HYDROTHERMAL VENT FAUNA, PHYSIOLOGY OF

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Hydrothermal Vent Environments Are Dynamic, Hot and Toxic

The hydrothermal vent environments, lying at the bottom of the ocean at depths of 2.5 km or more, were discovered in 1977 by a group of geologists exploring spreading centers at midocean ridges on the sea floor. As fissures open up in the earth's surface, lava is extruded onto the ocean floor and sea water is pulled towards the center of the earth so deeply that it comes into contact with hot, molten magma. The sea water is superheated and then discharged back into the environment through fissures in the ocean floor. As sea water moves from the center of the earth and into the vent habitat on the seafloor, it becomes laden with inorganic chemicals. In particular, hydrogen sulfide, an essential chemical in this unique environment, leaches into the water at depth, and water discharging into the environment can be highly enriched in this toxic but energy-rich chemical.

There are two types of hydrothermal vents. In those characterized by diffuse venting, sea water percolates out at a moderate rate and is approximately 10–20°C in temperature. As the bottom water temperature of the majority of the earth's deep ocean is about 2°C, these hydrothermal fluids are elevated in temperature, but rapidly mix with the surrounding sea water. One of the first hydrothermal vent environments discovered, Rose Garden at the hydrothermal vent environment near the Galapagos Islands, is an example of a diffuse vent habitat. In the black smoker environment of the hydrothermal vents, things are a lot hotter, such as at those on the Juan de Fuca Ridge off the coast from the state of Washington. This is a very dynamic, high-temperature environment where water issuing forth from large chimneylike structures can be as hot as 400°C in temperature.

In spite of the hydrogen sulfide-enriched environment, elevated temperatures, and the dynamic volcanic activity, numerous and varied animals cluster around these sites, taking advantage of the hard substrate provided by the extruded pillow lava. A typical vent environment begins with a stretch of pillow lava in the foreground, with clams wedged into the numerous fissures. At the heart of the vent environment are diffuse venting hydrothermal fluids or actively spewing white smoker chimneys and black smoker chimneys, teeming with life. Typical inhabitants include dense clusters of tubeworms and many free-ranging animals roaming in and out of the vent environment such as brachyuran crabs, galatheid crabs, numerous amphipods, a few species of fish, and a host of other smaller animals.

Chemosynthesis — The Basis of All Life in the Vent Environment

Possibly the most revolutionary outcome of the discovery of hydrothermal vents is the story of how life exists in this challenging habitat and the unique nature of the food chain and the source of basic energy in this remote location. Prior to the discovery of the hydrothermal vents, most biologists believed that all life depended upon the energy of sunlight and that the basis of all food chains was photosynthesis. When the hydrothermal vents were discovered, it was immediately clear that they represent a very enriched biological environment very remote from the surface sunlight. It was difficult to imagine that organic material could drift down in large enough quantities to provide the energy to fuel this environment. Other interesting data materializing rapidly after the discovery of the vents indicated that most of the animals, especially the large invertebrates, have no digestive systems. For example, the large tubeworm, *Riftia pachyptila*, has no mouth and no intestine; however, it is a large animal approximately 1.5 m in length and up to 2 cm in diameter, and large colonies of these animals flourish in the remote vent habitat.

The question of how animal life is supported in the deep sea communities of the hydrothermal vents became, and remains to this day, a focus of intense research. Several lines of evidence lead to the realization that some of the major invertebrates endemic to the vent environment harbor bacteria within their body cavities. Free-living bacteria in this environment and in our own backyard have been known for years to be able to use chemical energy as a basis of their metabolism. In the case of the free-living bacteria, there are many hydrogen sulfide-oxidizing bacteria that can use this chemical as the basis of their metabolic pathways and produce organic

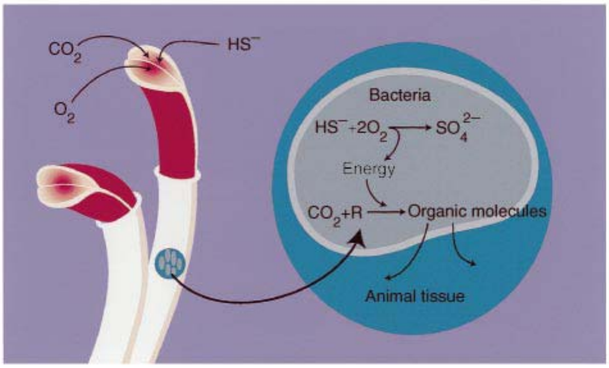

Figure 1 Chemosynthetic pathways in *Riftia pachyptila.*

compounds that form the basis of their nutrition. Hydrothermal vent animals harboring these chemical-utilizing bacteria within their body tissues as symbionts include the large tubeworm *Riftia pachyptila*, which has dense aggregations of bacteria in a residual gutlike organ, and the clam *Calyptogena magnifica*, which harbors bacteria in the gills. These symbiotic bacteria are able to utilize the inorganic chemical hydrogen sulfide, so plentiful in this environment, in a manner analogous to what plants do with energy from the sun. This process is therefore termed chemosynthesis rather than photosynthesis.

The symbiotic bacteria living within the bodies of the larger invertebrate animals have been demonstrated to oxidize hydrogen sulfide, and the energy released from this biochemical process is used to power the fixation of carbon dioxide into small organic compounds – just as in free-living bacterial sulfide oxidation. The Calvin–Benson cycle employed in both cases is the same metabolic pathway that is utilized by plants in photosynthesis to transform inorganic carbon dioxide into organic compounds that are then utilized as food higher up in the food chain. The critical difference with chemosynthetic metabolism is that, rather than using sunlight, these animals and bacteria utilize chemical energy to power that reaction and are completely independent of sunlight (**Figure 1**). The net result is that free-living bacteria in the environment and symbiotic bacteria living within animal tissues are able to live independently of sunlight by utilizing chemicals from the core of the earth, thus forming a very different basis for the food chain in the hydrothermal vent environment. The discovery of the hydrothermal vent environment was a fundamental discovery of a well-defined ecosystem that is completely independent of sunlight at any level of the food chain.

The Ecophysiology of the Giant Tubeworm *Riftia pachyptila*

One of the most dramatic and best-known of the animals endemic to the hydrothermal vent environment is the giant tubeworm *Riftia pachyptila*. Colonies of these worms are clumped together around effluent points in the hydrothermal vent habitat, growing toward and into the water that is percolating out from the seafloor. An individual animal lives inside a single, unbranched chitinous tube and the red structure protruding out of the end of the tube is the respiratory plume. The animal can retract the plume back into the tube if disturbed by a roaming predator. There is a collarlike vestimentum organ that positions the animal within the tube, and a large trunk region of the animal is filled with an organ termed the trophosome. This organ is believed to be the vestigial gut of the worm and is composed, literally, of masses of bacteria. A pool of coelomic fluid bathes the trophosome and contains a large-molecular-weight extracellular respiratory hemoglobin (**Figure 2**). *Riftia pachyptila* also has a separate pool of blood that contains high concentrations of an extracellular hemoglobin that circulates in an elaborate closed circulatory system powered by a heartlike structure in the vestimentum region. The blood is pumped in a complete circuit

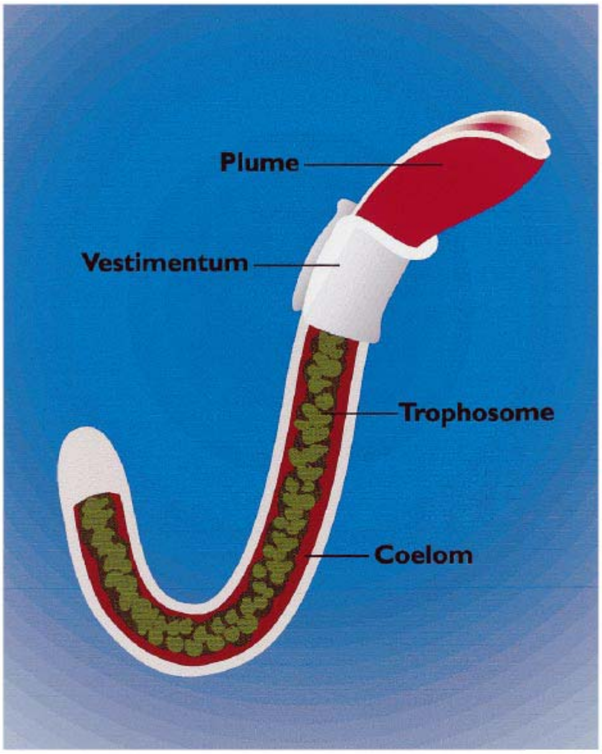

Figure 2 The external anatomy of *Riftia pachyptila.*

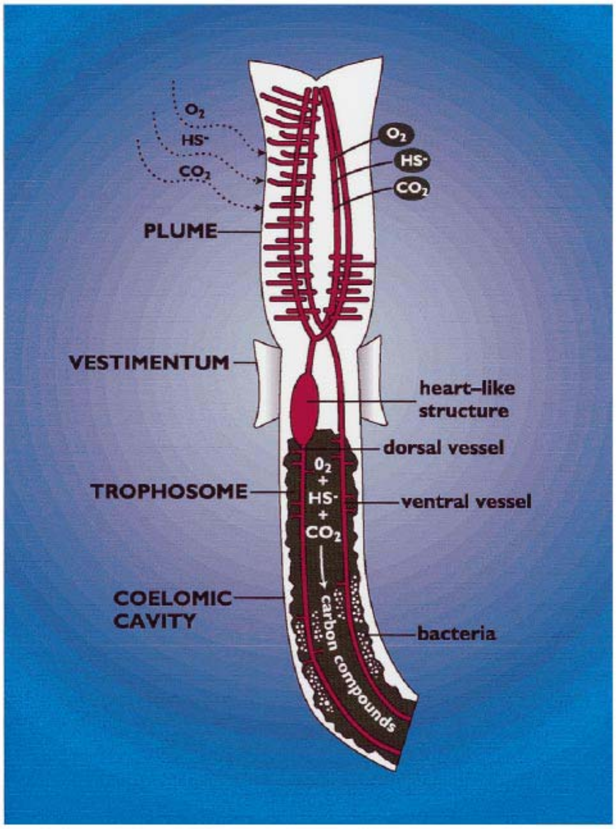

Figure 3 The internal anatomy of *Riftia pachyptila.*

from the respiratory plume to body tissues, and on to elaborate capillary beds in the region of the trophosome and bacteria (**Figure 3**). The red color of the blood is due to the high concentration of hemoglobin and gives the characteristic red color to the plumes.

The respiratory plume and the circulating hemoglobin are essential for the transport of the key metabolites oxygen, hydrogen sulfide, and carbon dioxide, which are the principal components of the metabolism of the symbiotic bacteria. The respiratory hemoglobins present in the plume and the coelomic fluid of the animal bind oxygen with a very high affinity. The binding is reversible and cooperative, such that oxygen uptake is enhanced at the respiratory plume, and oxygen delivery is augmented at the tissues and trophosome organ.

Hydrogen sulfide is a highly toxic molecule that typically acts in a similar manner to cyanide by binding at the iron center of cytochrome molecules and hemoglobin molecules, thus arresting aerobic metabolism. Although *Riftia pachyptila* and other hydrothermal vent animals utilize hydrogen sulfide for their metabolism, they also have tissues that are highly sensitive to sulfide poisoning. Detoxification of hydrogen sulfide is essential for aerobic life in this dynamic, chemically enriched environment. The key to the simultaneous needs for transportation and detoxification is the respiratory hemoglobin present in the plume and coelomic fluid. *Riftia pachyptila* hemoglobin binds hydrogen sulfide with a very high affinity. The toxic hydrogen sulfide is transported to the trophosome region in the center of the worm's body as a tightly bound molecule that cannot chemically interact with sulfide-sensitive tissues. Oxygen and sulfide are simultaneously bound to the hemoglobin at separate binding sites and are transported to the trophosome, where they are believed to be delivered to the symbiotic bacteria for metabolism. In this way hydrogen sulfide is taken up from the surrounding sea water and transported to the site of bacterial metabolism while interaction is prevented with other tissues, such as the body wall, that are highly aerobic and sensitive to the toxic effects of hydrogen sulfide. These unusual adaptations function for respiratory gas transport and metabolism as well as for detoxification and tolerance of toxic chemicals in what would be a very inhospitable environment for most animals.

Dense colonies of *Riftia pachyptila* flourish in a specialized microhabitat within the vent environment. The worms anchor themselves on the rocks where the hydrothermal vent fluid is issuing out into the seafloor. The base of the tube is bathed in hydrothermal fluid enriched in hydrogen sulfide and carbon dioxide, but devoid of oxygen. Temperatures are relatively elevated here, and a gradient develops along the length of the tube. The respiratory plume extends into ocean-bottom sea water that is 2°C in temperature, devoid of hydrogen sulfide and enriched in oxygen (**Figure 4**). By occupying the interface between the hydrothermal fluids and the surrounding bottom water, animals are exposed to both of these essential metabolites which are then taken up by the circulating hemoglobin and transported to internal tissues and symbiotic chemosynthetic bacteria.

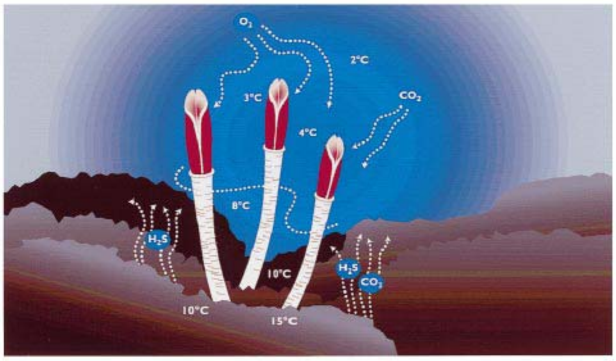

Figure 4 The microhabitat of *Riftia pachyptila.*

The Ecophysiology of the Giant Clam *Calyptogena magnifica*

The vesicomyid clam *Calyptogena magnifica* is a common inhabitant of hydrothermal vents that orients in the fissures of the pillow lava near the periphery of the vent environment. Individual clams can reach up to 20 cm in length. The clams position themselves in cracks in the pillow lava and wedge their muscular foot down into the region where the hydrothermal plume is percolating out (**Figure 5**). This water is enriched in hydrogen sulfide and is elevated in temperature. This position orients the siphon end-up into surrounding sea water and enables the uptake of oxygen and carbon dioxide. *Calyptogena magnifica* possess a high concentration of an intracellular, circulating hemoglobin that functions for oxygen binding and transport. The clam's blood also contains a separate component that binds hydrogen sulfide and transports this essential metabolite to internal symbionts in the gill region. In this manner, the clams are able to accumulate hydrogen sulfide from the hydrothermal fluids bathing the foot, and oxygen via binding to the circulating hemoglobin through gill ventilation at the siphon region. These essential metabolites are transported as bound substances to symbiotic chemosynthetic bacteria in the gill via the circulatory system of the clam, providing both essential respiratory gas transport and detoxification of toxic hydrogen sulfide. The vent clams, like the tubeworms, seek out, exploit, and flourish in a unique microhabitat in the hydrothermal vent community.

Other hydrothermal vent animals include the mytilid mussel *Bathymodiolus thermophilus* that also harbors chemosynthetic bacteria in its gill tissues. There are many free-ranging animals that are not fueled by chemosynthesis but may feed on the larger invertebrates that benefit from that symbiotic, chemoautotrophic metabolism. Animals such as the brachyuran crabs, *Bythograea thermydron*, that wander through the environment scavenging dead or dying material, numerous swarming amphipods, as well as slow-moving fishes, are plentiful. Along with the giant tubeworms, clams, and mussels, these animals benefit directly or indirectly from the chemical-based metabolism that supports this dynamic and robust deep-sea community. It is the specialized physiological adaptations for transport and detoxification of hydrogen sulfide and other processes essential for life that provide the underlying mechanisms that make this possible.

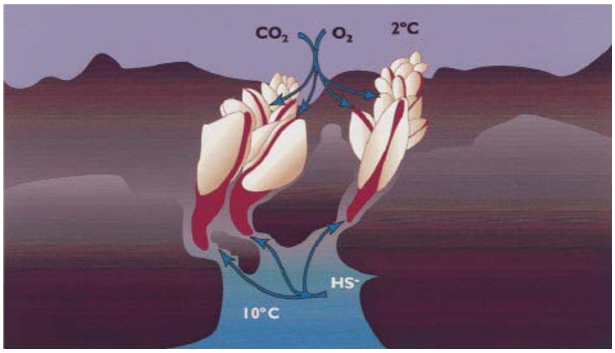

Figure 5 The microhabitat of *Calyptogena magnifica*.

Summary

A fascinating variety of marine invertebrates occur in dense assemblages in organically enriched deep-sea hydrothermal vent environments. Intensive studies on the hydrothermal vent fauna have been conducted since their discovery in the late 1970s. Many investigations have focused on the fact that these organisms, including vestimentiferan tubeworms and vesicomyid clams emphasized here, are nutritionally dependent upon the chemical-based metabolism of large populations of symbiotic bacteria that they harbor internally in dense concentrations. These bacteria utilize hydrogen sulfide as an energy source to fix inorganic carbon into nutrients. Hydrogen sulfide is extremely toxic to aerobic organisms in nanomolar to micromolar concentrations. However, uptake and transport of sulfide to internal symbionts is essential for the host animal's metabolism and survival.

Chemical-based metabolism, or chemoautotrophy, and detoxification of sulfide through binding to blood-borne components occur in vent tubeworms and clams, and are particularly well-characterized for the tubeworm *Riftia pachyptila*. These chemosynthetic endosymbiont-harboring worms simultaneously transport sulfide bound to the respiratory hemoglobin, providing an electron donor for the bacterial symbiont metabolism and protection against sulfide toxicity at the tissues.

How animals living in sulfide-rich environments like hydrothermal vent communities transport, metabolize, and detoxify hydrogen sulfide has been one of the major questions posed by hydrothermal vent researchers. The clarification of both the phylogenetic importance and the ecological status of these animals requires knowledge of their physiological adaptations to low oxygen conditions and high concentrations of sulfide, and provides answers to the puzzle of how these animals flourish in such seemly hostile environments.

See also

Deep-sea Ridges, Microbiology. Hydrothermal Vent Fluids, Chemistry of. Hydrothermal Vent Biota. Hydrothermal Vent Deposits. Hydrothermal Vent Ecology.

Further Reading

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HYDROTHERMAL VENT FLUIDS, CHEMISTRY OF

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Introduction

It was not until 1977 that we knew that fluids exit from the seafloor along the global midocean ridge system. With the first discovery of hydrothermal venting at the Galapagos Spreading Center, our ideas on how elements cycle through the oceans and lithosphere, and even how and where life on our planet may have originated were fundamentally and irrevocably changed. Although these fluids were only a few tens of degrees hotter than ambient sea water ($< 30°C$ vs. 2°C), on the basis of their chemical compositions it was immediately clear that these fluids were derived from reactions at much higher temperatures between sea water and the oceanic crust. Less than two years later, spectacular jets of hot ($\geqslant 350°C$) and black water were discovered several thousand kilometers away on the northern East Pacific Rise, and 'black smokers' and 'chimneys' (**Figure 1**) entered the oceanographic lexicon.

From a chemical oceanography perspective, hydrothermal venting and hydrothermal vent fluids provide both new source and sink mechanisms for elemental cycling in the ocean, and therefore possible resolutions to a number of the outstanding chemical flux imbalances. They therefore play a fundamental role in regulating the chemistry of the oceans through geological time. From a biological oceanography perspective, hydrothermal vents provide us with new ecosystems based on chemosynthetic, rather than photosynthetic energy. Of the > 500 new species discovered at these sites, the archea and other microbiological components are attracting increasing interest for both biotechnological applications and 'origin of life' questions on our own and other planets. From a physical oceanographic perspective, hydrothermal vents provide an input of both heat and materials into the oceanic mid-depth circulation. From a geological oceanographic perspective they provide an efficient means of removing heat from newly formed oceanic crust, as well as a means of altering the elements recycled into the mantle when the oceanic crust formed at spreading centers is later subducted back into the Earth's interior.