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**Deep-Sea Hydrothermal Vent Fauna: Evolution, Dispersal,
Succession and Biogeography**

Alexander Howe

ABSTRACT

Since their discovery in 1977, the ecological communities found at deep-sea hydrothermal vents have provided many surprises about life on Earth in extreme conditions and continue to instill much curiosity in scientists that study their systems as well as those simply interested in Earth's biodiversity. This review paper will attempt to provide a general overview of as many aspects of hydrothermal vents and their associated fauna as possible. The general geological processes that produce these systems and the chemosynthesis which sustains abundant life at these depths will first be covered. A basic overview of hydrothermal vent ecology, including some key organisms and general succession patterns will be taken up next. Dispersal ability, which plays a crucial role in facilitating the colonization of new habitat, structuring communities, and allowing for speciation through barriers to gene flow, will be considered. The biogeography of hydrothermal vent biotic assemblages globally will be an important topic and factors that influence it will be considered at length. Finally, what is currently known about the evolution of vent fauna will be briefly examined along with a theory which speculates on the origin of life on Earth at hydrothermal vents.

INTRODUCTION

Until 1977 and the discovery of a rich and functional ecosystem miles underwater at the Galapagos Rift in the eastern Pacific, biologists believed that sunlight was the only energy source potent and plentiful enough to sustain large-scale life. The organisms they discovered far below the photic zone, however, had evolved to capitalize on a wholly different energy source, which allowed them to survive and thrive under the extreme conditions of the deep-sea. Instead of photosynthesis, the bacteria that form the base of the food web in these unique ecosystems derive their energy from chemosynthesis, oxidizing reduced chemicals such as hydrogen sulfide and methane.

Since their initial discovery, scientists have been fascinated with all aspects of these ecosystems. Understanding the biochemical processes that allowed life to exist in such extreme environments was the first task, but broader questions of global biodiversity and ecosystem dynamics were soon raised. Because hydrothermal vents are both ephemeral and localized primarily to spreading plate boundaries, a fundamental question has centered on how vent fauna are able to disperse and colonize new habitats.

The mid-ocean ridges constitute the longest mountain chain on earth at over 80,000km long. It is not surprising that even after 30 years of exploration we have only seen a small fraction of the diversity of the deep. Still, as more and more pieces of the puzzle have been assembled, a global picture has begun to develop that allows researchers to tentatively answer some important questions about the biogeography and evolution of the vent fauna. Many questions remain to be answered and active research is being done in many fields as technology and research methods advance.

While they may be remote and seemingly inconsequential to our terrestrial existence, interest in hydrothermal vents extends beyond mere scientific curiosity. Some hypotheses about the origin of life center on these ancient geological systems and similar conditions may exist on other planets, suggesting the possibility of extraterrestrial life. In a more practical way, vent organisms may offer some unique natural products, such as high temperature tolerant enzymes.

Basic Geological Aspects of Vents and Seeps

Deep-Sea hydrothermal vents are the products of plate tectonics. At plate boundaries where two plates are spreading apart, magma from the Earth's mantle rises to fill in the fissure, creating new plate material composed primarily

of basalt. The force of the rising magma pushes the plate upwards, creating underwater mountains, or “mid-ocean ridges” as they are commonly called. Occurring at most plate boundaries, these are the longest mountain chains found on earth, stretching on for a combined total of over 80,000km. Their size, shape and topography can vary widely depending on a variety of factors such as their rate of spread. This occurs anywhere between 10 to 90mm per year, creating ridge widths between a few hundred and a few thousand yards. Mid-ocean ridges are not always found in a simple linear direction. Instead they frequently have cross-stitch zigzag formations called fracture zones (Van Dover C.L., 2000).

Hydrothermal vents form when seawater moves closer to the earth’s molten mantle through pores and fissures in the rocks at the mid-ocean ridges. The water reacts with the magma, becoming super-heated and taking on many dissolved minerals including iron, copper, and zinc. This includes hydrogen sulfide as well, which is vital to the primary-producer chemosynthetic bacteria that make up the base of the food-web in hydrothermal vent communities. The water also becomes acidic and anoxic. Because heated water is more buoyant than cold seawater, it rises up and exits back into the ocean through chimneys called smokers.

There is much variety to the types of smokers that exist, though two of the most common are white and black smokers. These differ in several important ways. Black smokers are hotter, with the exiting water temperatures in the range of 350°C to 400°C, while white smokers are generally between 250°C and 300°C. The names for the two chimneys come from the color of the water they spew. The water of black smokers is dark because the dissolved metals react with sulfur in the seawater to form metal sulfide minerals that are characteristically black in color. White have a slower flow, which allows the black metal sulfides to precipitate out before reaching the surface. The white color is due to the presence of the mineral anhydrite (Van Dover C.L., 2000).

The hydrothermal fluid exiting through the chimneys forms a rising plume that rapidly mixes with the ambient seawater until a neutral buoyancy is achieved. At this point the plume spreads horizontally away from the chimney it originated at, its direction dictated by the prevailing ocean currents. Rapid shifts in currents and the chemical composition of hydrothermal fluids can cause large changes in the local environment over very small distances. Concentration gradients of dissolved metals and chemicals can create vastly different microhabitats in close proximity. This, along with the relatively short life span of

most hydrothermal vents—usually on the order of only years to decades—creates a unique ecosystem where flexibility, adaptability, and dispersal are crucial to survival (Van Dover C.L., 2000; Micheli *et al.*, 2002).

Cold seeps are areas of the ocean floor in which hydrogen sulfide and methane are released into the open water. This can be from several different processes including reactions of seawater with certain types of sediments, hydrocarbon reservoirs (oil deposits) leaking through porous sediment, and even whale skeletons, which can host a wide variety of microbial and invertebrate life. Due to geological processes, cold seeps often occur closer to land masses along continental margins. They have a much more consistent and slow flow of chemicals than hydrothermal vents, and they persist much, much longer. Seeps can form varied topography over time with the methane reacting with seawater to form reef-like structures of carbonate (Sibuet M. & Olu K., 1998).

Vent and Seep Fauna

Hydrothermal vents and seeps typically occur at depths greater than 1000m: far below the end of the photic zone at approximately 450m (Dover *et al.*, 2002). Before the discovery of hydrothermal vent communities in 1977 (Lonsdale, 1977), it was widely assumed that the deep ocean was a desert of sparsely populated scavengers who relied on the small amount (less than 1%) of detritus that rained down from the photic zone. That there could be such productive ecosystems at these depths so far from sunlight was quite unexpected, though the process of chemosynthesis had already been discovered in the late 1800s (Jannasch & Mottl, 1985).

Chemosynthesis is the biological conversion of 1-carbon molecules, such as carbon dioxide and methane, into carbohydrates using the oxidation of inorganic compounds like sulfur dioxide and hydrogen gas for energy. While there are many different chemical pathways through which chemosynthesis can occur, some are more common than others. At hydrothermal vents, hydrogen sulfide is utilized most frequently as the reducing agent for deriving energy from, as evidenced by the ease of isolating sulfur-oxidizing bacteria and archaea from samples taken from vent communities (Ruby & Jannasch, 1982). At cold seeps, sulfur oxidizers are also present, but the most vital pathway utilizes methane as both the source of carbon and energy through oxidation (Jannasch & Mottl, 1985).

The common thread between both communities is the presence of a reduced compound (most commonly hydrogen sulfide or methane). The highly productive ecosystems of vents and seeps stem from the large influx of these reduced chemicals from below the earth's crust. In addition to the many strains of archaea and eubacteria that are adapted for life in chemosynthetic habitats, single celled eukaryotes are also common, though relatively little is known about their role or diversity. Bolidozoa and ciliates appear to be the main protist pioneers, while alveolates seem to dominate the deep sea in terms of diversity (Lopez-Garcia P *et al.*, 2003).

The invertebrate macro-fauna of hydrothermal vents and cold seeps have garnered much attention, as they primarily define the exotic look of the vent and seep communities. The most prominent members include specialized species of limpets, barnacles, bivalve mollusks, shrimp, vestimentiferan tubeworms and gastropods (Grassle, 1985). Since 1977, over 400 new species of vent fauna have been described (Dover *et al.*, 2002), and over 200 more have come from seeps (Sibuet M. & Olu K., 1998). Some animals, such as limpets and barnacles, graze or filter the chemosynthetic bacteria. Many more species including tubeworms, mussels, and clams, have developed amazing endosymbiotic relationships with the bacteria and host large colonies in specialized tissues (Grassle, 1985). Still others, such as polychaete worms and shrimp, have episymbiotic relationships with bacteria, hosting them on their exterior.

It takes a high level of specialization to live in such extreme habitats as vents and seeps, and reflecting this, many of the species described to date are endemic to these habitats (Van Dover C.L., 2000). However, there is evidence of relatedness between the biota of vents, seeps, and other chemosynthetic environments through shared taxa and even some species which can exist in more than one of these habitats (Sibuet M. & Olu K., 1998).

Some of the more interesting vent fauna include *Riftia pachyptila*, a giant tubeworm, which can grow up to two meters long in dense colonies and lives within a chitinous tube attached to the seafloor. The distinctive red plume at the "head" of the animal is retractable and contains vast quantities of hemoglobin. The hemoglobin can bind both oxygen and hydrogen sulfide, transporting this normally toxic chemical to the trophosome. This is a specialized organ that contains the endosymbiont bacteria which give the tubeworm large quantities of carbohydrates in exchange for other nutrients and a stable habitat (Van Dover

C.L., 2000; Childress & Fisher, 1992). Bivalves such as *Calyptogena magnifica* host their endosymbiont bacteria in vacuoles in their gills. Studies have shown that they can pass on the bacteria to their larvae, allowing them to begin development more quickly (Hurtado *et al.*, 2003). *Rimicaris exoculata* is a species of shrimp that is often found on or near the chimneys at hydrothermal vents. Unlike most other species of shrimp in the deep ocean, *R. exoculata* has no eye-stalks and instead has a pair of fused eyes that see in the infrared spectrum, allowing them to locate the superheated plumes of hydrothermal vent fluids (Van Dover C.L., 2000).

DISPERSAL AND GENE FLOW IN VENT COMMUNITIES

In addition to the unique characteristics of their chosen habitat, hydrothermal vent specialist species also face exceptional challenges in the dispersal and colonization of new habitats. Because hydrothermal vents occur consistently only along ocean-ridge plate boundary systems, vent fauna have a very narrow range of suitable habitats that they must reach in order to survive. The ephemeral nature of vents means that local communities can often be wiped out entirely, producing strong selection pressures for species that are good dispersers (Pond *et al.*, 2000). The qualities that vent invertebrates must possess include long-distance dispersal capabilities, high reproductive capacity, and quick development once established; all characteristics of weedy species (Dover *et al.*, 2002). Ambient temperatures of approximately 2°C throughout most of the deep ocean aid dispersal by slowing larval development, allowing for greater dispersal distances.

Colonization of new vent habitats is no easy matter, however, and there are many barriers to dispersal. Perhaps the most important of these is plate tectonics, which has led to vast changes in both the arrangement of the continents and seas, and has created many vicariant events that help to explain current biogeographical patterns of vent fauna diversity across the earth (Tunnicliffe *et al.*, 1996). Some important examples of this will be presented later in the paper.

Other important barriers occur due to the specificity of habitat required by vent animals and the narrow band that this habitat is found along. Ridge systems often have cross-axis fractures, which grow larger as plates spread apart, and are often tens of kilometers long (Tuunnicliffe V.C. & Fowler M.R., 1996). These discontinuities in an otherwise linear system cause gaps in suitable habitats and

can be difficult for dispersing larvae to navigate. Ocean currents play a large role as well, as most vent species rely on currents to transport them to suitable habitat. Ocean bathymetry (depth) is an important determinant of local currents. At mid-ocean ridges, currents are frequently along-axis, though frequent reversals in current can occur and currents may exist in opposite directions on either side of the ridge (Mullineaux & Manahan, 1998; Pond *et al*, 2000). Thus small differences in the location and timing of larvae dispersal can lead to very different dispersal directions and speeds.

Researching and understanding the dispersal capabilities of vent organisms is a difficult task, as deep-sea conditions must be recreated in a lab to examine physiological characteristics of organisms, and tracking dispersal routes *in situ* is not simple (Mullineaux & Manahan, 1998). Recently, studies have begun to examine the dispersal capabilities of certain vent invertebrates to assess how they are able to disperse and colonize new vent habitats tens and hundreds of kilometers away.

One such study examined the giant tubeworm *Riftia pachyptila* by looking at its larval lifespan in conjunction with water current analyses to assess its dispersal potential. Recreating *in situ* conditions of 2°C and 250atm, Marsh *et al.* (2001) found that the larvae of *Riftia pachyptila* could survive an average of 38 days before their protein and lipid stores ran out, giving them rarely more than 100km of dispersal potential based on local patterns of ocean currents. While currents often ran along the ridge axis, frequent reversals in current patterns occurred on the order of every 15-25 days at the test site. This led to a “random-walk” movement pattern of a test parcel designed to imitate the movement of a larva, often transporting it some distance off the ridge axis. The researchers found that only 39% of test larvae stayed within 25km of the ridge, highlighting the low chances of an individual finding suitable habitat.

Marsh *et al.* (2001) also noted that a longer lifespan was not always a benefit to survival, as the longer a larva spent in the currents, the more likely it was to be swept off axis. Many larvae may never disperse from parent’s vent site, as large numbers of larvae become trapped in the swirling hydrothermal vent plume and may simply drift back down to the same vent. At one study location a much different current regime was seen with a fast, unidirectional flow for 60 days. Dispersal potential at this rate was estimated at 245km, highlighting the importance that a favorable current can play in dispersal.

The shrimp *Rimicaris exoculata*, which is found in great numbers at vent communities along the Mid-Atlantic Ridge—and more recently at the Indian Ridge system (Dover *et al.*, 2001)—is also a very capable disperser. It uses very different mechanisms than *Riftia pachyptilla*, however, with a free-swimming, planktotrophic, post-larval stage that feeds on photosynthetically derived material, allowing it to survive for long periods as far as 100km away from vent sites (Pond *et al.*, 2000). This adaptation likely aids its dispersal capabilities by allowing it to survive when its planktonic stage is blown off course by cross-axis currents. Its adult form is also a very capable swimmer, which may have some impact on its ability to move between vent sites.

Several species of mussels from the genus *Bathymodiolus*, another species with a free-swimming planktotrophic larval stage, have also been the target of gene flow studies to determine dispersal capabilities and barriers. Craddock *et al.* (1995) examined allozyme loci and mitochondrial restriction length polymorphisms for several discrete populations of *Bathymodiolus thermophilus* that spanned from 9-13°N on the Eastern Pacific Rise ridge system to the Galapagos Rift ridge system, which intersects it running east to west. They discovered no significant barriers to dispersal with nearly identical genetic identities between populations. Won *et al.* (2003) built upon this work by returning to the same region and sampling over a much wider range of 4,900km, spanning from 13°N to 32°S along the Eastern Pacific Rise, and including the same locations on the Galapagos Rift. Their findings corroborated the work of Craddock *et al.* (1995), but also expanded upon it as they found significant genetic divergence (4.4%) from populations above and below the Easter Microplate (located northwest of Easter Island). The Easter Microplate formed around 4.5Mya and significant cross-axis current flow has been predicted based on the bathymetry of the region. These current patterns offer a compelling explanation for the genetic divergence seen between populations above and below the microplate, and it would seem that it has formed a strong barrier to dispersal for these mussel populations and likely many other vent fauna.

COMMUNITY SUCCESSION

Due to the transient nature of hydrothermal vents, vent fauna must frequently contend with both slowly expiring vent habitats, as well as vents that violently explode due to volcanic activity. While some vent sites are lost, new ones will spring up elsewhere as shifting magmatic currents beneath the Earth's

crust alter energy patterns. This recurrent habitat alteration causes succession dynamics at vents to cycle regularly, leading to similar patterns of colonization that researchers have observed.

After a natural eruption that occurred at a vent site on the East Pacific Rise, researchers had a perfect opportunity to examine succession dynamics at hydrothermal vents. They discovered that the vestimentiferan tubeworms *Tevnia jerichonana* and *Riftia pachyptila* were the first to colonize the bare basalt around the vent. These species quickly grew to visually dominate the site. Soon after the initial tubeworm establishment, the mussel *Bathymodiolus thermophilus* followed. Eventually, it overgrew the tubeworms. Gastropods—limpets and snails—came to be the most numerically abundant of the vent fauna (Shank *et al*, 1998).

Govenar *et al.* (2004) performed a clearing experiment at a vent site also located on the East Pacific Rise to examine community succession with late successional species present. They removed the tubeworms present in several plots and transported several hundred *Bathymodiolus thermophilus* mussels to the cleared sites. Following this alteration, all of the adult mussels transplanted to the cleared plots migrated away—something the researchers had not anticipated. New tubeworm propagules soon reached the site and grew quickly in the open habitat. Following their arrival, the pattern of succession described above began. Particularly interesting from their observations of the biotic composition of the plots one year after the initial alteration was the presence of *Bathymodiolus thermophilus* juveniles attached to the base of *Riftia pachyptila* tubes. This suggests that while conditions at the cleared vent site were not within the tolerable range of mussels, the presence of *Riftia pachyptila* is integral in allowing for greater biodiversity. Thus the researchers posited that tubeworms add complexity and heterogeneity to vent habitats in the Pacific Ocean, thereby increasing the species diversity that can exist by providing more microhabitats with conditions suitable to different species such as mussels, limpets, snails and shrimp.

BIOGEOGRAPHY

Provinces

Due to the unique and varied set of dispersal barriers that vent and seep organisms face, coupled with the global distribution of habitats throughout the

world's oceans, the specialist fauna of these habitats display broad patterns of biodiversity and community composition that can differ wildly. Because of this, biologists have named a total of six biogeographical "provinces" to date, with more likely as new regions are explored (Dover *et al.*, 2002; Shank, 2004).

The distinct assemblage of species present defines each hydrothermal vent biogeographic province. The Pacific Ocean, which has been the most heavily studied, is host to three of these provinces. The *Riftia pachyptila* tubeworm dominated eastern Pacific has become the most "prototypical" vent assemblage for portrayal of hydrothermal vents in the media, likely due to the original discovery of these unique habitats at the Galapagos Rift. The back-arc basins of the western Pacific form another province and are characterized by unique species of barnacles, snails, and mussels that are not seen in the eastern Pacific or the Atlantic. The Northeast Pacific ridge system found off the coast of Northwestern United States forms the third province in the Pacific Ocean. Its community structure closely resembles that of the eastern Pacific, though its ecosystem hosts unique species of those organisms (Shank, 2004).

In the north Atlantic, two provinces have been identified to date, with the shallower vents in the north and deeper vents further south both host to different species of shrimp and mussels. The most distinct aspect of these sites in comparison to their Pacific counterparts is the absence of any species of tubeworm. No exploration has been done south of the equator or into the arctic of the Atlantic, which may yield unique biotic assemblages as well (Shank, 2004).

2001 marked the first exploration of vents in the Central Indian Ocean and the biotic assemblage observed there constitutes the 6th province. This province is particularly interesting due to the geographical setting of the Indian Ocean between the Atlantic and Pacific and its possible role in linking the biota of the two oceans. More surveys are needed before generalizations can be made about how this linkage may be occurring, however. The fauna here is most closely allied to that of the Pacific, hosting primarily unique, but similar species to the vents of the eastern Pacific, however the vent shrimp *Rimicaris exoculata*, found in great numbers at vent sites in the Atlantic, is also present here (Dover *et al.*, 2001).

Vicariance

All vent invertebrates share a common reliance on the same chemosynthetic bacteria that make up the base of the food-web and share similar

adaptations for the extreme conditions of the deep-sea. Even so, the diversity of the life found at hydrothermal vent ecosystems, just like that of terrestrial ones, is very high and is growing higher as new species are discovered with nearly every new dive. In order to understand why hydrothermal vent sites around the world differ in their biotic composition so drastically, biologists are examining the processes and factors that have influenced the evolutionary pathways of vent organisms.

Similarly to terrestrial systems, allopatric speciation caused by vicariant events in the deep oceans over geological time is likely responsible for much of the diversity that we see today. This vicariance is influenced by a number of different factors, several of which have already been touched upon. Scientists have identified four major factors that are believed to primarily influence the biogeography of chemosynthetic ecosystems of the deep-sea (Shank, 2004):

- Seafloor and mid-ocean ridge topography
- Deep-sea currents
- Plate tectonics
- Stepping-stone habitats (i.e. whale falls, wood falls, cold seeps and seamounts)

The seafloor's bathymetry can vary wildly across the world's oceans and this in turn can directly influence current patterns. Due to the key role currents can play in the dispersal of vent fauna, many gene flow studies have been conducted to date in order to indirectly examine this aspect shaping hydrothermal vent biogeography (Chevaldonne *et al.*, 1997; Hurtado *et al.*, 2004; Marsh *et al.*, 2001; Vrijenhoek, 1997; Won *et al.*, 2003). Currents play a clear role in both hindering and aiding vent fauna in dispersing and colonizing new vent sites. When currents run along the plate boundaries where most hydrothermal vents are found, they play an integral role in moving the larvae of vent fauna to new locations. Currents are rarely, if ever, static, and as the Marsh *et al.* (2001) study on *Riftia pachyptila* larval dispersal shows, currents can often shift and blow larvae off of a ridge axis which in most cases will result in their death. Vent fauna have most clearly adapted to the low probability of successful colonization by adopting the r-selective traits characteristic of weedy species; these include long-distance dispersal capabilities, high reproductive capacity and quick development once established (Dover *et al.*, 2002).

The topography of mid-ocean ridges is a critical determinate of vent biogeography, as it is primarily along this narrow range that vent habitats are

found and thus it provides a vital limitation to where vent fauna must disperse in order to colonize new habitat. Large faults, called fracture zones, are common along ridges and break up their otherwise predominantly linear geometry. The size of the fracture zones and the rift valley that runs down the middle of the ridge system can vary greatly, with the rate of plate spreading largely dictating the topography of the plate boundary where the ridge is found. The East Pacific Rise, for example, spreads at a much faster rate than the Mid-Atlantic Ridge. Accordingly, fracture zones in the Pacific are significantly smaller—on average ten kilometers—while fracture zones in the Atlantic can be hundreds of kilometers long (Shank, 2004). The spreading rate of the plates also affects how wide and deep the rift valley is. Narrow and shallow rift valleys are characteristic of the Pacific Ocean (200 meters wide and 10 meters deep on average), while the Atlantic's rift valleys are much deeper and wider (2 kilometers deep and 1 kilometer wide on average) (Shank, 2004). With large fracture zones and wide and deep rift valleys in the Atlantic, hydrothermal vent fauna found there may have a much more difficult time dispersing between vent habitats than their Pacific cousins do.

While no vent sites have been explored to date in the South Atlantic, it is hypothesized that the biotic assemblages found there may be quite different than those that have been observed at sites in the North Atlantic (Shank, 2004). This is due to a section of the Mid-Atlantic Ridge at the Equator where gargantuan fracture zones are found, called the Romanche and Chain Fracture Zones. Here the fractures are so wide, deep, and long that bottom currents are channeled through at around 1 million cubic feet per second (Shank, 2004). This may create a nearly impenetrable wall for larvae attempting to disperse into or out of the North Atlantic and could at least partially explain the distinctive biotic assemblage existing there. Similarly, more research is needed to determine if the Drake Passage between the southern tip of South America and Antarctica is acting as a barrier or aid to the dispersal of vent fauna between the Pacific and the Atlantic. The Antarctic Circumpolar Current may act as a wall between the two oceans, or it may aid larvae in quickly moving them to new habitats.

Plate tectonic history is a vital component for gaining a broader understanding of current vent assemblage biogeography. As with terrestrial ecosystems, the movement of the earth's plates has created many vicariant events that likely explain much of the biodiversity that we see today. Tunnicliffe *et al.* (1996) examined plate tectonic history in conjunction with what is currently

known about the species found at the different biogeographic provinces. Their analysis suggests that current vent assemblages are closely linked to the timing of the movement of the plates.

One clear example of how plate tectonics can create vicariance for hydrothermal vent animals is shown in the closely related species of the Juan de Fuca and East Pacific Rise ridge systems. These used to be part of a continuous ridge, but the advance of the North American plate westward broke up the ridge 30 million years ago into the two parts we see today (the San Andreas Fault in California is the terrestrial continuation of the East Pacific Ridge) (Tunnicliffe *et al.*, 1996). Consequently the organisms at the Juan de Fuca Ridge were functionally isolated from the East Pacific Ridge and with the absence of gene flow they began to evolve along a different evolutionary pathway. The northeastern tubeworms (*Ridgea piscesae*), for example, have skinnier tubes than their southeastern cousins (*Riftia pachyptila*), from whom they diverged.

The interface of plate tectonics and biological niche differences between vent fauna have also been proposed for explaining the differences we see between the Pacific and Atlantic. It has been suggested that the salinity of the newly forming Atlantic may have been considerably higher than the ancient Pacific due to the infant Atlantic's shallow depth. The shrimp that dominate in the Atlantic are known to be more tolerant to high salinities, so it is possible that they were able to gain a foothold in these environments earlier and prevented the tubeworms of the Pacific from ever gaining a foothold (Shank, 2004).

Similarly, the rate of spreading of the Atlantic and Pacific plates may partially explain the differences in the biotic assemblages observed between the two oceans' vent sites. The Pacific, with its fast spreading rate, has a quicker turnover of vent sites with more frequent eruptions that wipe out all life present. This may favor the tubeworms that are often the first to colonize new vent habitats and could explain their prevalence in the Pacific (Shank, 2004). Conversely, the Atlantic, with its slower spreading rate, has longer-lived vents that may be more amenable to the mid to late-stage succession shrimp that dominate there.

Finally, other chemosynthetic based ecosystems may hold some answers to questions about vent fauna evolution and dispersal. Seamounts (undersea volcanoes that form over hotspots) may act as stepping-stones to other vent habitats and could allow vent species to disperse in non-linear ways and reach other ridge sections that they could not normally get to. They may also act as

refugia for vent species, providing a stable habitat from any deep-sea mass extinctions and acting as a source for re-colonization of hydrothermal vents (Shank, 2004).

Cold seeps—much longer-lived and more geologically stable than hydrothermal vents—may also provide an intermediate chemosynthetic environment for vent species. Similarly, whale and wood falls have been discovered that are host to entire ecosystems of chemosynthetic organisms, analogous in their composition to vent sites. There is even some overlap in the species that inhabit all of these chemosynthetic habitats. Unlike most detritus that rains down from the shallow waters above, wood and whale bones are not quickly decomposed, leading to relatively stable environments that allow for the development of complex ecosystems. The bacteria that decompose this organic matter have hydrogen sulfide as one of their metabolic waste products, allowing for the overlap between seep and vent fauna. Especially along whale migratory routes or river mouths where trees may be washed out from heavy floods, these special habitats may be important conduits for the movement of various chemosynthetic organisms, though how important they may be is not yet known.

EVOLUTION

Similar to their potential role in aiding dispersal for vent organisms, other chemosynthetic habitats such as cold seeps, whale falls, and tree falls may have played an important role in facilitating the adaptation for and colonization of vent habitats over evolutionary time. Distel *et al.* (2000) provides some compelling evidence for this evolutionary trajectory in the mussel subfamily Bathymodiolinae, which is composed of species endemic to various chemosynthetic habitats. Based on 18S rRNA sequence data from the different species in this subfamily, there is remarkable genetic similarity (>98.5% for the whole family, >99.7% between vent and seep taxa). This suggests a recent common ancestor and evolutionary split between species within this family, and thus a relatively rapid diversification between these different environments. Although the evidence is not conclusive, the suggested phylogeny based on the same genetic analysis places a species of mussel found only at whale and wood fall sites as the basal member of this monophyletic clade. If this proves to be true, then it would point to an earlier association with whale and wood falls and a subsequent adaptive radiation to vent and seep environments. As whale and wood fall environments are commonly found at shallower depth than cold seeps and hydrothermal vents,

this evolutionary progression would fit well with a model of incremental colonization of deeper and deeper marine environments by vent invertebrates.

In Little & Vrijenhoek (2003), the authors examine the literature on vent and seep fossil remains as well as molecular clock studies aimed at predicting the age of certain extant species. Their goal was to investigate the hypothesis that vent fauna are relic species that evolved in the Paleozoic (>245Mya). Under this hypothesis, hydrothermal vents acted as stable refugia during major oceanic extinction events such as during the Cenomanian-Turonian boundary near the end of the Mesozoic (~91Mya), or at the end of the Paleozoic when anoxic conditions prevailed.

Their findings, however, indicate that at least the ecologically dominant modern vent fauna are not living fossils and instead have their evolutionary origins more recently than the Paleozoic. Vestimentiferan tubeworms, for instance, have had their age estimated from molecular clocks calibrated by the vicariant event that separated the East Pacific Rise from the Juan de Fuca Ridge. Based on this calibration their age is estimated to be somewhere between 50 to 126 Mya, placing their origin in the mid-Cenozoic to late Mesozoic. Vesicomylid clams have had their molecular clock calibrated by fossil records and their common ancestor is predicted to have lived only 22-44 Mya during the Cenozoic. The subfamily of mussels discussed above, Bathymodiolinae, is predicted to have diverged from other mytilids 56-94 Mya during the mid Mesozoic to early Cenozoic. It is expected that the split between vent and seep lineages occurred as recently as 22 Mya. Finally, bresiliid shrimp have left no fossil record, but a molecular clock calibration borrowed from related taxa suggests they may have diversified sometime in the past 20 million years.

While there are many problems with both the fossil record of hydrothermal vent habitats as well as the use of molecular clocks to predict the age of lineages, the authors still made the assessment that the two lines of evidence generally corroborated one another. As gaps in the fossil record are filled in, new light may be shed on the ages of some vent fauna. However, it would seem that based on the more recent origins of many of the dominant vent fauna in the late Mesozoic to Cenozoic, hydrothermal vents have not been immune from extinction events that have affected diversity in the photic zone. It may be possible, as Shank (2004) suggests, that other habitats such as seamounts or seeps may have acted as refuges for chemosynthetic fauna. By protecting the biotic assemblages found there from deep-sea catastrophes, they were able to

subsequently reseed those environments. Subsequent adaptive radiation of those newly colonizing species may have led to the modern biotic assemblages. This may have occurred multiple times across geological time, and could explain why many of the current species we see at hydrothermal vents seem to be relatively young.

The Origin of Life?

Though most vent invertebrates likely have their origin in the photic zone, subsequently adapting to the deep sea and hydrothermal vents, at least one theory on the origin of life on Earth postulates that the first proto-ecological systems occurred at hydrothermal vents. In Martin & Russell (2003), the authors point to several important features of the hydrothermal vent that makes it a good candidate for abiogenesis (the origin of life). Because the smokers at hydrothermal vents are made of porous metal sulfides, the “micro-caverns” that exist in these structures may have been a key to the organizing of organic molecules that can spontaneously form given the right conditions. These micro-caverns could provide the necessary three-dimensional structure that would allow for temperature and chemical concentration gradients. These gradients could have been crucial to the synthesis of monomers and polymers of amino acids in the absence of catalyzing protein enzymes. The micro-caverns would also allow for sufficiently high concentrations of key chemicals to build-up, increasing the likelihood of the catalyst of certain reactions. Hydrothermal vents provide a constant source of energy and reduced chemicals that would also be an important factor in the synthesis of some key organic molecules. An important element of this theory is that a lipid membrane, the presence of which is how we currently define “life”, is not actually necessary until all cellular functions are present due to the presence of the hydrothermal vent chimney’s micro-caverns providing a similar structural function.

Under this theory, the rise of archaeobacterial and eubacterial lineages occurred independently of one another, but in similar environments. One of the fundamental differences between both lineages is a different lipid membrane composition, and under this theory of independent origins the different lipid membranes could easily have arisen due to chemical differences between habitats. The authors estimate this origin at approximately 3.8 billion years ago, with the eukaryotic lineage arising from a symbiotic event between eubacteria and archaeobacteria around 2 billion years ago. This theory has important

implications for extraterrestrial life, as similar conditions to those at hydrothermal vents are expected to prevail on certain planets and moons within our solar system. However, this proposed mechanism for abiogenesis has not been proven and it is not currently clear whether it could actually work. Still, it is an interesting component of a discussion about hydrothermal vents and suggests a potentially crucial role they may have played in facilitating life's origin.

CONCLUSION

As pieces of the biogeographical and evolutionary puzzle of hydrothermal vent life are put together through the collaborative work of scientists in different fields, a broader picture of life at these extreme conditions is slowly coming together. Many aspects remain unclear however. For instance, what role might other chemosynthesis-based ecosystems play, both in the evolutionary history, as well as the dispersal of different vent fauna? How have past climatic events affected, if at all, the biodiversity at these seemingly buffered ecosystems? Did life originate at hydrothermal vents and what implications might this have on our understanding of the potential for extraterrestrial life?

Many of these questions may not be answered for some time, if at all. However, research is active and ongoing in this field. In order to fill in some key gaps in our understanding—particularly on the unique and fascinating biogeography of vent fauna—researchers are targeting some areas specifically. Some important areas include the South Atlantic, which should help to reveal the extent to which the Romanche and Chain Fracture zones located at the Equator are acting as barriers to dispersal between the North and South Atlantic. The seafloor off the coast of New Zealand and the Chile Rise should be informative locations for examining the interplay of different chemosynthetic environments such as whale falls, wood falls, seeps and vents. The East Scotia Rise, located in the Drake Passage, will provide important information regarding the role this narrow passageway plays in dispersal between the Pacific and Atlantic. Finally, the Gakkel Ridge in the Arctic Ocean, previously thought not to have hydrothermal vents due to its ultra-slow spreading speed, will be an incredibly interesting location to explore, as it has existed in relative isolation from any other mid-ocean spreading centers for millions of years. It is possible that an entirely unique fauna has developed here over that time period.

Even with our current knowledge, though, it is clear that we do already understand a great deal about hydrothermal vents and the ecosystems that they

support. What this knowledge points to is an incredibly fascinating system quite unlike any other that we've encountered. Life has once again shown its amazing ability to evolve and adapt to survive in conditions that would seem to be impossible to exist in. Whatever questions or interests may stimulate an individual, hydrothermal vents are an important topic for furthering our understanding of the diversity of life and the conditions under which it can exist.

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