead of the oxidation of hydrogen sulfide. Carbon 14 studies indicate that the vent field has been around for approximately 30,000 years. Scientists speculate that these newly discovered vent fields may last for hundreds of thousands of years (Boetius, 2005).

Due to differences in the geology and chemistry of this vent site, the nature of the community associated with Lost City is substantially different from black smoker communities. Instead of large clusters of sessile invertebrates, organisms are smaller and are found in less densely aggregated groups (Kelly et al, 2005a). Currently, no evidence suggests the existence of symbiotic relationships between animals and the chemoautotrophic microorganisms forming the bottom of the food chain. Instead it appears that the marine invertebrates gain energy from grazing on vent-associated carbonates and microbial biofilms. Gastropods and amphipods have been found living in channels of actively venting carbonate sites that range in temperatures between 10-40 degrees C. Polycheates, nematodes, ostracods, stromatopods and bivalves inhabit hydrothermally active flanges and spires. Larger, more mobile animals found at the site include wreckfish, cut-throat eels, and geryonid crabs (Kelley et al, 2005b).

At this point, no one knows how common serpentine hydrothermal vent systems may be. Peridotites can exist in extensive ranges and, with the right geological conditions, it is possible there may be many as yet undiscovered hydrothermal vent systems and communities similar to those found at Lost City.

Why study hydrothermal vents?



Carbonate chimney from Lost City
http://oceanexplorer.noaa.gov/explorations/05lostcity/background/chimney/chimney.html
Ocean Explorer, National Oceanic and Atmospheric Administration (14th Street & Constitution Avenue NW, Room 6217, Washington, DC 20230)

The prospect of studying hydrothermal vents presents a number of challenges, as site locations are frequently remote, found at great depths, and samples can require considerable ingenuity and complicated equipment to be obtained. Considering these challenges, one might ask what the value is of studying these remote biological communities. Their existence presents a number of intriguing questions and the possibilities for even more intriguing answers. Since their discovery, scientists have speculated that life on earth may have first evolved under conditions similar to those found at hydrothermal vents (Little & Vrijenhoek, 2003). Genomic studies suggest that some of the thermophilic microorganisms found at hydrothermal vents come from very ancient lineages (Teske et al, 2003). Furthermore, a number of scientists have suggested that the environment at vent sites might be similar to conditions on other planets. The chemosynthetic model may offer a glimpse of what conditions might be faced by life in extraterrestrial systems. Studies of succession and vent biogeography provide a basis of comparison to address how other aquatic and terrestrial communities found in isolated systems develop and are populated. On a more immediately practical side, vent microorganisms might offer useful natural products and new biotechnologies, such as high temperature tolerant enzymes (Deming, 1998). Studies of vent invertebrates, such as *Riftia pachyptila*, also show interesting body chemistries that help these organisms adapt to the stresses of the environment (Yancey, 2005). Whatever the questions that stimulate an individual, the discovery of hydrothermal vent communities has expanded our knowledge of the diversity of life and our understanding of the range of conditions in which life on earth can thrive.

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