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HUMIDITY

See **EVAPORATION AND HUMIDITY**

HYDROTHERMAL VENT BIOTA

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On 17 February 1977, the deep-submergence vehicle *Alvin* descended 2500 m to the crest of the Galapagos Rift spreading center to first visit an ecosystem that would forever change our view of life in the deep sea. Cracks and crevices in the ocean floor were emanating fluids with temperatures up to 17°C. None of the bizarre organisms clustering around these 'hydrothermal vents' had ever been encountered; they comprised new species, genera, families, superfamilies, and bizarre 'tubeworms,' up to 2 m long, which were subsequently placed in a new phylum (Vestimentifera) (**Figure 1**). Since the Galapagos Rift discovery, numerous hydrothermal vent sites have been found throughout the world's oceans and over 500 new species have been described from these regions. **Figure 2** depicts many of the major hydrothermal systems from which organisms have been collected to date. Fluids with temperatures as high as 403°C exit from polymetallic sulfide chimneys in many of these regions (**Figure 3**).

Figure 1 A cluster of vestimentiferan tubeworms (*Riftia pachyptila* and *Tevnia jerichonana*), together with a zoarcid fish (*Thermarces andersoni*) and brachyuran crabs (*Bythograea thermydron*) inhabiting low-temperature hydrothermal vents at 9°50′N along the East Pacific Rise (depth 2500 m).

Most ecosystems on earth ultimately rely on photosynthesis, with the energy source being solar. In marked contrast, deep-sea hydrothermal ecosystems are based predominantly on chemosynthesis, with the energy source being geothermal. Many of the chemosynthetic microbes are fueled by hydrogen sulfide, which is present at low-temperature vents in concentrations up to several hundred micromoles per liter and at high-temperature vents in concentrations up to 100 milimoles per liter. These microbial organisms can be either ‘free-living’ (in the water or on the surface of various substrates) or symbiotic in association with certain vent organisms. The vestimentiferan tubeworms *Riftia pachyptila* and

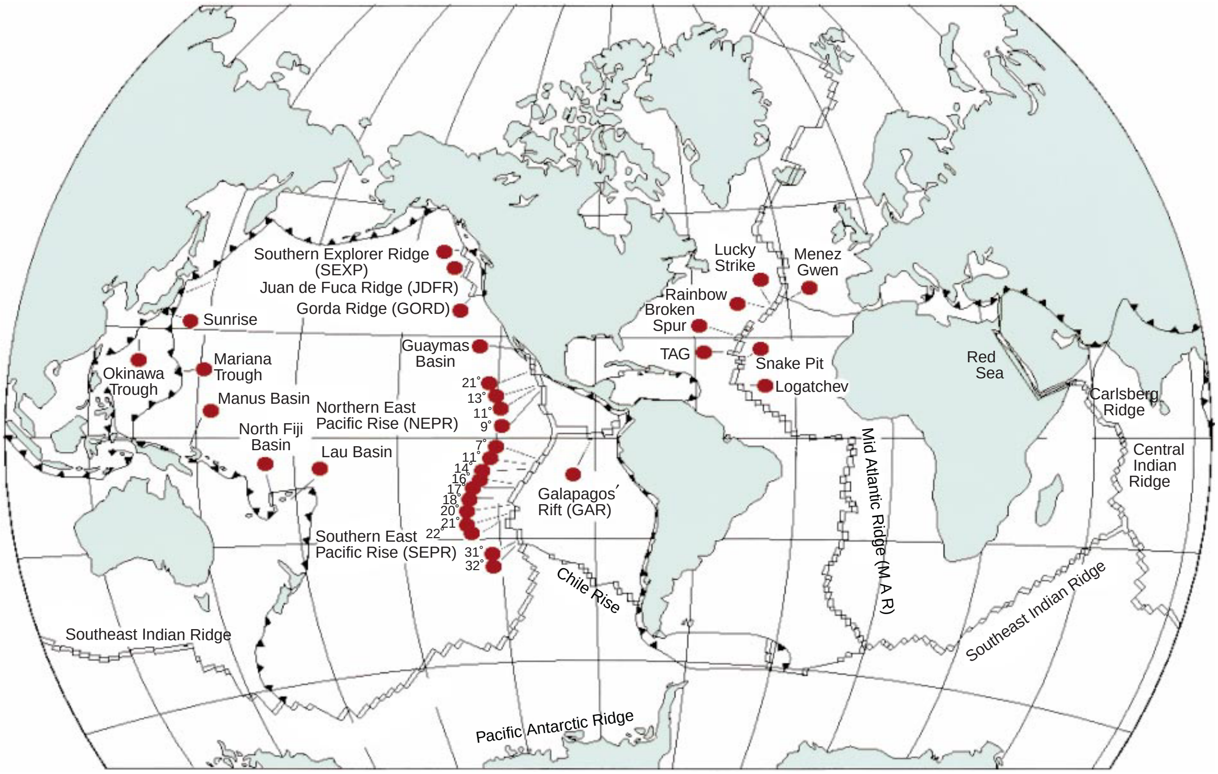

Figure 2 Deep-sea hydrothermal vent sites along mid-oceanic and back-arc ridge systems from which vent organisms have been collected to date. Numbers indicate approximate latitude of site along the East Pacific Rise.

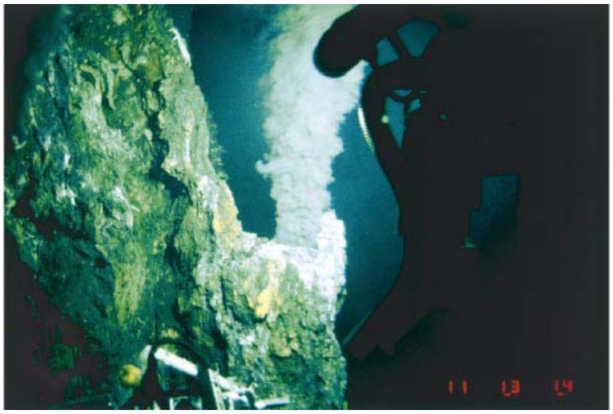

Figure 3 A 'black smoker' polymetallic sulfide chimney at 20°50′N along the East Pacific Rise (depth 2615 m). Temperatures as high as 403°C have been recorded at the orifice of such edifices from which mineral-rich fluids emanate violently in many deep-sea hydrothermal systems.

Tevnia jerichonana (**Figures 1**, **4**, **5**, and **6**), for example, each have a specialized 'tissue,' known as the trophosome, which is comprised entirely of chemosynthetic bacteria. The tubeworms have no mouth, no digestive system, and no anus; in short, no opening to the external environment. Hydrogen sulfide diffuses across cell membranes and is transported via the hemoglobin-containing circulatory system to the trophosome, where it is utilized by the associated symbionts. Mussels (*Bathymodiolus thermophilus*) (**Figures 7** and **8**) and vesicomyid clams (*Calyptogena magnifica*) (**Figure 9**), common along both the Galapagos Rift and East Pacific Rise (EPR), represent two of the other dominant members of the vent megafauna that house chemosynthetic symbionts. In the case of each of these bivalves, the symbionts are associated with the gills and both species have modified feeding apparatuses relative to those of shallow-water related species (likely a result of their predominant reliance on the associated symbionts for nutrition). Closely related mussels and clams within the families Mytilidae and Vesicomyidae are common constituents of the fauna associated with vents along mid-oceanic ridge and back-arc spreading centers (as well as at many cold-water hydrocarbon seeps) throughout the world's oceans. All of these bivalve mollusks retrieved to date appear to contain thiotrophic ('sulfur-feeding') or methanotrophic ('methane-feeding') chemosynthetic symbionts.

It should be mentioned that, while chemosynthetic bacteria play a critical role in food chains associated with many vent systems, there are numerous other microbes at the vents belonging to two other recognized kingdoms. Both eukaryotes and Archaea occupy specialized niches within various vent ecosystems and certain Archaea, which have been isolated from environments associated with high-temperature sulfide chimneys, have been reported to occupy the most primitive 'node' on the phylogenetic tree of life. Such reports have led to considerable speculation as to whether or not life itself may have originated in hydrothermal vent environments.

At various high-temperature vent sites, numerous organisms colonize the sides of active sulfide edifices. **Figure 4** depicts a sulfide edifice (named 'Tubeworm Pillar') that is 11 m high, the sides of which are covered with tubeworms (both *R. pachyptila* and *T. jerichonana*), crabs, zoarcid fish, and a

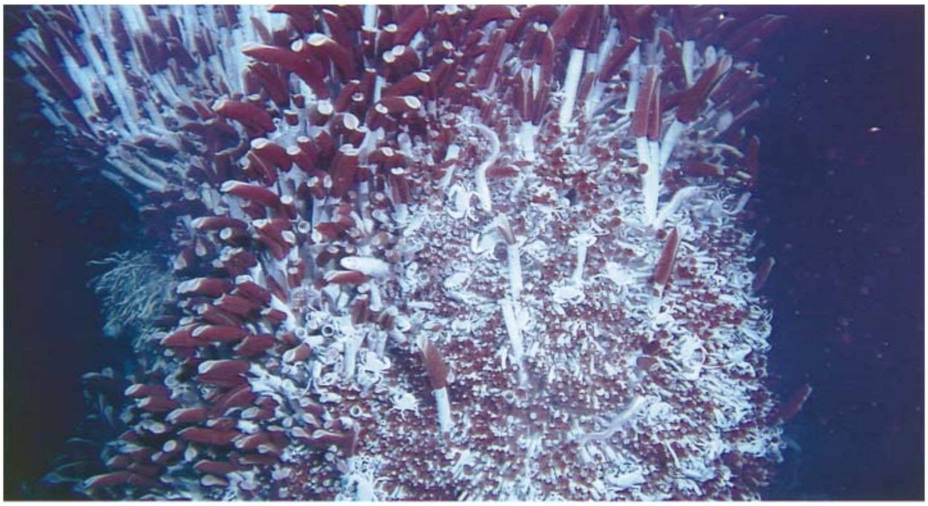

Figure 4 A portion of an 11 m high polymetallic sulfide edifice known as Tubeworm Pillar at 9°50′N along the East Pacific Rise (depth 2500 m). The top two-thirds of the edifice is covered with vestimentiferan tubeworms, both *Riftia pachyptila* (larger organisms) and *Tevnia jerichonana* (smaller organisms), as well as numerous brachyuran crabs (*Bythograea thermydron*) and zoarcid fish (*Thermarces andersoni*).

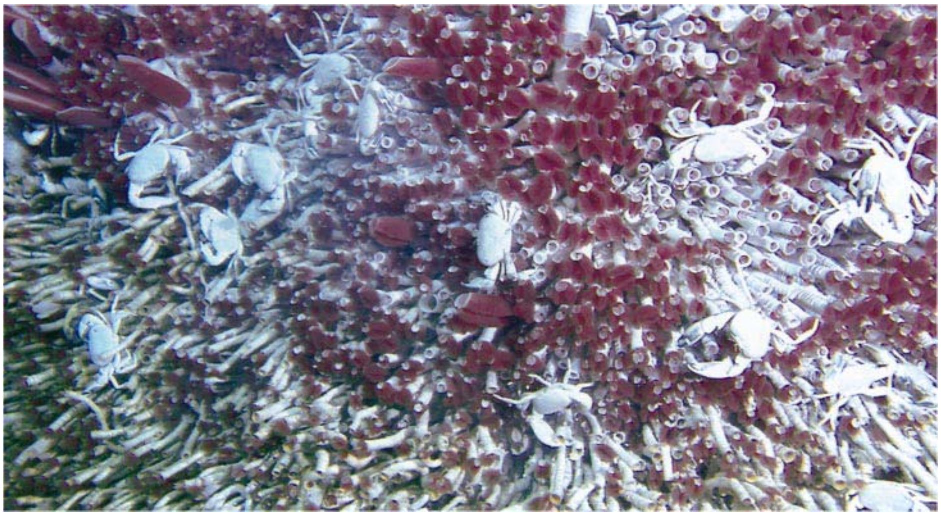

Figure 5 Higher magnification of the side of Tubeworm Pillar (depicted in **Figure 4**), showing tubeworms (*Riftia pachyptila* and *Tevnia jerichonana*) and scavenging brachyuran crabs (*Bythograea thermydron*).

spectrum of smaller, associated vent fauna. At other sites, the sides of 'black smoker' chimneys are frequently covered with the tubes of polychaetes, such as *Alvinella pompejana*, a 'Pompeii' worm named after the submersible *Alvin* (**Figure 10**). This organism has been reported to routinely withstand long-term exposure to temperatures ranging from 2°C to 35°C and short-term exposure to temperatures in excess of 100°C, rendering this annelid perhaps the most eurythermal organism on the planet.

In addition to the numerous species of bivalves, such as mussels and clams mentioned earlier, there are myriad other common mollusks at vents, including numerous gastropods, particularly archeogastropod limpets. Thirteen different gastropod species have been reported from vents along the narrow range of the East Pacific Rise from 9°17′N to 9°54′N. These organisms can achieve high population densities and are found on a wide variety of substrates including the tubes of *Riftia pachyptila* and the shells of *Bathymodiolus thermophilus* (**Figures 8** and **11**). Limpets graze on free-living microbes that coat the majority of surfaces associated with both low-temperature and high-temperature (e.g., sulfide chimney) vents. Over 100 species of mollusks have been collected to date from the mid-oceanic and back-arc spreading centers visited to date.

Virtually all of the invertebrates inhabiting deep-sea hydrothermal vents have planktonic larval

Figure 6 Close-up image of a cluster of *Tevnia jerichonana*, together with a brachyuran crab (*Bythograea thermydron*) and a zoarcid fish (*Thermarces andersoni*). Note the 'accordion-like' morphology of the tube of this species of vestimentiferan tubeworm.

Figure 7 A dense population of mussels (*Bathymodiolus thermophilus*) inhabiting a low-temperature hydrothermal vent field along the East Pacific Rise. Associated fauna in the field of view include tubeworms (*Riftia pachyptila*), brachyuran crabs (*Bythograea thermydron*), zoarcid fish (*Thermarces andersoni*), and a galatheid crab (*Munidopsis subsquamosa*) (lower left).

stages. These free-swimming stages serve as the primary means of dispersal between isolated vent systems, which can be separated by hundreds of kilometers. The larval stages can be either planktotrophic (feeding within the water column) or lecithotrophic (utilizing yolk reserves for nutrition). In either case, it appears that the early life history stages of the vast majority of vent organisms are capable of staying in the water column for considerable lengths of time (likely months in the case of many vent species). Such extended planktonic durations facilitate passive transport over vast distances via ocean currents (velocities of ocean currents between 15 and 30 $\mathrm{cm\,s^{-1}}$ are commonly encountered along the crest of ridge systems).

Numerous crustaceans inhabit the vent environment and represent perhaps the dominant scavengers of the ecosystem. Brachyuran crabs (e.g., *Bythograea thermydron* on the Galapagos Rift and the East Pacific Rise) (**Figures 1, 5, 6**, and 7) appear to be one of the earliest colonizers of hydrothermal vent environments. When new vents were formed during the April, 1991 volcanic eruption along the crest of the East Pacific Rise at 9°50′N, several regions were referred to as 'crab nurseries' owing to the relatively large abundance of crab larvae (megalopae) in areas of low-temperature discharge. Eleven months after the eruptive event, the region was populated by tremendous numbers of large crabs. These were frequently observed to be holding with their claws various substrates, such as empty tubeworm tubes or pieces of basalt covered with microbial mats, and voraciously scraping the surfaces with their mouth parts, suggesting that microbes and/or their products may represent an important source of nutrition for these organisms. They are also frequently seen extending their claws into the tubes of *Riftia pachyptila* and will readily devour the tissues of any tubeworm or mussel damaged during routine submersible activities. They are easily captured in 'crab traps' baited with a wide variety of dead fish. Intraspecific attacks appear to be relatively common occurrences and crabs with only one claw or a missing leg are frequently seen on the bottom, presumably reflecting an encounter with another crab.

Galatheid crabs (e.g., *Munidopsis subsquamosa*) (**Figure 12**) inhabit peripheral areas of the vents during earlier stages of succession and, as hydrogen sulfide levels gradually decrease over time, they are commonly encountered in central areas as well, often among tubeworms and mussels. While these 'squat lobsters' may also be scavengers, they are seldom, if ever, caught in traps. One chance encounter with a relatively large dead octopod in the peripheral area of a vent revealed a large quantity of

Figure 8 Close-up of mussels (*Bathymodiolus thermophilus*) attached to the tubes of the tubeworm *Riftia pachyptila*. Limpets (*Lepetodrilus elevatus*) are seen attached to the external surfaces of both the mussel shells and tubeworm tubes.

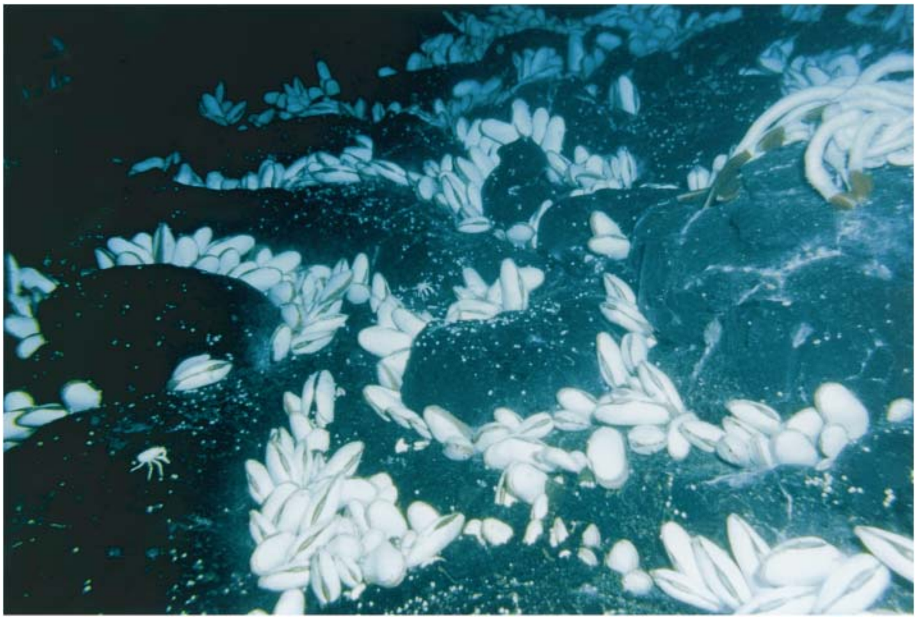

Figure 9 Vesicomyid clams (*Calyptogena magnifica*) line cracks and crevices from which low-temperature fluids are venting in an area known as Clam Acres at 20°50′N along the East Pacific Rise (depth 2615 m). This species is common at many vent sites that are believed to be in relatively late stages of succession along the Galapagos Rift and the entire stretch of the East Pacific Rise from 21°N to 18°S.

galatheid crabs on the carcass and a noticeable absence of brachyuran crabs or other vent organisms (**Figure 13**). Close-up imagery revealed that the crabs were actively feeding on the dead tissues of the carcass. Galatheids that have been collected to date have generally been 'transported' back to the surface in random regions of the submersible itself. The carapaces of this species are frequently covered with fine, filamentous bacteria (**Figure 12**).

Numerous species of shrimp (**Figure 14**) have been encountered at vent sites visited to date along ridge axes in all ocean basins. At several sites (e.g., the TAG hydrothermal vent field) along the Mid-Atlantic Ridge, thousands of shrimp are frequently seen 'swarming' on top of one another, completely carpeting the sides of large sulfide chimneys. It has been suggested that a large 'eye spot' on the back of the carapace of the shrimp is capable of sensing long-wavelength light emitted by high-temperature smokers. Shrimp are also relatively common inhabitants of vents visited to date in the western Pacific (e.g., at the Alice Springs vent field along

Figure 10 The polychaete *Alvinella pompejana* emerging from its tube on the side of a black smoker chimney at 9°50′N along the East Pacific Rise. It has been suggested that the organism may be the most eurythermal invertebrate on the planet, capable of withstanding short-term exposures to temperatures ranging from less than 2°C to in excess of 100°C.

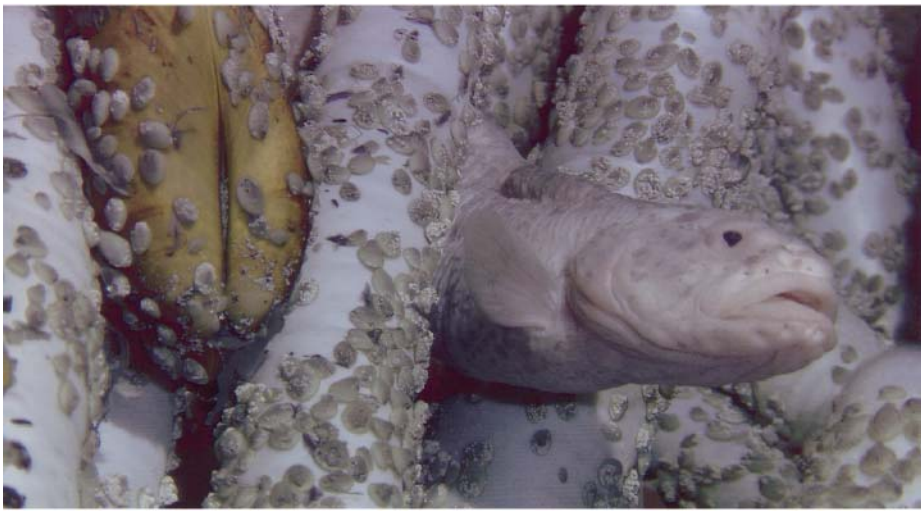

Figure 11 Limpets (*Lepetodrilus elevatus*) coating the surfaces of the tubes of *Riftia pachyptila* and the shell of *Bathymodiolus thermophilus* (left). A zoarcid fish (*Thermarces andersoni*) is seen emerging from the tubeworm tubes.

the back-arc spreading center in the Mariana Trough).

Other smaller, common vent-endemic crustaceans include numerous species of amphipods, copepods, and leptostracans. *Halice hesmonectes*, an amphipod common at various vent sites along the East Pacific Rise is frequently seen 'swarming' above mussel and tubeworm colonies in regions of active low-temperature venting. It has been reported that these dense swarms represent the highest concentration of planktonic invertebrates in the ocean.

Serpulid polychaetes (**Figure 15**) are common inhabitants of the peripheral area of many vent fields. Commonly referred to as 'feather dusters,' they were seen extending over large expanses of lava during the early expeditions to the Galapagos Rift in 1977 and 1979 and were subsequently reported at numerous vents along the East Pacific Rise. Their small tubes, which generally reach lengths of about 5 cm, consist of calcite. When the tentacular plumes are withdrawn into the tube, a small 'plug' seals the tube from the external environment.

Numerous species of apparently vent-endemic fish have been reported from hydrothermal systems along ridge systems throughout the world's oceans. *Bythites hollisi* is a bythitid that was encountered on the first dive to the Galapagos Rift vent field in 1977. Bythitids have been observed in large numbers at several other vent sites, such as the hydrothermal field at 9°50′N along the East Pacific Rise (**Figure 16**). One large 'pit,' with a diameter of several meters, from which cloudy, shimmering

Figure 12 A galatheid crab (*Munidopsis subsquamosa*) with filamentous bacteria on its carapace. This species is a common inhabitant of peripheral vent environments and is also frequently observed in ambient deep-sea environments.

Figure 13 Numerous galatheid crabs (*Munidopsis subsquamosa*) on and in the immediate vicinity of the carcass of a cirrate octopod approximately 50 m from an active hydrothermal vent at 9°50′N along the East Pacific Rise. Close-up imagery revealed that the crabs were actively feeding on the dead tissues of the carcass.

water was emanating, had a concentration of over 20 bythitids, which were frequently observed with their heads projecting downward into the cloudiest portions of the water at the base of the pit.

Zoarcids (eel pouts) are common members of the vent fauna at various sites along the East Pacific Rise and the Mid-Atlantic Ridge, with several different species having been encountered at the various vent fields visited to date. The common species that inhabits many East Pacific Rise vents is *Thermarces andersoni* (**Figures 1, 4, 6,** and **11**). From analyses of extensive video footage and stomach contents of retrieved specimens of this species, it appears to commonly feed on a wide range of organisms, including bacteria, amphipods, leptostracans, and shrimp. It has also been observed scavenging on the plumes of specimens of vestimentiferan tubeworms that have been damaged in the process of sampling or maneuvering with the submersible.

Enteroptneusts, commonly referred to as 'spaghetti worms' were first observed in 1977 draped over pillow lava in peripheral regions of the Galapagos Rift vent field. Few individuals were observed at any of the other many vent fields visited over the next 20 years throughout the world. In 1997, six years after the volcanic eruption at 9°50′N along the East Pacific Rise, numerous enteroptneusts were observed at distances ranging from a few meters to a few hundred meters from active vent sites within the region. No individual organisms were observed living in direct association with venting fluids or at distances in excess of a kilometer from active hydrothermal systems. This unusual, soft-bodied invertebrate may represent an organism that is uniquely adapted to an ecotone between active vents and the ambient deep sea. Analyses of video images of numerous individuals taken with a high-resolution video camera system equipped with a macro-lens (**Figure 17**) have revealed behavioral patterns suggesting that the organism may be 'grazing' directly on basaltic surfaces, potentially consuming microbes or organic substances ultimately originating in the vent environment.

One of the most unusual and spectacular organisms inhabiting vent ecosystems is the vestimentiferan tubeworm *Riftia pachyptila* which

Figure 14 The shrimp *Alvinocaris lusca* perched atop a tube of *Riftia pachyptila* at a low temperature vent along the East Pacific Rise.

Figure 15 Serpulid polychaetes in the peripheral area of a vent field at 9°50′N along the East Pacific Rise.

thrives at numerous vent fields along the Galapagos Rift and East Pacific Rise (**Figures 1, 4**, and **8**). As mentioned earlier, it lives in a symbiotic relationship with chemosynthetic bacteria concentrated within its body. Such a relationship provides an internal, hydrogen sulfide-nourished ‘garden’ that, in turn, nourishes the tubeworm. Although the mechanism by which the host obtains energy from the bacteria is unclear, the energy transfer appears remarkably efficient. An unique opportunity to determine the growth rate potential of *R. pachyptila* arose as a result of the April, 1991 volcanic eruptive event at 9°50′N along the East Pacific Rise mentioned above. In March, 1992, no *R. pachyptila* were present within the region, which had been devastated by the eruption. By December, 1993, less than 2 years later, huge colonies of this tubeworm had colonized the active low-temperature vents; the tube lengths of many individuals were in excess of 1.5 m (**Figures 18** and **19**). Such growth rates of more than 85 cm y^{-1} increase in tube length represent the fastest rates of growth documented for any marine invertebrate. It is interesting to note that one of the other fastest-growing marine invertebrates is the giant clam *Tridacna squamosa*, a bivalve that has a symbiotic association with photosynthetic algae (zooxanthellae). The efficiency with which energy is transferred from the symbiont to the host in certain invertebrates may well be a contributing factor to the remarkable growth rates of these organisms. The rapid succession of a tubeworm-dominated vent community over the 5-year period following the April, 1991 eruption is dramatically illustrated in **Figures 18** and **19**.

Figure 16 The vent fish *Bythites hollisi* emerging from a high-temperature vent region known as Hole-to-Hell at 9°50′N along the East Pacific Rise. The species is common at various vent fields along the Galapagos Rift and East Pacific Rise.

Figure 17 The enteroptneust *Saxipendium coronatum* (commonly known as a 'spaghetti worm') on the surface of basalt about 30 m from an active low-temperature vent field at 9°50′N along the East Pacific Rise. The image was taken with a prototype high-resolution, video camera system equipped with a macro-lens.

Inhabitants of deep-sea hydrothermal vents are among the most spectacular and unusual organisms on the planet. Given the relatively small number of vent ecosystems found to date, many questions have been raised concerning whether conservation measures need to be taken to protect vent communities from anthropogenic disturbances. Any assessment of the potential consequences of anthropogenic impacts needs to consider that the organisms inhabiting deep-sea hydrothermal vents thrive in an environment that is constantly being altered radically by geological process. Periodic devastation of entire biological communities is a relatively common occurrence as volcanic and tectonic processes proceed along active ridge axes. Over the past two decades we have learned that many vent communities are remarkably resilient. Populations of essentially all vent organisms indigenous to regions decimated by massive volcanic eruptions have, like a Phoenix rising from the ashes, reestablished themselves in less than a decade. This remarkable resilience in the face of huge natural disasters has profound implications as one considers the potential impacts of exploitation of precious mineral and biological resources associated with active hydrothermal systems throughout the world's oceans.

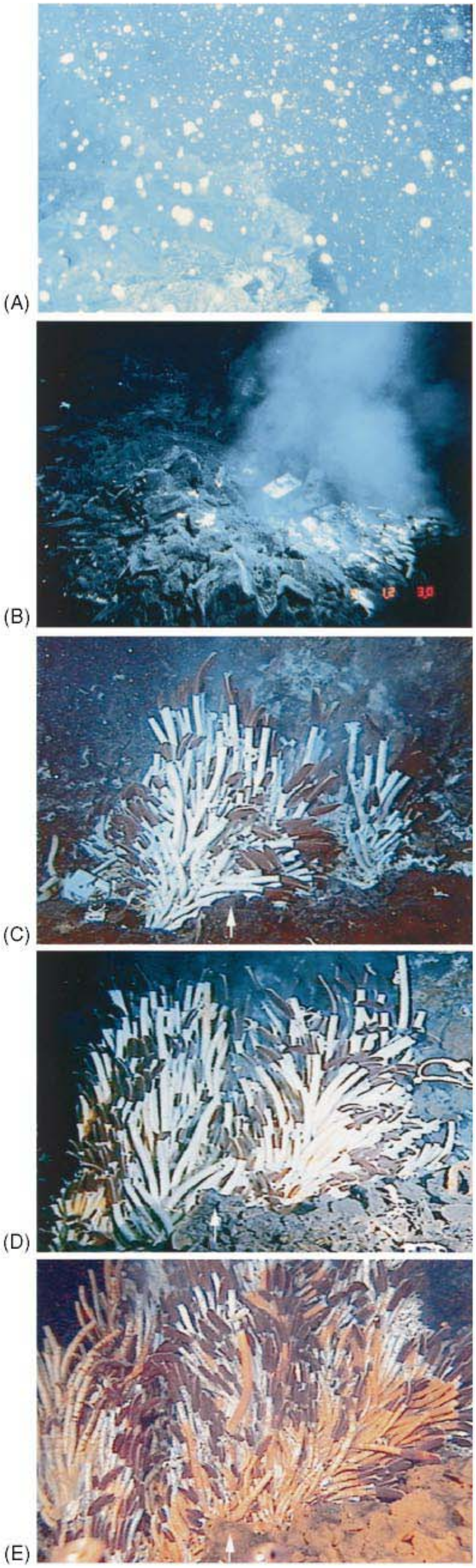

Figure 18 (Right) Temporal sequence of vent community development at a low-temperature vent in a region known as Hole-to-Hell at 9°50′N along the East Pacific Rise. This was the site of a volcanic eruption in April, 1991 that entirely decimated previously existing communities within the region. The field of view of each image and the heading of the camera system utilized are approximately the same for each image taken at the following times: (A) April, 1991; (B) March, 1992, (C) December, 1993; (D) October, 1994; and (E) November, 1995. (Shank *et al., 1998*.)

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See also

Deep-sea Ridges, Microbiology. Hydrothermal Vent Ecology. Hydrothermal Vent Fauna, Physiology of.

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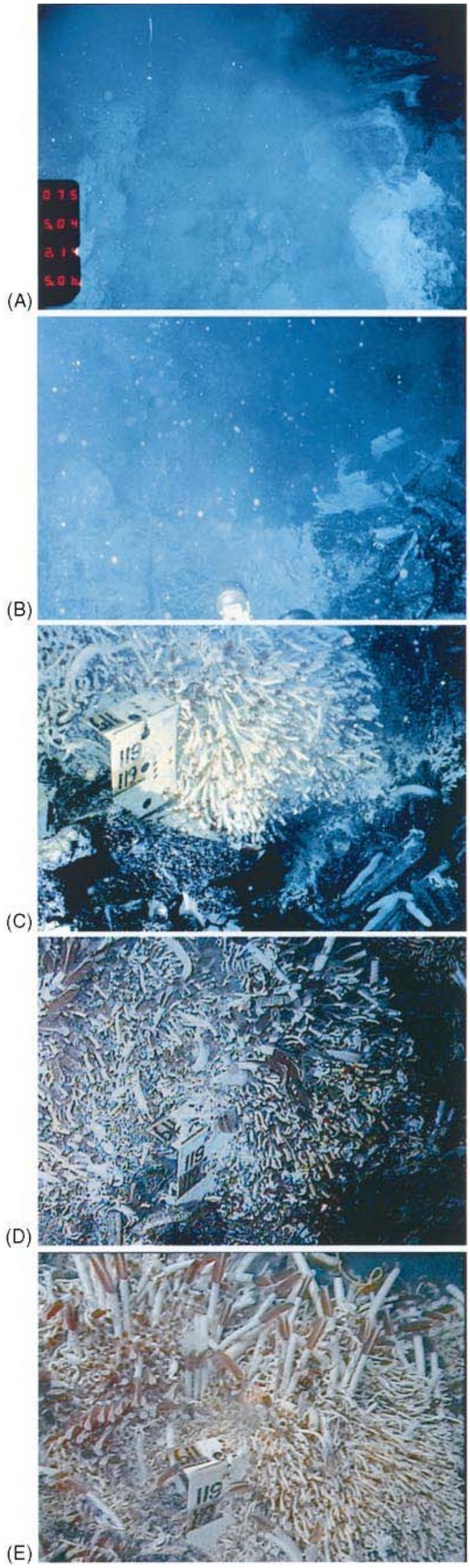

Figure 19 (Left) Temporal sequence of vent community development at a low-temperature vent located approximately 500 m from the community depicted in **Figure 18**. This was also a region that was buried with fresh lava by the April, 1991 volcanic eruptive event, decimating previously existing communities within the area. The field of view of each image and the heading of the camera system utilized are approximately the same for each image taken at the following times: (A) April, 1991; (B) March, 1992; (C) December, 1993; (D) October, 1994; and (E) November, 1995. (Shank *et al.,* 1998.)