

Biogeography and chemosynthetic adaptation of deep-sea hydrothermal vent organisms

Won-Kyung Lee^{1,2}, Yong-Jin Won^{2*}

요약: The mid-ocean ridge systems are complex geologic structures that create new oceanic crusts at the marine plate boundary. They have a total length of about 65,000 km and are distributed globally. At these plate boundaries, seawater subjected to deep-sea hydraulic pressure enters the interior of the seafloor along cracks in the crust and then becomes heated by the magma heat source beneath the oceanic crust and gushes back to the seafloor's surface. This erupted hot seawater is mixed with heavy metals and other chemical compounds generated through the reaction between the seawater and the rocks of the oceanic crust and leached out, significantly impacting the deep sea's chemical composition. This kind of water circulation that erupts like hot spring water in the ocean crust is called hydrothermal vents and is distributed throughout the global ocean along plate boundaries. For the first time in 1977, earth scientists who began exploring deep-sea hydrothermal vents near the Galapagos Islands discovered a previously unknown ecosystem around these vents. Surprisingly, marine invertebrates and microorganisms thrived in this extreme oceanic environment where light could not reach. This discovery sparked the idea that an ecosystem different from a terrestrial one based on photosynthesis using solar energy may exist on Earth. Afterward, based on the circulation of chemicals operated by the Earth's internal heat and the organic synthesis by marine bacteria and archaea, this ecosystem came to be called the 'chemosynthesis-based ecosystem.' Furthermore, due to over 40 years of ocean exploration and biological research, our understanding of the biogeography and evolution of the species of hydrothermal vent communities has deepened.

키워드: mid-ocean ridge systems, hydrothermal vents, biogeography, chemosynthesis, chemosynthesis-based ecosystem

¹*Division of Biomedical Research, Korea Research Institute of Bioscience and Biotechnology, Daejeon, Republic of Korea*

²*Division of Ecoscience, Ewha Womans University, Seoul, Republic of Korea*

*Corresponding author: won@ewha.ac.kr

Geographic distribution of the hydrothermal vent ecosystem

Since the discovery of the first deep-sea hydrothermal vent and its dense biological community specially adapted to this environment in the Galapagos Rift in 1977 (Weiss et al. 1977; Corliss et al. 1979), the continuing deep-sea exploration and research for more than 40 years has led to the discovery of new hydrothermal vent communities. These deep-sea hydrothermal vent communities were known to be distributed like oases in the desert along the volcanic fields of mid-ocean ridges and subduction zones at ocean floor plate boundaries (Tunnicliffe 1991). The history of deep-sea exploration has revealed the full extent of

hydrothermal vent distribution worldwide. As our understanding deepens about the geographical distribution of deep-sea hydrothermal vent animals, the more interesting they become. For deeper understanding, it is necessary to have comprehensive knowledge of both the physicochemical and geological characteristics of habitats, as well as the biological characteristics of these organisms. First, let's look at the geological characteristics of deep-sea hydrothermal vents. Deep-sea hydrothermal vents distribute geographically isolated over distances spanning from tens to hundreds of kilometers (Baker et al. 2016). This spatial distribution is also closely connected to the formation process of deep-sea hydrothermal vents, which serve as a habitat for vent animals. Deep-sea hydrothermal vents are sites on the seafloors where the heated water surges and is discharged through cracks in the crust. They typically form in areas with dynamic tectonic activity around the plate boundaries, where new oceanic crust formed due to rising magma (Figure 1). Hydrothermal vents are distributed along the mid-ocean ridge (MOR), where plates spread apart as they move in opposite directions. They are also found in the back-arc basin (BAB) within the subduction zone, where one plate converges with another, and in seamount areas with volcanic activity on the ocean floor.

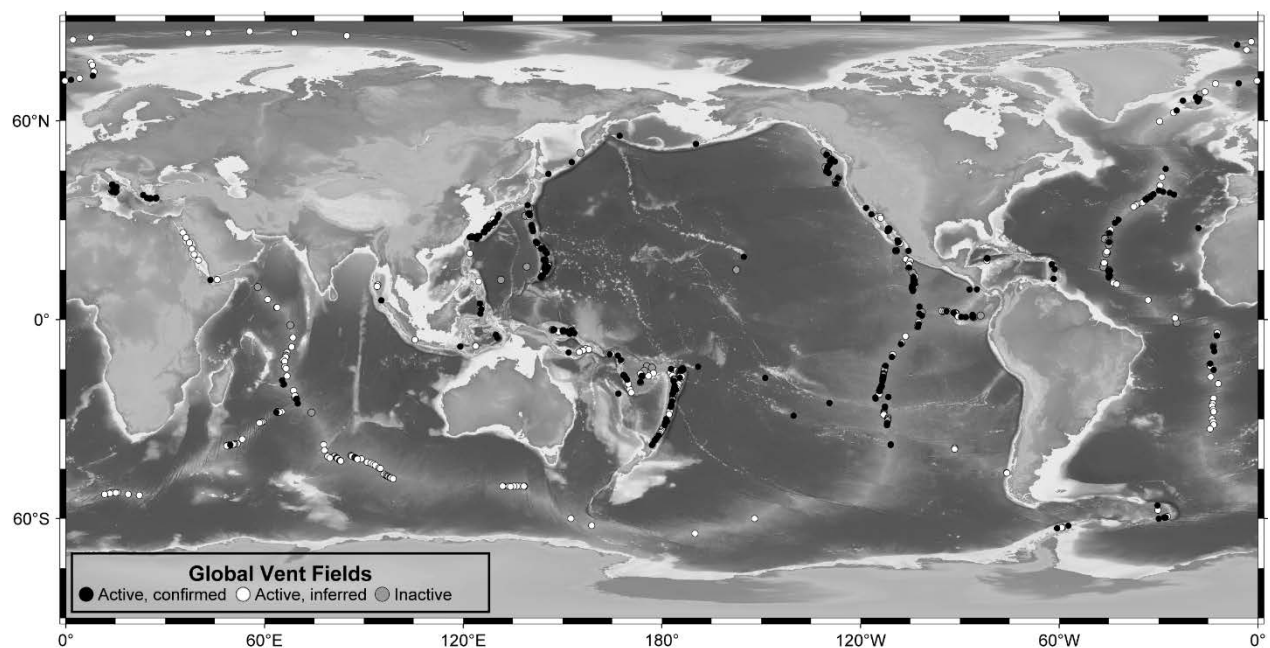


Figure 1. Distribution map of deep-sea hydrothermal vents discovered in the world's oceans. Three different types of hydrothermal vents are shown: active (confirmed), active (inferred), and inactive hydrothermal vents, respectively.

The MOR is a geological structure formed by the cooling process resulting from the

transfer of heat from the earth's interior to the surface, driven by mantle convection and upwelling. It forms an extensive underwater mountain range that stretches across the seafloor, at depths of about 2,000-3,000 m. One can easily imagine the MOR by thinking of the Earth as a baseball and the MOR as stitched threads on the baseball. The total length of MOR that runs along the sea floor adds up to 65,000 km, which makes MOR the single largest geological structure on earth's surface. Also, if one opens a map of the ocean floor and traces along the MOR, one can observe its continuous path encircling the Pacific, Atlantic, and Indian Oceans all around the globe. This path even extends around Antarctica and reaches the Arctic Sea. However, the MOR is not uniformly connected, featuring sparsely interspersed empty spaces and shifts in ridge axes due to transform faults. Meanwhile, the BABs are densely distributed in the western Pacific Ocean. The BABs are formed by the geological process of subduction, where one oceanic plate converges with another, leading to the expansion which is accompanied by rising and melting of the mantle, creating hydrothermal vents on the sea floor. The structure of BABs in the western Pacific Ocean is patchy which is geographically spaced apart and thus biological connectivity has been expected to be much weaker than linear continuous ridges. These characteristics of geological structure are related to connectivity and significantly influence the distribution and endemism of animals living near hydrothermal vents (Mitarai et al. 2016).

Second, let us explore the biological characteristics of the deep-sea hydrothermal vent. It is known as a chemosynthetic-based ecosystem because it relies on chemical compounds such as hydrogen, methane, and hydrogen sulfides dissolved in vent fluid. In this ecosystem, chemosynthetic autotrophic bacteria are the primary producers that synthesize organic compounds by utilizing oxidizing chemical energy. These bacteria are like plants in photosynthesis-based terrestrial environments. However, how do these chemosynthesis-based primary producers provide nutrients and energy to other animals? Interestingly, hydrothermal vent animals form a symbiotic relationship with these chemosynthetic autotrophic bacteria, gaining nutrients and energy from them. For example, deep-sea vent mollusk mussels have sulfur-oxidizing or methane-oxidizing symbionts in their gill cells, absorbing nutrients by dissolving them within the cells (Duperron et al. 2005; Won et al. 2008; Jang et al. 2020). This intracellular symbiotic relationship is widely observed in deep-sea vent clams, snails, and tubeworms (Vrijenhoek 2010c). Annelid vent tube worms show an extreme example of an anatomical evolution in which they lost digestive organs due to their inability to digest or consume nutrition by themselves. Another form of symbiosis is ectosymbiosis. In this case, bacteria are 'farmed' on the surface of organisms and the organisms consume them directly. Examples are vent shrimps (Guri et al. 2012) and crabs (Thurber et al. 2011). Overall, interruptions in hydrothermal water supply resulting from changes in magma activity

might lead to the cutoff of chemical energy sources and primary production, eventually posing a threat to the existence of the hydrothermal vent ecosystem (Dick 2019). Therefore, the tectonic activity also affects the temporal stability of the vent ecosystem as well as its spatial distribution.

Chemosynthesis-based ecosystems also appear in completely different environments. In 1983, a community of organisms that had settled in a new environment was discovered on the deep seafloor of the escarpment off Florida in the Gulf of Mexico (Paull et al. 1984). This biological community is called a cold-seep ecosystem because it is formed in the same cold temperature range as the surrounding seawater. Here, fluids rich in hydrocarbons, such as hydrogen sulfide and methane, seep out from the seafloor sediments. For this reason, species such as tube worms and mussels, which are very similar to those inhabiting hydrothermal vents, inhabit these areas. Another type of chemosynthetic ecosystem has been discovered in microhabitats such as whale carcasses and trees that have sunk to the seafloor. In 1987, a whale carcass was discovered in the deep sea off California. As the organic matter of the whale carcass was decomposed by decomposing microorganisms, an environment was created with high concentrations of reduced compounds, and a community of organisms similar to vent fauna adapted to this environment was discovered (Smith et al. 1989). In this way, it can be seen that organisms specially adapted to this environment have evolved in the ocean's chemosynthetic ecosystem, which was created by different mechanisms. Additional research has revealed that these organisms having adapted to chemosynthetic environments have very high taxonomic and evolutionary affinity. This means that at some point in the past, species descended from a common ancestor adapted and evolved to different places and environments around the bottom of world oceans (Peek et al. 1997; Distel et al. 2000; Jones et al. 2006; Dutilleul et al. 2008; Lorion et al. 2013; Kiel 2016).

Spreading rate of Mid Ocean Ridge

The stability of deep-sea hydrothermal vent ecosystem is closely linked to particularly the spreading rate of oceanic plates (Juniper and Tunnicliffe 1997; Vrijenhoek 1997). The fast-spreading ridges have dynamic volcanic activity, resulting in earthquakes and volcanic eruptions which destroy hydrothermal vents where vent animals inhabit. At the same time, new hydrothermal vents are created frequently. Frequent formations of new hydrothermal vents lead to the geographical proximity of habitats for vent animals. As evidence, hydrothermal vents formed in tight geographic intervals on the East Pacific Rise, which has the greatest magma activity and the fastest plate spreading rate (>140 mm per year) on Earth (Bird 2003). Also, the periodic extinction of biological communities due to the eruption of the submarine volcano has been observed, which led to the study of the succession of vent communities

(Tunnicliffe et al. 1997; Shank et al. 1998; Mullineaux et al. 2010). Conversely, on the ridges with a slow spreading rate, destruction or the formation of new hydrothermal vents due to volcanic activity is rarely observed. This results in relatively distant geographic locations between vent habitats (Beaulieu, et al. 2015). The Mid-Atlantic Ridge serves as an example with slow spreading rate (20-50mm per year), exhibiting sporadic formation of new hydrothermal vents and very distantly dispersed hydrothermal vents.

In addition to the geographical distribution of hydrothermal vents, their temporal persistence also varies depending on the region. In areas with dynamic magma activity, such as the MOR of the East Pacific, the rate of formation and extinction of hydrothermal vents is high due to frequent lava eruptions (Vrijenhoek 1997). On the other hand, the duration of hydrothermal vents at MOR with slow or moderate expansion rates is estimated to be as long as 1,000 years or more (Van Dover et al. 2002; Vrijenhoek 2010a). The Rainbow Vent Field in the Atlantic Ocean and the Juan de Fuca Ridge in the Northeast Pacific Ocean may be examples. Overall, these spatiotemporal characteristics play a crucial role in shaping the connectivity and dispersal patterns of animals inhabiting hydrothermal vents.

Evolutionary response to the instability of hydrothermal vent ecosystem

In barren areas where there is no hydrothermal activity, habitat discontinuity is inevitable. However, to adapt to the deep-sea hydrothermal environment, where instability exists in hydrothermal water supply, hydrothermal vent animals have evolved several characteristics in common. They have developed an ability to travel far distance to settle in a new habitat and, after settlement, to grow rapidly and reproduce at an early stage to survive in an unstable environment. For these characteristics, deep-sea biologists sometimes compare deep-sea hydrothermal animals to 'weeds' in terrestrial ecosystems (Vrijenhoek 2010b). However, the distinct life history of each species leads to different geographical connectivity even in the same deep-sea hydrothermal environment.

Among various biological characteristics, larval migration plays a pivotal role in determining the geographical distribution of species. Most deep-sea hydrothermal vent animals migrate along ocean currents during their larval stage and mature into adults after settling in a new habitat. From this point on, they no longer migrate. The distance traveled during the larval period can be predicted by the survival time estimate of each species and the dispersal mechanism along the ocean currents. A representative example is the case of deep-sea mussels, which are commonly found in all oceans. Deep-sea mussels undergo a planktotrophic larval stage which enables them to swim (Laming et al. 2018). This adaptation ensures relatively longer survival periods as they can feed while traveling and facilitates migration to distant habitats through free swimming (Lutz et al. 1980; Arellano and Young

2009). Another example is tube worms, one of the prominent vent animals. Tube worms undergo a lecithotrophic larva stage. During this larval stage, tube worms can survive for approximately 6 weeks by feeding on the nutrients in the egg yolk (Marsh et al. 2001). Considering the flow of the deep-sea ocean currents in the East Pacific, tube worms are estimated to travel about 100-200 km. Based on the habitat distribution along the East Pacific Rise, this travel distance is sufficient to find a new vent habitat. Pompeii worms, an annelid polychaetes observed in the eastern Pacific, also go through a lecithotrophic larva stage like tube worms, but their eggs are much heavier restricting their ability to move along the ocean currents (Pradillon and Gaill 2003). Nevertheless, it has been proven through laboratory experiments that the larval development of the Pompeii worm stops when the water temperature drops below 2° C and continues to develop when the water temperature rises again (Pradillon et al. 2001). This means that their larvae could halt development when the water temperature drops, conserving the time to travel by drifting with the current until they reach a suitable environment where the water temperature rises. The characteristic of this developmental process, referred to as Prolonged Larval Duration (PLD), implies high dispersal potential for new habitats.

Hydrothermal vent animals with distinct geographical characteristics

In addition to the geological characteristics of ocean ridges, deep-sea hydrothermal animals show the distribution of geographic separation influenced by the ocean currents, depth, and topographical characteristics. Abiotic factors that block the dispersal of animals are called physical (or dispersal) barriers. As mentioned earlier, the effectiveness of dispersal barriers may vary depending on the species-specific life historical traits. The effects of physical barriers have been studied extensively across several species found in the eastern Pacific region. The following are the examples of animals in this region. Along the MOR in the eastern Pacific Ocean, there is a rift valley called ‘Hess Deep’ near the equator. This is a long, narrow valley formed between two parallel faults. The water depth of the Hess Deep Rift is approximately 6,000 m, and the valley crosses the northern and southern regions of the East Pacific Rise. Tube worms of the genus *Riftia* and pompeii worms of genus *Alvinella*, as well as various species of gastropods, such as snails and limpets, exhibit geographic subdivision, partitioned into northern and southern regions (Hurtado et al. 2004; Johnson et al. 2008; Plouviez et al. 2009; Coykendall et al. 2011; Jang et al. 2016). In contrast, deep-sea mussels of genus *Bathymodiolus* and scale worms of genus *Branchiopolynoe* living in symbiosis with deep-sea mussels, inhabit the same region but are largely unaffected by the physical barrier. This species-specific effect also has significant implications for research on hydrothermal vent animals inhabiting other ocean ridges (Hurtado

et al. 2004; Plouviez et al. 2009; Johnson et al. 2013).

As proven by the exploration of deep-sea hydrothermal vents over 40 years, one of the most representative biogeographical characteristics of hydrothermal organisms is their high endemism. Local endemism means that a species distribution is restricted to a specific region. On average, about 70% of hydrothermal species are endemic, found only in certain regions but are not found in any other. Biological communities of hydrothermal vents around the world are divided into five to eleven distinct provinces based on vent fauna (Tunnicliffe et al. 1998; Van Dover et al. 2002; Bachraty et al. 2009; Rogers et al. 2012). The discrepancy among studies arises from variations in the geographical scope, the number of species studied, the level of phylogenetic classification applied, and the specific statistical models utilized for comparative analysis. However, in general, vent fauna can be divided into distinct groups within each region. Due to the structural features of the MOR, hydrothermal vent habitats are restricted to small areas and considerable distance exists between them, which serve as the primary criteria for delineating biogeographic regions in the entire ocean. This is because hydrothermal vent animals have a clear limit in their overall migration distances.

According to the updated information in InterRidge Vents Database Version 3.4 in 2020 (Figure 1), more than 700 hydrothermal vents have been discovered since the first discovery of hydrothermal vents near the Galapagos Islands in 1977, and although not confirmed, approximately 600 more vents are expected to exist (Beaulieu and Szafranski 2020). Information regarding the biogeographic distribution of deep-sea hydrothermal ecosystems will continue to be updated, incorporating research findings on newly discovered hydrothermal vent fields and fauna through ongoing exploration.

사사

We thank Dong-Sung Kim in KOIST, Sung-Hyun Park in KOPRI, and other scientists in these institutes for their help on our cruises to the Antarctic and Indian Ocean. We are grateful to Prof. Seung-Sup Kim for his generosity in providing us with the world hydrothermal vent map. .

References

- Arellano SM, Young CM. 2009. Spawning, development, and the duration of larval life in a deep-sea cold-seep mussel. *The Biological Bulletin* 216:149-162.
- Bachraty C, Legendre P, Desbruyeres D. 2009. Biogeographic relationships among deep-sea hydrothermal vent faunas at global scale. *Deep Sea Research Part I: Oceanographic Research Papers* 56:1371-1378.
- Baker ET, Resing JA, Haymon RM, Tunnicliffe V, Lavelle JW, Martinez F, Ferrini V, Walker SL,

- Nakamura K. 2016. How many vent fields? New estimates of vent field populations on ocean ridges from precise mapping of hydrothermal discharge locations. *Earth and Planetary Science Letters* 449:186-196.
- Beaulieu SE, Baker ET, German CR. 2015. Where are the undiscovered hydrothermal vents on oceanic spreading ridges? *Deep Sea Research Part II: Topical Studies in Oceanography* 121:202-212.
- Beaulieu SE, Szafranski KM. 2020. InterRidge Global Database of Active Submarine Hydrothermal Vent Fields Version 3.4. PANGAEA.
- Bird P. 2003. An updated digital model of plate boundaries. *Geochemistry, Geophysics, Geosystems* 4.
- Corliss JB, Dymond J, Gordon LI, Edmond JM, von Herzen RP, Ballard RD, Green K, Williams D, Bainbridge A, Crane K. 1979. Submarine thermal springs on the Galapagos Rift. *Science* 203:1073-1083.
- Coykendall DK, Johnson SB, Karl SA, Lutz RA, Vrijenhoek RC. 2011. Genetic diversity and demographic instability in *Riftia pachyptila* tubeworms from eastern Pacific hydrothermal vents. *BMC evolutionary biology* 11:96.
- Dick GJ. 2019. The microbiomes of deep-sea hydrothermal vents: distributed globally, shaped locally. *Nature Reviews Microbiology* 17:271-283.
- Distel DL, Baco AR, Chuang E, Morrill W, Cavanaugh C, Smith CR. 2000. Do mussels take wooden steps to deep-sea vents? *Nature* 403:725-726.
- Dubilier N, Bergin C, Lott C. 2008. Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. *Nature Reviews Microbiology* 6:725-740.
- Duperron S, Nadalig T, Caprais J-C, Sibuet M, Fiala-Médioni A, Amann R, Dubilier N. 2005. Dual symbiosis in a *Bathymodiolus* sp. mussel from a methane seep on the Gabon continental margin (Southeast Atlantic): 16S rRNA phylogeny and distribution of the symbionts in gills. *Applied and Environmental Microbiology* 71:1694-1700.
- Guri M, Durand L, Cuffe-Gauchard V, Zbinden M, Crassous P, Shillito B, Cambon-Bonavita M-A. 2012. Acquisition of epibiotic bacteria along the life cycle of the hydrothermal shrimp *Rimicaris exoculata*. *The ISME journal* 6:597-609.
- Hurtado LA, Lutz RA, Vrijenhoek RC. 2004. Distinct patterns of genetic differentiation among annelids of eastern Pacific hydrothermal vents. *Molecular Ecology* 13:2603-2615.
- Jang S-J, Ho P-T, Jun S-Y, Kim D, Won Y-J. 2020. A newly discovered *Gigantidas* bivalve mussel from the Onnuri Vent Field in the northern Central Indian Ridge. *Deep Sea Research Part I: Oceanographic Research Papers* 161:103299.
- Jang S-J, Park E, Lee W-K, Johnson SB, Vrijenhoek RC, Won Y-J. 2016. Population subdivision of hydrothermal vent polychaete *Alvinella pompejana* across equatorial and Easter Microplate boundaries. *BMC evolutionary biology* 16:1-15.

- Johnson S, Warén A, Vrijenhoek RC. 2008. DNA barcoding of *Lepetodrilus* limpets reveals cryptic species. *Journal of Shellfish Research* 27:43-51.
- Johnson SB, Won Y-J, Harvey JB, Vrijenhoek RC. 2013. A hybrid zone between *Bathymodiolus* mussel lineages from eastern Pacific hydrothermal vents. *BMC evolutionary biology* 13:1-18.
- Jones W, Won Y, Maas P, Smith P, Lutz R, Vrijenhoek R. 2006. Evolution of habitat use by deep-sea mussels. *Marine Biology* 148:841-851.
- Juniper SK, Tunnicliffe V. 1997. Crustal accretion and the hot vent ecosystem. *Philosophical Transactions of the Royal Society of London. Series A: Mathematical, Physical and Engineering Sciences* 355:459-474.
- Kiel S. 2016. A biogeographic network reveals evolutionary links between deep-sea hydrothermal vent and methane seep faunas. *Proceedings of the Royal Society B: Biological Sciences* 283:20162337.
- Laming SR, Gaudron SM, Duperron S. 2018. Lifecycle ecology of deep-sea chemosymbiotic mussels: a review. *Frontiers in Marine Science* 5:282.
- Lorion J, Kiel S, Faure B, Kawato M, Ho SY, Marshall B, Tsuchida S, Miyazaki J-I, Fujiwara Y. 2013. Adaptive radiation of chemosymbiotic deep-sea mussels. *Proceedings of the Royal Society B: Biological Sciences* 280:20131243.
- Lutz R, Jablonski D, Rhoads D, Turner R. 1980. Larval dispersal of a deep-sea hydrothermal vent bivalve from the Galapagos Rift. *Marine Biology* 57:127-133.
- Marsh AG, Mullineaux LS, Young CM, Manahan DT. 2001. Larval dispersal potential of the tubeworm *Riftia pachyptila* at deep-sea hydrothermal vents. *Nature* 411:77-80.
- Mitarai S, Watanabe H, Nakajima Y, Shchepetkin AF, McWilliams JC. 2016. Quantifying dispersal from hydrothermal vent fields in the western Pacific Ocean. *Proceedings of the National Academy of Sciences* 113:2976-2981.
- Mullineaux LS, Adams DK, Mills SW, Beaulieu SE. 2010. Larvae from afar colonize deep-sea hydrothermal vents after a catastrophic eruption. *Proceedings of the National Academy of Sciences* 107:7829-7834.
- Paull CK, Hecker B, Commeau R, Freeman-Lynde R, Neumann C, Corso W, Golubic S, Hook J, Sikes E, Curran J. 1984. Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. *Science* 226:965-967.
- Peek A, Gustafson R, Lutz R, Vrijenhoek R. 1997. Evolutionary relationships of deep-sea hydrothermal vent and cold-water seep clams (Bivalvia: Vesicomidae): results from the mitochondrial cytochrome oxidase subunit I. *Marine Biology* 130:151-161.
- Plouviez S, Shank TM, Faure B, Daguin-Thiebaut C, Viard F, Lallier FH, Jollivet D. 2009. Comparative phylogeography among hydrothermal vent species along the East Pacific Rise reveals vicariant processes and population expansion in the South. *Molecular Ecology* 18:3903-3917.

- Pradillon F, Gaill F. 2003. Oogenesis characteristics in the hydrothermal vent polychaete *Alvinella pompejana*. *Invertebrate Reproduction and Development* 43:223-225.
- Pradillon F, Shillito B, Young CM, Gaill F. 2001. Deep-sea ecology: Developmental arrest in vent worm embryos. *Nature* 413:698-699.
- Rogers AD, Tyler PA, Connelly DP, Copley JT, James R, Larter RD, Linse K, Mills RA, Garabato AN, Pancost RD, et al. 2012. The discovery of new deep-sea hydrothermal vent communities in the southern ocean and implications for biogeography. *PLoS biology* 10:e1001234-e1001234.
- Shank TM, Fornari DJ, Von Damm KL, Lilley MD, Haymon RM, Lutz RA. 1998. Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents (9° 50' N, East Pacific Rise). *Deep Sea Research Part II: Topical Studies in Oceanography* 45:465-515.
- Smith CR, Kukert H, Wheatcroft RA, Jumars PA, Deming JW. 1989. Vent fauna on whale remains. *Nature* 341:27-28.
- Thurber AR, Jones WJ, Schnabel K. 2011. Dancing for food in the deep sea: bacterial farming by a new species of yeti crab. *PLoS One* 6:e26243.
- Tunnicliffe V. 1991. The biology of hydrothermal vents: ecology and evolution. *Oceanogr Mar Biol Annu Rev* 29:319-407.
- Tunnicliffe V, Embley RW, Holden JF, Butterfield DA, Massoth GJ, Juniper SK. 1997. Biological colonization of new hydrothermal vents following an eruption on Juan de Fuca Ridge. *Deep Sea Research Part I: Oceanographic Research Papers* 44:1627-1644.
- Tunnicliffe V, McArthur AG, McHugh D. 1998. A biogeographical perspective of the deep-sea hydrothermal vent fauna. *Advances in Marine Biology* 34:353-442.
- Van Dover CL, German C, Speer KG, Parson L, Vrijenhoek R. 2002. Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* 295:1253-1257.
- Vrijenhoek RC. 1997. Gene flow and genetic diversity in naturally fragmented metapopulations of deep-sea hydrothermal vent animals. *Journal of Heredity* 88:285-293.
- Vrijenhoek RC. 2010a. Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations. *Molecular Ecology* 19:4391-4411.
- Vrijenhoek RC. 2010b. Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations. *Molecular Ecology* 19:4391-4411.
- Vrijenhoek RC. 2010c. Genetics and evolution of deep-sea chemosynthetic bacteria and their invertebrate hosts. *The vent and seep biota: Aspects from microbes to ecosystems*:15-49.
- Weiss RF, Lonsdale P, Lupton J, Bainbridge A, Craig H. 1977. Hydrothermal plumes in the Galapagos Rift. *Nature* 267:600-603.
- Won Y-J, Jones WJ, Vrijenhoek RC. 2008. Absence of cospeciation between deep-sea mytilids and their thiotrophic endosymbionts. *Journal of Shellfish Research* 27:129-138.