⟨ Review ⟩

Deep-sea Hydrothermal Vents: Ecology and Evolution

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ABSTRACT: The discovery of deep-sea hydrothermal vents and their ecosystems is a monumental landmark in the history of Ocean Sciences. Deep-sea hydrothermal vents are scattered along the global mid-ocean ridges and back-arc basins. Under sea volcanic phenomena related to underlying magma activities along mid-ocean ridges generate extreme habitats for highly specialized communities of animals. Multidisciplinary research efforts during past three decades since the first discovery of hydrothermal vents along the Galapagos Rift in 1977 revealed fundamental components of physiology, ecology, and evolution of specialized vent communities of micro and macro fauna. Heterogeneous regional geological settings and tectonic plate history have been considered as important geophysical and evolutionary factors for current patterns of taxonomic composition and distribution of vent faunas among venting sites in the World Ocean basins. It was found that these communities are based on primary production of chemosynthetic bacteria which directly utilize reduced compounds, mostly H_2S and CH_4, mixed in vent fluids. Symbioses between these bacteria and their hosts, vent invertebrates, are foundation of the vent ecosystem. Gene flow and population genetic studies in parallel with larval biology began to unveil hidden dispersal barrier under deep sea as well as various dispersal characteristics cross taxa. Comparative molecular phylogenetics of vent animals revealed that vent faunas are closely related to those of cold-water seeps in general. In perspective additional interesting discoveries are anticipated particularly with further refined and expanded studies aided by new instrumental technologies.

Key words: Chemosynthetic bacteria, Hydrothermal vent, Mid-Ocean Ridge, Molecular Phylogenetics, Symbioses

INTRODUCTION

The spectacular nature of deep-sea hydrothermal vent community at a depth of 2,500 m seafloor was first discovered by the aid of the man submersible deep-sea research vessel (DSRV) Alvin along the Galapagos Rift near the Galapagos Islands in 1977 (Corliss and Ballard 1977) (Fig. 1 and 2). Since the discovery of dense animal communities at deep-sea hydrothermal vents along the Galapagos Rift, continuing worldwide explorations have identified unusual faunal assemblages of vent communities that thrive like oases of life at seafloor spreading centers. Up to date, these communities have been continuously discovered, and also various biological samples were taken from hydrothermal vents. For example some representative hydrothermal vents are known to reside in the Galapagos Rift, along the East Pacific Rise, in Guaymas Basin, along the Gorda, Juan de Fuca, and Explorer ridges, in the western Pacific at the Mariana Trough, Manus Back Arc Basin, Lau Basin, North Fiji Basin, and Okinawa Trough, along the Mid-Atlantic Ridge, and in the triple junction of Indian Ocean ridges (for reviews, see Lutz and Kennish 1993, Tunnicliffe et al. 1998, Van Dover 2000, Van Dover et al.

2001, Watabe and Hashimoto 2002) (Fig. 1). As shown in Fig. 1 the number of most known vents locates in places where expeditions are relatively easier than to remote regions, such as near Antarctic. Vent habitats look like islands isolated by distance along spreading ridge axis. Furthermore heterogeneity in temporal distribution of venting sites due to fluctuation of geologic activities exists and influence vent communities (Shank et al. 1998). Tunnicliffe et al. (1998) counted the number of known vents as about thirty up to that time and these vents were mostly located in the Pacific and Atlantic. Since then new hydrothermal vent sites have been added to the list and species lists have grown rapidly. For example recently the southern most hydrothermal vent at thirty eight degree latitude in the Pacific-Antarctic ridge was explored and during this expedition a new species of blind deep-sea crab, which even leads to establish a new family of Galatheoidea (Crustacea, Decapoda, Anomura), was added to the whole list of animals from vents (Macpherson et al. 2005). Fig. 1 illustrates the distribution and location of the representative hydrothermal vents and cold water seeps, which have different geological settings to vents and mostly locate continental margins, around world where scientific investigations have been done and/or biological samplings have been un-

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dertaken. As seen in the Fig. 1, deep-sea hydrothermal vents are scattered along the global mid-ocean ridge (MOR) system, in back-arc spreading centers, and seamounts. The MOR on the map is shown as somewhat like zigzag lines. These lines certainly represent a center where fresh sea crusts are newly formed and simultaneously sea floors begin to spread out onto opposite directions. Differing from the MOR, subduction zones are the places where one ocean crust runs down to the other plates, and thus back- arc basin is shaped near. On the other hand, cold-water sulfide/hy drocarbon seeps were also found to support similar highly specialized faunal assemblages at sea bottom, having different geological settings from the hydro-thermal vents (Paull et al. 1984, Olu et al. 1996, Sibuet and Olu 1998).

The discovery of deep-sea hydrothermal vent communities at such extreme environments where sun light never reaches and atmospheric pressures are several hundreds times higher than surface water was one of the most important discoveries in the history of Ocean Sciences. Deep-sea hydrothermal vents are characterized by super-heated venting (often reaching over 380 Celsius degrees on the axis of the East Pacific Rise), which are driven by magma activities be-low ocean crust (Spiess et al. 1980). As soon as superheated mi-neral-rich and corrosive hydrothermal fluid vents out, it quickly mixes with cold sea water (1~2 Celsius degrees), creating ambient water temperature about 10 to 20 Celsius degrees. Hydrothermal fluids gush out through rock-structures like a chimney which was formed by precipitation of minerals, when venting fluids interacted with sea water. Usually water temperatures at places where vent animals reside are of ambient range (Van Dover 2000). It was summarized that there were 443 hydrothermal vent invertebrate species known to generic level and/or at least published (Tunnicliffe et al. 1998). The authors recognized that many more were under study and were not determined onto generic level although their taxonomic status was known to ordinal or family level. Among hydrothermal vent faunas, mussels, clams, tube worms, crabs, shrimps, and snails are the most conspicuous macro fauna than other taxa (Grassle 1986). Particularly three phyla, mollusks, arthropods, and annelids, are pre-ponderant (Van Dover 1990, Tunnicliffe et al. 1998).

Survival of vent and seep communities depends on chemosynthe-tic primary production by microbes that exploit reduced compounds, mostly H_2S and CH_4 (see review by Fiala-Medioni and Felbeck 1990, Fisher 1990, Cavanaugh 1994, Nelson and Fisher 1995). The high chemosynthetic primary production at hydrothermal vent pro-vides nutrition directly to populations of vent fauna. Unexpected existence of prosperous deep-sea ecosystem at hydrothermal vent intrigued strong interests to many biologists, particularly to taxono-mists, microbiologist and physiologists. Therefore a series of resear--ches has been dedicated to untangle the mystery of energy source
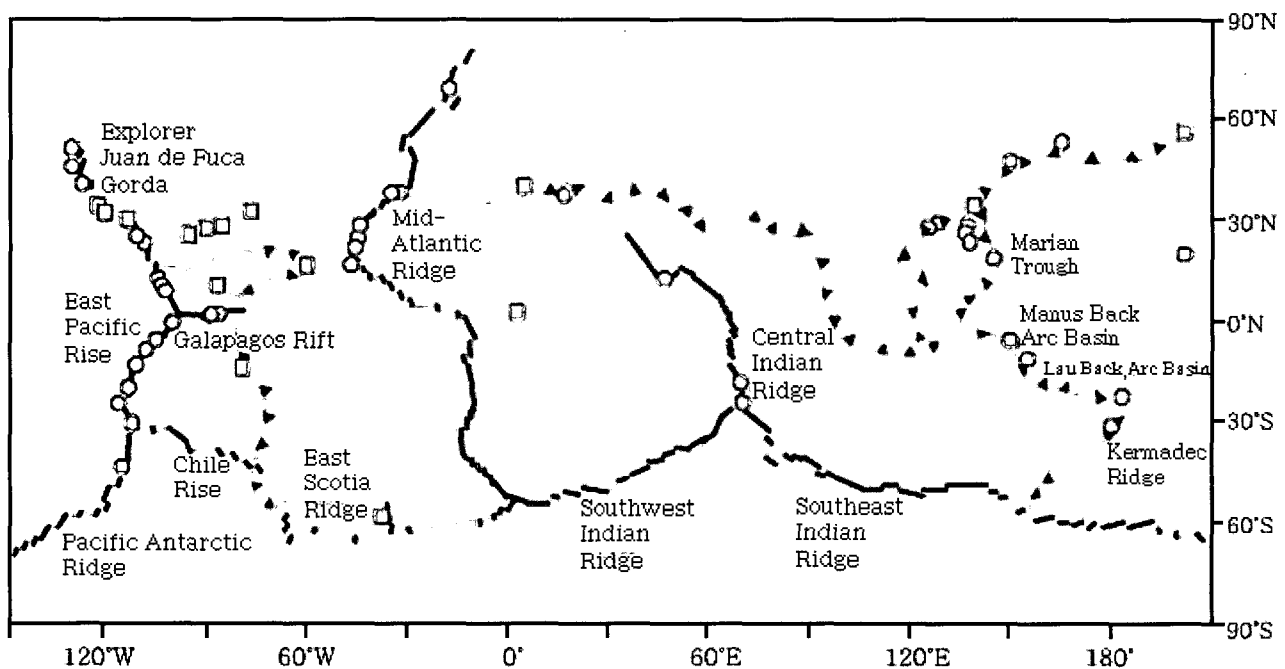

Fig. 1. The mid-ocean ridge system. Thick lines are mid-ocean ridges and thin lines besides the thick ones represent transform faults. Single line with pointers are subduction zones showing the direction of subduction. Open circles mark hydrothermal vent sites known around world oceans. Open rectangles mark cold-water seeps, mostly along continental margins. Modified from Vrijenhoek (1997) and Tunnicliffe and Fowler (1996).

for the ecosystem of hydrothermal vents over a decade since the discovery of vent. Many microbiologists and physiologists focused their research efforts on finding a basis of energy flow in food chains within the vent ecosystem. As the results, growing number of literatures on bacterial chemosynthesis and symbiotic association of these micro organisms and their host, vent invertebrates, were produced in this period (see review by Cavanaugh 1994). Symbiotic relationships between many of the invertebrates and chemoautotrophic bacteria were established widely as a basis for nutrition in related taxa from vents and seeps, as well as in other marine animals that inhabit in sulfide rich coastal sediments (Cavanaugh et al. 1981, Felbeck 1981, Rau 1981, Cavanaugh 1983, Stein et al. 1988, Cary et al. 1997). Chemoautotrophic symbionts exploit reduced compounds available in the vent fluids; for example, carbon fixation occurs through oxidation of reduced sulfur compounds (Rau and Hedges 1979, Felbeck et al. 1981, Powell and Somero 1985, Belkin et al. 1986, Herry et al. 1989) or methane gas (Childress et al. 1986, Cavanaugh et al. 1987, Cary et al. 1988). In short, vent ecosystem was built on the chemosynthesis and symbiosis without depending on photosynthesis.

On the other hand, considerable attentions have been paid to ecological and evolutionary connections among highly specialized and fragmented deep-sea hydrothermal vent communities. Deep-sea chemosynthetic communities are distributed in discrete habitat islands that are typically separated by wide geographical gaps, occasionally over several hundreds to thousands kilometers apart. The patchy and ephemeral nature of these vent habitats raised a series of questions concerned with colonization and dispersal capabilities of vent-endemic animals. Investigations of dispersal modes of the invertebrates have been conducted by studying the dispersal potential of larvae (Lutz et al. 1980, Turner et al. 1985, Lutz 1988, Mullineaux et al. 1995, Tyler and Young 1999, Marsh et al. 2001, Pradillon et al. 2001) and by assessing realized dispersal, or gene flow (Black et al. 1994, Karl et al. 1996, Vrijenhoek 1997). In addition, faunal affinities between the hydrothermal vents and cold seeps have raised question about evolutionary relationships of invertebrate taxa (Craddock et al. 1995a, Black et al. 1997, Peek et al. 1997, Halanych et al. 2001, Goffredi et al. 2003) In general vent and seep fauna turned out to be close relationship each other. Furthermore unusual benthic fauna associated with whale falls and sunken woods at deep-sea floor also were known to have close evolutionary relationship with fauna from vent and seep communities (Distel et al. 2000a, Rouse et al. 2004, Jones et al. 2005).

BIOGEOGRAPHY

Study of biogeography of vent fauna began as new hydrothermal

vents on different ridges were found. Since the first discovery of vent communities on the Galapagos Rift, additional hydrothermal vents on the northern East Pacific Rise were found (Spiess et al. 1980). Thereafter comparisons of taxonomic composition among global vent communities have been undertaken with great interests. Currently six biogeographic provinces are known (Van Dover 2000, Van Dover et al. 2001). According to Tunnicliffe et al. (1998) current biogeography of vents are characterized as the followings; (i) vent faunas exhibit extensive provincialism, (ii) over 75% of vent species occur at local venting sites, (iii) vent faunas between basins show greater similarity than to the nearby normal deep-sea fauna, (iv) overall composition of vent faunas consists of three major phyla, Arthropoda (35%), Mollusca (34%), Annelida (23%), (v) despite high productivity, vent communities show low diversity of species and also seemingly simpler trophic structure than other marine communities, (vi) sulphide-rich cold seeps and organic masses (wood and animal carcasses) show close evolutionary affinity to those of vent at higher taxonomic level, but not in species level. Interestingly the authors explained the endemism with relative recency of vent faunas and added a hypothesis of independent penetration to vents by many lineages. The pattern of taxonomic distribution and composition of vent faunas appeared to be related to tectonic plate history (Van Dover 1990, Tunnicliffe and Fowler 1996). Pathways along mid-ocean ridges were suggested as a major migration route between vents (Tunnicliffe and Fowler 1996). A recently found hydrothermal vent invertebrates in two venting sites (Kairei and Edmond) in Indian Ocean ridge demonstrated that most organisms have close evolutionary relationships with western Pacific vent faunas rather than to Mid-Atlantic faunas with except for shrimp (Van Dover et al. 2001). Fig. 2 shows some representative vent animals from the vents of the Central Indian Ocean ridges, particularly with newly found scaly snail which differs from all known mollusks by having its foot covered by scales containing iron sulfide (pyrite and greigite) (Waren et al. 2003, Goffredi et al. 2004). Combining molecular dating of some vent faunas, vent biologists hypothesized that Cenozoic tectonic history and oceanic circulation patterns have played important roles for contemporary biogeographic patterns (Van Dover et al. 2002).

Interestingly a comparison of fissile data and molecular phylogenies of several dominant hydrothermal vent and seep taxa showed that most modern vent animal groups arose relatively recently and that taxonomic composition of vents has changed considerably through time, despite of significant discrepancies between both data sets (Little and Vrijenhoek 2003). Once it was suspected that hydrothermal vent faunas might be a relic of antiquity having a long evolutionary history from Palaeozoic, because several relic species are found only at hydrothermal vents (Newman 1985).
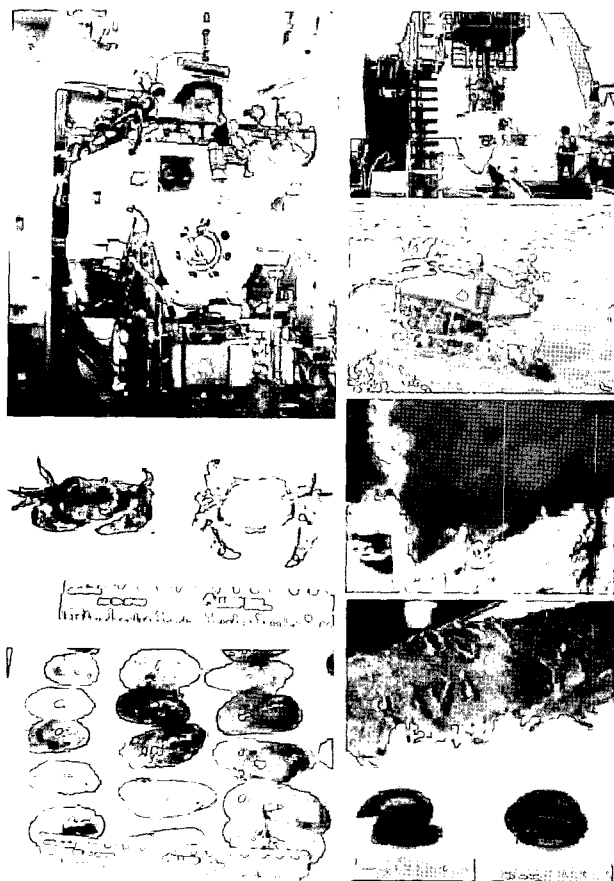
Fig. 2. Deep-sea man submersible research vessel (DSRV) *Alvin* on board. A launching moment of the *Alvin* into sea. Lowering deep-sea remote operating vessel (ROV) *Jason* into sea water. Blacker smoker and rock chimney of hydrothermal vent in East Pacific Rise. Stalked barnacles on a rock-chimney of hydrothermal vent. A newly discovered gastropod, scaly foot snail (family indeterminate) from the Kairei vent site in the central Indian Ocean ridge. *Bathymodiolous* mussels collected from the same vent, and arranged according to their size. Brachyuran crabs from the same site. An identical ruler is repeatedly shown for comparisons of body size (full size of 15 cm). Photos and explanations are arranged from upper left to clockwise order.

However, molecular dating of origin of some dominant animal groups (vestimentiferans, bathymodiolins, vesicomyids and bresiliids) do not exceed Jurassic period even with conservative calibration of the molecular clocks (Little and Vrijenhoek 2003).

ADAPTATION AND SYMBIOSIS

In the beginning of exploration of hydrothermal vent, vent biologists were overwhelmed by unseen anatomies of vent animals which

seemingly reflected their adaptation to deep-sea hydrothermal vent environments. For example some annelids, bivalve mollusks, and gastropods showed partial to entire loss of digestive organs and instead development of specialized cells (bacteriocytes) that house symbiotic bacteria within cytoplasm of various tissues (Boss and Turner 1980, Felbeck 1981, Rau 1981, Kenk and Wilson 1985, Fiala-Medioni et al. 1986, Endow and Ohta 1989). Remarkably vent vestimentiferan tubeworms (Annelida: Siboglinidae) completely lost digestive organs, so a taxonomist put these animals even on a rank of new phylum, Vestimetifera (Jones 1985), although recently the taxonomic status was resolved by morphological, embryological, and molecular analyses as belonging to the phylum, Anelida (Kojima et al. 1993, Rouse and Fauchald 1995, Young et al. 1996, McHugh 1997, Southward 1999). These, mouthless, gutless, adult vestimentiferan tubeworms rely entirely on sulfur-oxidizing endosymbionts for their nutrition. Symbionts are housed in specialized cells (bacteriocytes) located in a large organ called the trophosome. Vesicomyid clams (Bivalvia: Vesicomyidae) also depend on sulfur-oxidizing endosymbionts housed in gill epithelium (Felbeck et al. 1981, Rau 1981), but they possess reduced or vestigial digestive systems (Boss and Turner 1980). *Bathymodiolus* mussels (Bivalvia: Mytilidae) also contains symbiotic bacteria; however these mussels have a complex pattern in housing endosymbionts. Some species have only sulfur-oxidizing endosymbiotic bacteria in specialized bacteriocytes of gill tissue, and others house methanotrophic microbes, and some house both types of symbionts (Fisher et al. 1987, Cavanaugh et al. 1992, Distel et al. 1995, Robinson et al. 1998). In addition, endosymbiotic bacteria appear not only epithelial cell of gill but also in soft tissue of mantle (Fiala-Medioni et al. 2002, Salerno et al. 2005).

Symbiotic relationships between invertebrates and endosymbiotic bacteria have evolved repeatedly in distantly related invertebrate taxa from hydrothermal vents and cold-water sulfide/hydrocarbon seeps (Cavanaugh et al. 1981, Felbeck 1981, Rau 1981, Cavanaugh 1983, Stein et al. 1988, Cary et al. 1997). Such obligatory nature of symbioses between invertebrate hosts and chemoautotrophic bacteria raised questions about mechanisms for transmission of endosymbionts to the next generation. Acquisition mode of symbionts has important implications for survival strategy of hydrothermal vent animals. An assurance of food source via endosymbionts might guarantee likely survival at unpredictable environments such as ephemeral vent habitats. This type of biological tie may lead to optimal adaptation to their habitats. However, a strict tie between a host and a symbiont might raise problem when they are laid in new environments. Most hydrothermal vent invertebrates have larval stage affected by water regime in their life histories (Tyler and Young 1999) So, released larvae can opportunistically settle to different environments where adaptation between host and endosymbionts are

not likely optimal. Under this context a few molecular studies gave insight into the evolution and adaptation of symbioses between vent animals and their endosymbiotic bacteria.

The hypothesis that sulfur-oxidizing, endosymbiotic bacteria associated with deep-sea hydrothermal vent animals are transmitted vertically between generations was examined in a group of conspicuous deep-sea animals. Studies of Vesicomyid clams showed that these clams vertically inherit their endosymbionts via transovarial mechanism and showed significant congruence of genetic diversification of host clams and their symbionts at both population and species level (Endow and Ohta 1990, Cary and Giovannoni 1993, Peek et al. 1998, Hurtado et al. 2003). Whereas, studies of vestimentiferan tubeworms suggested a horizontal transmission from environment (Jones and Gardiner 1988, Southward 1988, Edwards and Nelson 1991, Cary et al. 1993, Di Meo et al. 2000). These two groups appear to represent both ends of transmission mode of endosymbionts. Other taxa might be placed between these two ends. In case of *Bathymodiolus* mussels, environmental acquisition mode was strongly suggested (Won et al. 2003a).

Differences in the mode of transmission of symbionts have showed contrasting phylogenetic topologies of host-symbiont pairs (Feldman et al. 1997, Peek et al. 1998, Nelson and Fisher 2000). While vertical transmission in vesicomyid clams (Endow and Ohta 1990, Cary and Giovannoni 1993, Hurtado et al. 2003) has resulted in cospeciation (e.g. parallel evolutionary trees) between clam host species and their associated symbionts (Peek et al. 1998), horizontal transmission mode in vestimentiferan tubeworms has resulted in non parallel phylogeny between hosts and their symbionts (Feldman et al. 1997, Nelson and Fisher 2000).

GENE FLOW AND DISPERSAL PATTERN

Molecular systematic studies have greatly increased our understanding of organismic dispersal, population differentiation, and mechanisms of speciation in marine organisms (Palumbi 1994). Species that occupy deep sea habitats are thought to be relatively homogeneous, because the abyssal zone is continuous and uniform across vast distances (Gage and Tyler 1991), and because many of its inhabitants possess planktonic larvae or juveniles stages capable of dispersing in the water column (Scheltema 1986, Young 1994). Characterized as patchy and ephemeral (Grassle 1985, Van Dover and Hessler 1990, Tunnicliffe et al. 1998), discrete vent fields may be separated by large distances ranging from a few kilometers to hundreds and/or thousands of kilometers. A series of gene flow studies among populations of hydrothermal vent animals focused on vents in the Galapagos Rift and northern East Pacific Rise showed different pattern of dispersal (stepping-stone dispersal, island model dispersal,

and ridge-scale isolation) (France et al. 1992, Black et al. 1994, Craddock et al. 1995b, Vrijenhoek 1997, Black et al. 1998). Further studies that involved a larger area about 5,000 km wide in eastern Pacific region revealed unseen aspect of dispersal patterns of vent organisms (Won et al. 2003b, Hurtado et al. 2004). A role of ocean currents were seriously inferred for larval dispersal rates along spreading ridges in these regions. For example a topographic feature of the Easter Microplate and its associated deep-sea circulations coincided with genetic discontinuity between northern and southern populations of several vent species, and thus manifest east-to-west circulations, which are off-axis direction to the ridge in this region (Lupton and Craig 1981, Fujio and Imasato 1991), was interpreted to have played a role as a dispersal barrier to larvae of different species. Although the extent of impediment by currents varied among different taxa, probably due to other confounding effects, a general congruent pattern of genetic structures in this region highly suggests that deep-ocean currents be an important factor for shaping contemporary biogeography of vent faunas.

Addition to spatial variation of suitable vent habitats along spreading ridges, a temporal variation in them also raises another important issue in ecology and evolution of vent faunas. Volcanic eruptions cause extinction of vent habitats. A volcanic eruption between 9° 45′ N and 9° 52′ N on the East Pacific Rise in 1991 provided a chance to observe ecological succession of deep-sea hydrothermal vents during five years (Shank et al. 1998). Photographic and chemical time-series analyses during this period revealed a sequence of colonizing events like a following order and a continuing trend of decrease of H_2S concentration: microbial mats, mobile vent fauna (e.g. amphipods, copepods, and galatheid and brachyuran crabs), Vestimentiferan tube worm *Tevnia jerichonana*, other Vestimentiferan *Riftia pahyptila*, mussels *Bathymodiolus thermophilus*, galatheid crabs and serpulid polychaetes. The authors hypothesize that the above events might be general sequence of biological succession along the northern East Pacific Rise.

Population genetic studies on migration rate between isolated populations and genetic diversity among different taxa shed a light on the possible long term effects of habitat structure and ecological succession events on spreading mid-ocean ridge system. When vent species were categorized into early colonizer (appearing within 2 years of vent formation) and late colonizers (after 2 years), genetic diversity between these two groups were significantly separated with early colonizers having twice the genetic diversity of the late colonizers (Vrijenhoek 1997, Vrijenhoek et al. 1998). It has been hypothesized that the late colonizers would have smaller metapopulation size and thus be more prone to lose genetic diversity due to population bottlenecks and founder events (Vrijenhoek 1997, Vrijenhoek et al. 1998).

MOLECULAR PHYLOGENY

Vents and seeps share several species and more taxa at generic and family level. Faunal affinities between vents and other sulphide/ hydrocarbon rich cold seeps and organic masses cast a testable hypothesis of common origin of these highly specialized animals. Molecular phylogenetic studies were undertaken to illustrate origin and age of faunas from chemosynthetic communities (Craddock et al. 1995a, Black et al. 1997, Peek et al. 1997, Halanych et al. 2001, Goffredi et al. 2003). These molecular phylogenetic approaches revealed that the most taxa belonging to the chemosynthetic communities are truly close relatives each other than any other marine invertebrates, and also ages of vent taxa are much younger than Paleozoic origin. On the basis of morphological characteristics early vent biologist speculated that vent faunas are Palaeozoic relic (Newman 1985). While molecular data mostly estimated origin of some vent taxa as recent as between Cretaceous and Tertiary, some fossil records dated the relative of two modern vent taxa to be Palaeozoic (e.g. vestimentiferan-like tube worms and monoplacophoran mollusks) (Little and Vrijenhoek 2003).

Additionally invasions of deep-sea hydrothermal vents by marine invertebrates were hypothesized to occur via a wood/bone-to-seeps/ vents and a historical progression form shallow-water to deep-water habitats in case of Bathymodiolus mussels (Craddock et al. 1995a, Distel et al. 2000b). This hypothesis was supported in that vent species might represent a monophyletic group except for one lineage showing habitat transition from vent to seep (Won et al. 2002, Jones et al. 2005). The direction from shallow to deep ocean is consistent with a hypothesis posited by Jacobs and Lindberg (1998). They suggested that global anoxic/dysoxic events during the late Cretaceous and early Tertiary would have caused mass extinction of vent communities. Thus vent habitats were reinvaded by animals from other refugia, such as coastal vents and seeps. This extinction/repopulation hypothesis seems to be consistent with an onshore-offshore diversifications of other non-vent marine invertebrates animals. This scenario may be the case in deep-sea mussels, because they showed a general diversification pattern from shallow to deep invasion. Currently fossil records from ancient vent sites are very sparse. In future it would be very interesting to see if recurrent extinction/repopulation events would have led to extant taxa in deep-sea hydrothermal vents. Therefore further molecular phylogenetic analyses for other non-analyzed taxa are also needed.

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