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The Biology of Hydrothermal Vents: A Short Summary of Recent Findings

J. Frederick Grassle
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts

The internal heat of a planet, mostly of radioactive origin, in theory would provide an alternative to incoming radiation though we have little precedent as to how an organism could use it.—G.E. Hutchinson (1965)

The large clams, mussels, and vestimentiferan worms at hydrothermal vents two and a half kilometers deep are exceptions to the view that life depends directly or indirectly on the sun. Primary production of food for larger animals occurs by microbial chemosynthesis using energy from the reaction of sulfides and other reduced compounds in heated sea water emanating from the sea floor (Jannasch and Wirsen, 1979; Karl et al., 1980; Ruby et al., 1981). Chemosynthetic production has long been known from anaerobic-aerobic boundaries but the vent animals are the only ones known to thrive on chemosynthetic products derived from volcanic energy.

Dense beds of large animals (Figure 1) were first seen in 1977 from *Alvin* (Corliss and Ballard, 1977, Corliss et al., 1979), and large bivalves were seen independently in Deep-Tow photographs (Lonsdale, 1977). The first biology expedition to vents in 1979 included physiologists, biochemists, microbiologists, ecologists and taxonomic specialists on various animals occurring at the vents. Prominent species concentrated at Galapagos vents belong to four new families or subfamilies of annelid, pogonophoran, gastropod and crustacean (Desbruyeres and Laubier, 1981; Jones, 1980; McLean, 1981; Williams, 1980), and several more new families are likely to be described from material already collected. Among the smaller animals new genera of barnacles (Newman, 1979), leeches (Burrison, 1981), polychaetes (Maciolek, 1981) and copepods (Humes and Dojiri, 1980) have been described. Many of the animals are spectacular, but the diversity of species is low compared with deep-sea environments elsewhere (Galapagos Biology Expedition Participants, 1979, Sanders, pers. comm.).

Nucleotide analyses showed the vent water was several times (2.5-5x) more productive than surface water in the same area and orders of magnitude more productive than near-bottom water collected away from the vents (Karl et al., 1980). Earlier circumstantial evidence indicated sulfur bacteria growing in the vents (Corliss et al., 1979), but none of the microorganisms had been isolated and there were no estimates of productivity. All 95 strains of bacteria later isolated from Galapagos vent water could incorporate CO₂ in the presence of reduced sulfur and oxygen (Ruby et al., 1981). Since the sulfur-oxidizers need oxygen and the vent water above 8-10°C contains no detectable oxygen (Corliss et al., 1979), most free-living bacterial growth must occur in subsurface, basaltic caverns and lacunae peripheral to the main flow of vent water. Clumps and mats of bacteria become entrained by the more rapidly flowing water at elevated temperatures (up to 23°C in the Galapagos Rift). Temperatures slightly above ambient are detectable in crevices peripheral to the main vents where clams (*Calyptogenia magnifica*) as long as 30 cm are concentrated (Turner, 1981). *Calyptogenia* from 21°N on the East Pacific Rise experience temperatures at least 2°C above ambient (Killingley et al., 1981). Clams, mussels, (an undescribed mytilid) and the red-plumed worm, *Riftia pachyptila* contain symbiotic bacteria enabling them to gain food by taking up reduced sulfide and CO₂ from vent water (Cavanaugh et al., 1981; Felbeck, 1981; Felbeck et al., 1981). The *Riftia* live in the warmest water at the Galapagos Rift, while some clams and mussels survive at temperatures only slightly above the ambient 2°C. Studies of ratios of stable carbon and nitrogen isotopes further indicate that mussels, clams, and *Riftia*

gain food from a nonphotosynthetic pathway (Rau and Hedges, 1979; Rau, 1981a,b; Williams et al., 1981). Other molecules such as H_2 , NH_3 , NO_2 , Fe^{2+} , and Mn^{2+} may play a role in chemosynthesis (Ruby et al., 1981).

Aside from the unusual organisms and metabolism of reduced sulfur and metals, the most interesting findings concern rates of metabolism and growth and the age structure of vent organisms. Over large areas of the deep sea, metabolic rates, microbial activity and growth rates are often low (Jannasch et al., 1971; Grassle, 1977, 1980; Smith, 1978; Smith and Hessler, 1976). These low rates are associated with relatively stable habitats low in food for growth. For vent animals rates of growth are within the range normal for shallow-water relatives (Childress and Mickel, 1982; Galapagos Biology Expedition Participants, 1979; Rhoads et al., 1981; Turekian, 1979; Turekian and Cochran, 1981; Williams et al., 1981). Although evidence to the contrary had already been accumulating, the vent studies clearly set to rest the idea that a hostile environment consisting of high pressures and low temperatures had prevented the evolution of normal or fast life processes. The metabolic rate and growth of mussels at hydrothermal vents is food supply dependent (K.L. Smith in Hiatt, 1980; Rhoads et al., 1981), i.e., growth rates are highest close to the presumed source of molecular and bacterial energy. Rates may also evolve in response to rapid changes in temperature and food supply through fluctuation or cessation of the hydrothermal circulation. Estimates of heat loss from high temperature vents ($350^\circ C$) on the East Pacific Rise indicate episodic vent activity with individual vents lasting for 1-10 years (MacDonald et al., 1980). Other evidence for short vent duration comes from the size of sulfide deposits and the age of *Calyptogena* shells at sites where active venting is no longer present. Shell fragments placed at 2700 m depth in the same region as the vents indicate dissolution rates on the order of 25 years or less (Killingley et al., 1981). Fields of eroded clam shells (Corliss et al., 1979; Crane and Ballard, 1980; Francheteau et al., 1980) indicate recently inactive vents.

In an environment where the food supply may abruptly be curtailed it is advantageous for individuals to grow to sexual maturity as rapidly as the food supply allows in order to maximize the number of offspring released into the plankton to colonize new vents. The scarcity of stable environments with elevated supplies of energy for growth and metabolism have prevented ecologists from separating the role of environmental change from that of elevated food supply.

The biology of the dispersal stages of vent organisms remains unknown. The mussels have planktonic larvae of the sort known to feed in the surface waters (Lutz et al., 1980) but this species has one of the most restricted distributions of any of the vent animals. The late larval stage of the crab (*Bythograea thermydron*) has eye pigment that is subsequently lost in the adult (Williams, 1980) suggesting an early existence in surface waters. How larvae can locate new active vent sites only tens of

meters across, separated, by hundreds, and perhaps thousands of kilometers, remains a mystery.

Four hydrothermal vent sites have been sampled: the Galapagos Rift, $11-13^\circ N$, $21^\circ N$ and $27^\circ N$ (Guaymas Basin) on the East Pacific Rise. Vents with associated fauna are known only from photographs at $20^\circ S$ and $45^\circ N$ (Juan de Fuca Ridge). Over this enormous geographic range there are marked similarities in the faunas, but some striking differences between vent systems are apparent.

Mussels (Mytilidae) have been found only on the Galapagos Rift and at $11-13^\circ N$ and *Calyptogena magnifica* is found only on the Galapagos Rift and at $21^\circ N$ (D. Desbruyeres and J.P. Grassle, pers. comm.). A different species of *Calyptogena*, (*Calyptogena pacifica*) is found in the Guaymas Basin and near hydrothermal deposits in the San Diego Trough off California (Felbeck et al., 1981; R. Turner, pers. comm.). The only fish that orients toward the flow of vent water is the pink bythitid from the Galapagos that swims head down in the vents. This fish has been seen nowhere else. Vents at $11-13^\circ N$ and 21° have a predatory zoarcid living in association with the vent community (Desbruyeres, pers. comm.; Spiess et al., 1980). The most interesting animal found since the Galapagos expedition is the pompeii worm, *Alvinella pompejana* belonging to a new subfamily of polychaetes, *Alvinellinae* (Desbruyeres and Laubier, 1980). The "snow balls" associated with venting water at 32° to $330^\circ C$ were made up of tubes secreted by *Alvinella* (Figure 2, Rise Project Group, Spiess et al., 1980). This animal was also found at $11-13^\circ N$ along with a new genus of alvinellid (D. Desbruyeres, pers. comm.). The new alvinellid genus occurs commonly near the hottest water ($>300^\circ C$) at the Guaymas Basin site and occurs very rarely at the Galapagos Rift. The actual temperatures at which the worms live are much lower than those measured inside the "snow balls" and white smokers (D. Desbruyeres, pers. comm.).

Riftia pachyptila (F. Riftiidae) occurs at $11-13^\circ N$, $21^\circ N$, Guaymas Basin, and the Galapagos Rift, but the other family of vestimentiferans (F. Lamellibrachiidae) has been found only at $11-13^\circ N$, $21^\circ N$ and at $32^\circ N$ off California and $45^\circ N$ off Oregon. The undescribed spaghetti-like enteropneust, and the rhodaliid siphonophore seen on the periphery of the vents in the Galapagos (Galapagos Biology Expedition Participants, 1979) have not been seen elsewhere. There have been reports of a somewhat different looking siphonophore at $21^\circ N$ and a different enteropneust-like worm at $20^\circ S$ (R. Ballard, pers. comm.). Corals and sponges seen commonly away from vents at all sites do not occur within the vent communities.

The Guaymas Basin is of particular interest because hydrothermal fluid comes up through a thick covering of pelagic sediments. Mounds hundreds of meters long and tens of meters high are covered with thickets of *Riftia pachyptila* (Figure 3). The sediments around these mounds are covered with creamy patches of "fur" tens

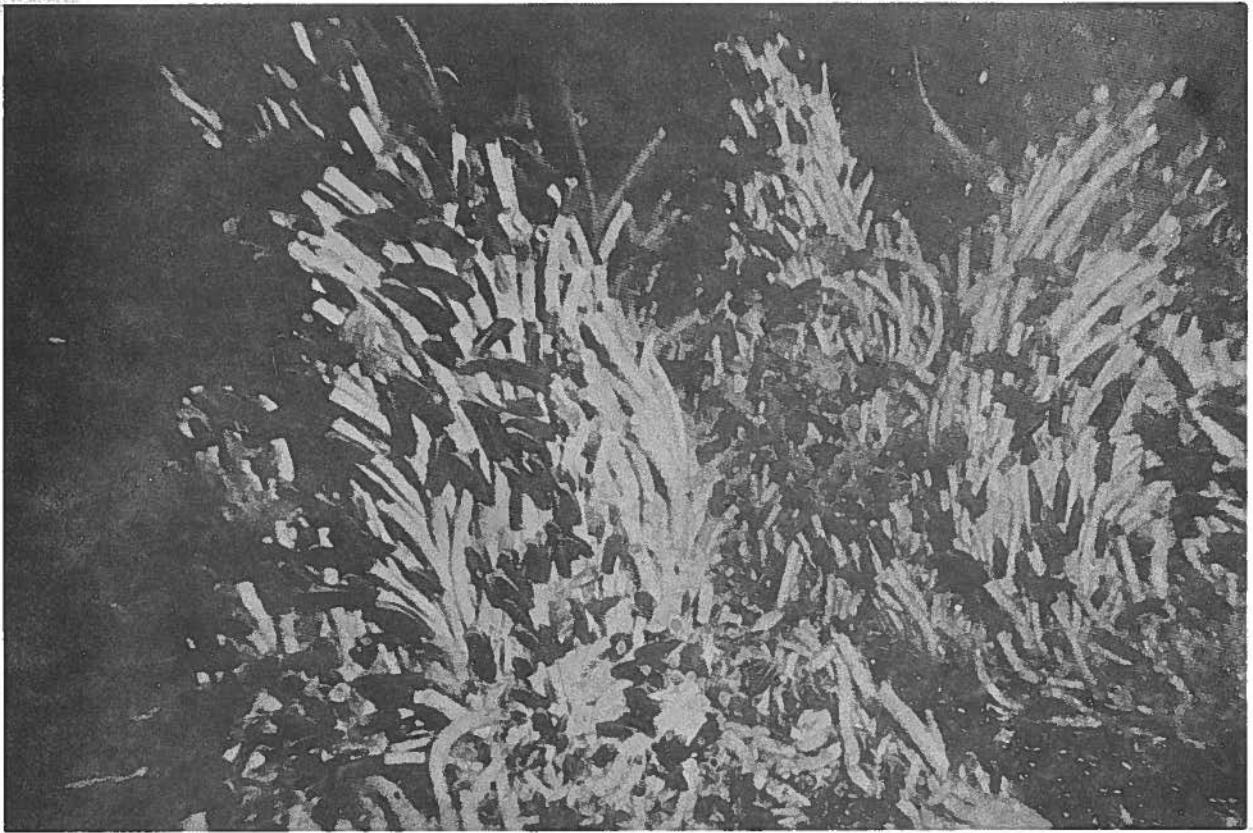


Figure 1. *Riftia pachyptila* of the "rose garden" vent on the Galapagos Rift. (Photo by K. Crane.)

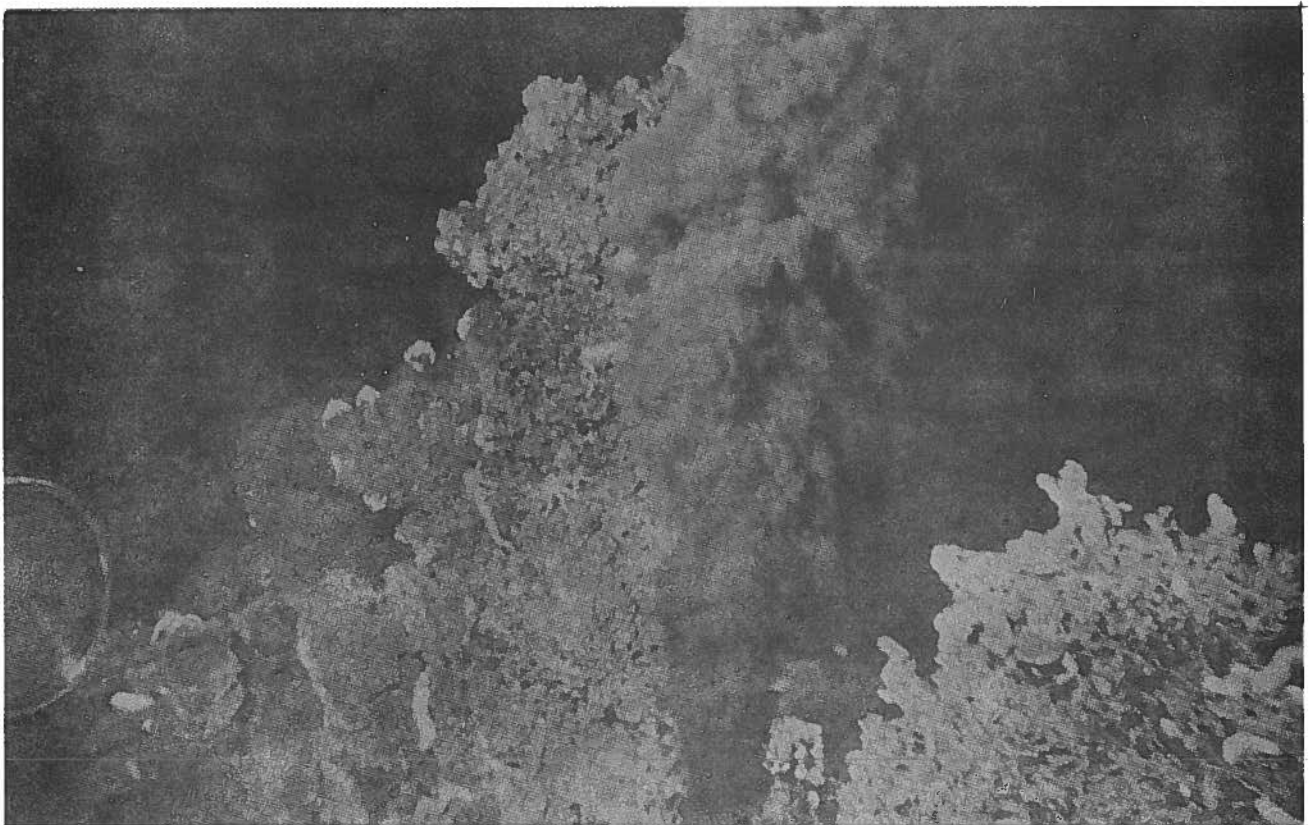


Figure 2. *Riftia pachyptila* and "snow ball" made of the tubes of the pompeii worm, *Alvinella pompejana* at 21°N. (Photo by J. Edmond.)

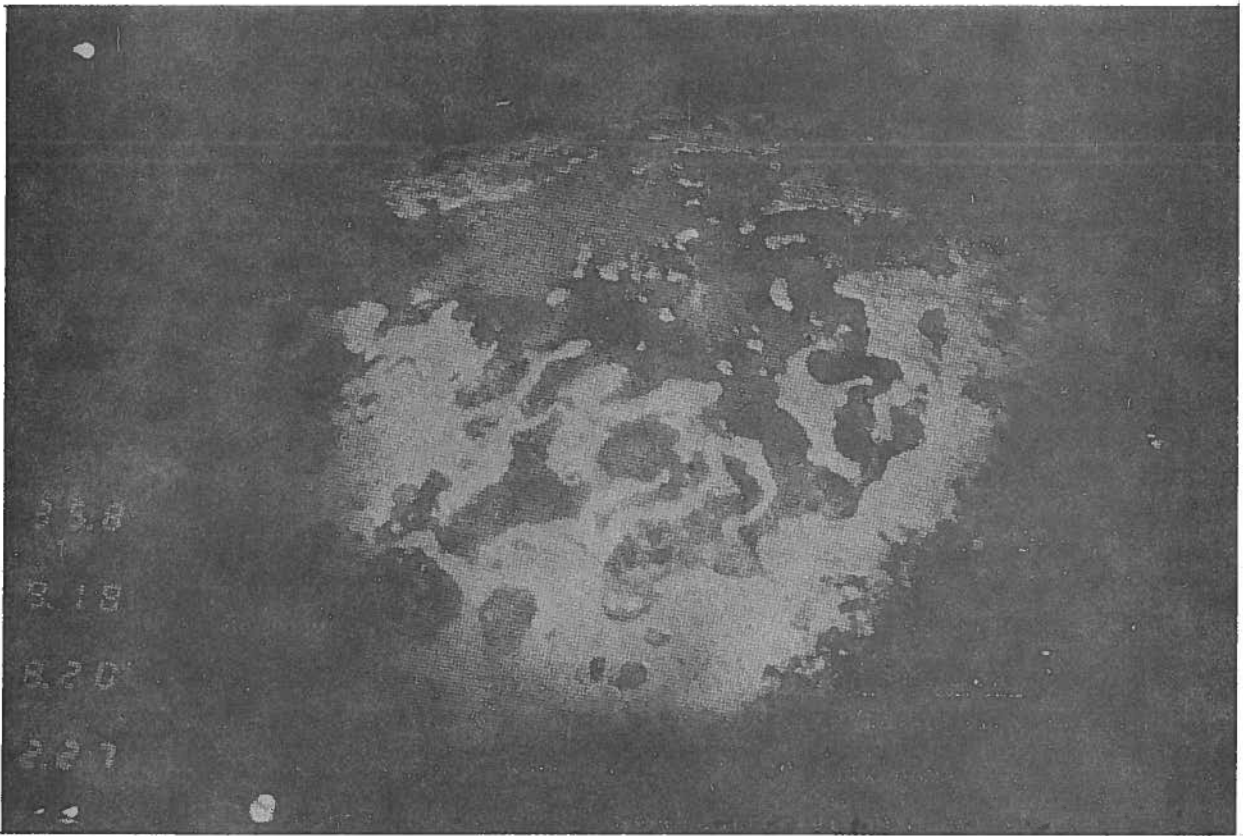


Figure 3. *Riftia pachyptila* and bacterial mat of *Beggiatoa* sp. at Guaymas Basin. (Alvin external camera.)

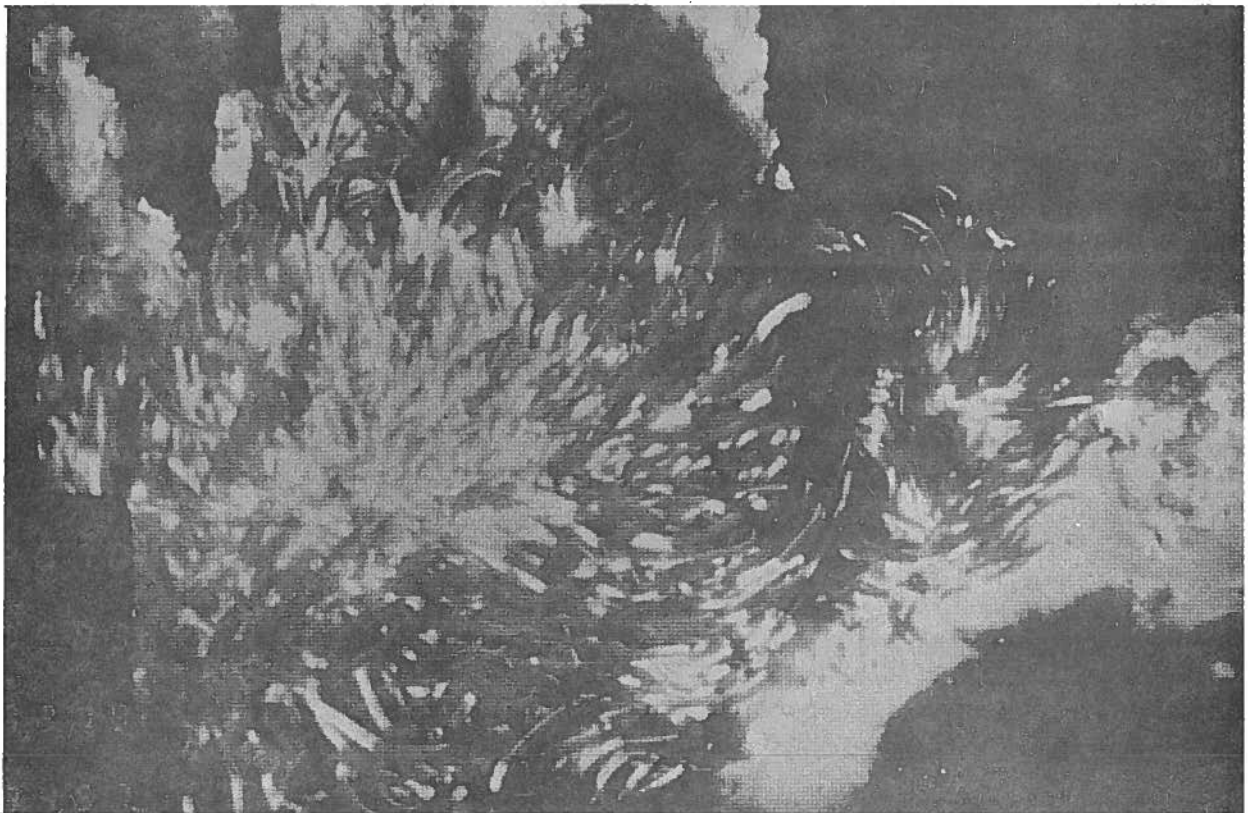


Figure 4. Mats of *Beggiatoa* sp. on the sediment surface at Guaymas Basin. (Alvin external camera.)

of meters wide—dense mats of bacterial filaments belonging to the genus *Beggiatoa* (Figure 4). Some of these filaments are greater than 110 μ in diameter, larger than any other known bacteria. Sediments under the patches smelled strongly of H₂S and contained small *Calyptogena pacifica* in densities up to 60 per 225 cm² box core. An adjacent core contained an even higher density of a *Nuculana*-like protobranch bivalve. Other grayish patches of sediment were saturated with hydrocarbons formed at high temperature from the pelagic sediments (Simoneit and Lonsdale, 1982). A small polychaete, *Ophryotrocha* was found to survive in these sediments despite the hydrocarbon concentrations. Thickets of black corals were common near the base of the mounds giving credence to the suggestion that a few animals on the periphery of vents gain food from particles swept toward the vents by convection currents (Hessler, 1981).

Our initial findings indicate punctuated strings of oases girdling the ocean floor two km below the surface. Our image of life in the deep sea has been altered, and more surprises are likely in the near future.

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J. Frederick Grassle is Associate Scientist at the Woods Hole Oceanographic Institution. He completed his doctorate at Duke University in 1967, spent two years in Australia at the University of Queensland and has been in Woods Hole since 1969. He has worked on coral reefs, population biology of polychaete worms, and the ecology of shallow-water and deep-sea benthic communities. He was chief scientist and coordinator of the Galapagos Rift Biology Expedition.

