23 August 1985, Volume 229, Number 4715 **SCIENCE**

Hydrothermal Vent Animals: Distribution and Biology

J. Frederick Grassle

Summary. Hydrothermal vent communities characterized by large clams, mussels, and vestimentiferan worms thrive on chemosynthetic microbial production. There are similarities in the animal distributions at vent communities from 20°S to 46°N on the Mid-Ocean Ridge in the Pacific Ocean and at cold sulfide seeps in the Gulf of Mexico. Vent communities, consisting of at least 16 previously unknown families of invertebrates, are at least 200 million years old. Since the life-span of a vent is only tens of years, the species survive by rapid growth and widespread dispersal of larvae with the subsequent colonization of new vents.

Large clams, crabs, mussels, and worms are found at a number of deep-sea oases fed by hydrothermal fluid and a profusion of microbial growth (Fig. 1). The list of new vent species and families continues to grow (Table 1). The total number of new families is expected to reach 16. The best studied vents are located at depths of 2500 to 2600 m along the Galápagos Rift and the East Pacific Rise. New vent communities continue to be found, the latest ones on an axial seamount on the Juan de Fuca Ridge at a depth of 1570 m, on a passive continental margin at a depth of 3266 m at the base of the Florida Escarpment, and at 700 to 800 m at a petroleum seep in the central Gulf of Mexico (*1*). These findings raise interesting questions about the evolution of metabolic, growth, and reproductive rates and about the distribution and dispersal of marine organisms.

Zonation and Distribution

The zonation of animals with distance from sites of maximum hydrothermal discharge has been described by Hessler and Smithey for the Galápagos Rift vents, which were studied with the submersible *Alvin* in 1979 (*2*, *3*). Animals closest to the vents are exposed to temperatures ranging from the ambient temperature, 2.01°, to ~15°C. The tube worm *Riftia* and the limpet *Neomphalus* live deep in vent depressions. Mussels, the shrimp *Alvinocaris*, an anemone, and another species of limpet live among the *Riftia* tubes. The giant white clam (*Calyptogena magnifica*) lives in crevices away from *Riftia*. Many mussels are attached at some distance from the central vent zone at temperatures close to 2.01°C. A large scale worm, *Branchipolynoe*, lives symbiotically with mussels but is occasionally observed swimming away from its host. Intervening rock surfaces are covered with another species of anemone and serpulid "feather duster" worms. A galatheid crab and a turritid gastropod are also common in this area. The peripheral zone is characterized by the siphonophore *Thermopalia*, and an enteropneust, *Saxipendium coronatum*, draped over rocks like strands of spaghetti. The vent communities are also distinguished by the absence of corals, sponges, and bryozoa commonly found on rocky surfaces elsewhere in the deep sea. Echinoderms are extremely rare.

There are differences in the relative numbers of *Riftia*, mussels, and clams at three carefully studied Galápagos vent areas (Rose Garden, Mussel Bed, and Garden of Eden). The abundances in each of the vent fields depend on the flow patterns of hydrothermal fluid and possibly on the amounts of particulate material suspended in the water. At the Rose Garden site, the westernmost vent, shimmering water marks a zone of rapid mixing along a large fissure filled with the largest *Riftia* seen. The Mussel Bed site has a wall of mussels on a steep slope, and the most rapid flows are in sites 1 to 2 m in diameter with only a few *Riftia*. On one occasion, removal of mussel clumps revealed *Riftia* underneath. The Mussel Bed site (visited in 1979) is located slightly lower down the same slope than the Clambake I site, described by geologists in 1977 (*3*). The third site (Garden of Eden) was visited in both 1977 and 1979 and at least part of the vent field seems to have changed little over this period. Quantitative comparisons are not possible, but the area occupied by *Riftia* may have shrunk somewhat from the 40-m patch in the 1977 *Angus* photographs (*5*). Limpets are particularly common on the rock surfaces at this site; mussels and clams are rare.

Animal distributions at these sites relate to the flux of hydrothermal fluid and the chemical environment which may vary independently of temperature. At the small scale of separation of the Galápagos vents, each species occurs at all vents and chance colonizing events do not result in differences in species composition between vents. A detailed *Angus* photographic survey of a 30-km stretch of the Galápagos Rift showed nine vents with living communities and three vents with only dead bivalve shells present to record earlier evidence of hydrothermal flows (*5*). The greatest distance between living communities was ~8 km.

A similar survey of the East Pacific Rise from 12°38′N to 12°54′N indicated

---

The author is a senior scientist in the Biology Department of Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.

24 active vents (*5*). Of these, 22 occurred over ~8 km of ridge axis from 12°47′ to 12°51′N. A 7-km stretch with massive sulfide deposits but no active vents separated these 22 vents from the two remaining vents near 12°41′ and 12°43′N. Another survey of a stretch of ~30 km near 21°N on the East Pacific Rise located 14 active vents spread over 6 km and a single "black smoker" (350°C) 6.5 km from any other vent (*5*). Large segments of ridge axis are inactive, and, because of the offset distance at fracture zones, vent fields may be separated by hundreds of miles. None of these sites has been surveyed by direct observations or close-up photographs in sufficient detail to permit comment on the presence or absence of individual species.

Only the following sites have been surveyed by biologists: three Galápagos vents, three vents at 13°N, a single vent area at 21°N, the Guaymas Basin vents, the Juan de Fuca Ridge axial seamount, and the Florida Escarpment in the Gulf of Mexico. White *Calyptogena*-like clams have been observed at all these sites as well as at 20°S on the East Pacific Rise and in the San Clemente Basin off California. Living *Calyptogena magnifica* have been verified only at the Galápagos vents and at 21°N, but empty shells have been collected from 13°N (*6*). The Guaymas Basin and San Clemente Basin have *Calyptogena pacifica*, and on the Florida Escarpment the *Calyptogena* are a new species (*7*). An unnamed Galápagos Rift mussel has also been collected at 13°N and seen in photographs from 17°S. Electrophoretic studies of genetic variation indicate that the mussel population at 13°N is distinct from the Galápagos population (*8*). New species of mussels have been found at the Guaymas Basin and the Florida Escarpment (*7*). A minimum of 13 limpet species belonging to at least five new families have been collected at 21°N. Of these, 11 species were found at 13°N and six were collected from the Galápagos Rift (*7, 9*). Two of the species were collected in the Guaymas Basin; none of the 21°N species have been found at the Juan de Fuca seamount (*9*).

The red-plumed *Riftia* is the only representative of the Riftiidae, the recently described second family of Vestimentifera. These tube worms occur at the Galápagos, at 13°N, at 21°N, and at the Guaymas Basin and give these vent areas their exotic appearance. Since the Galápagos collections were made, the complexity of the distribution pattern of Vestimentifera at each new vent area has increased (Fig. 2) (*10*). In addition to *Lamellibrachia barhami* (the genus first seen off California in 1966) and *Riftia pachyptila*, there are now at least six more undescribed species (*10*).

Alvinella pompejana, the animal living at the highest temperature of up to 40°C, was not found in the Galápagos Rift vents. It has been found only at 13°N and 21°N. However, another genus of this new subfamily, *Paralvinella*, has been found at the Galápagos vents and the Guaymas Basin. Yet another species of the same subfamily has been collected from the Juan de Fuca Ridge (*4, 11*).

The general pattern that emerges is of a fauna exhibiting many similarities and distributed from the Galápagos Rift north along the East Pacific Rise into the Gulf of California. The Pacific and Gulf of Mexico sites have similar large animals but different species. The Juan de Fuca vent fauna is distinct from that of other vent sites with the exception of the small polychaete *Amphisamytha galapagensis* (*1*).

Table 1. Recently described species found at hydrothermal vents. Most of the smaller species from Galápagos also occur at 21°N.

Megafaunal vent species
Alvinella pompejana Desbruyeres and Laubier 1980 (Polychaeta), Pompeii worm
Alvinocaris lusca Williams and Chace 1982 (Decapoda), vent shrimp
Branchipolynoe symmytilida Pettibone 1984 (Polychaeta), scale worm
Bythograea microps de Saint Laurent 1984 (Decapoda), brachyuran crab
Bythograea thermydron Williams 1980 (Decapoda), brachyuran crab
Calyptogena magnifica Boss and Turner 1980 (Bivalvia), giant clam
Cyanograea praedator de Saint Laurent 1984 (Decapoda), brachyuran crab
?*Diplacanthopoma* sp. (Vertebrata), vent fish
Neomphalus fretterae McLean 1981 (Gastropoda), limpet
Riftia pachyptila Jones 1980 (Vestimentifera), giant tube worm
Saxipendium coronatum Woodwick and Sensenbaugh 1985 (Enteropneusta), spaghetti worm
Thermopalia taraxaca Pugh 1983 (Siphonophora), dandelion
Smaller vent species
Galápagos
Amphisamytha galapagensis Zottoli 1983 (Polychaeta)
Bathybdella sawyeri Burreson 1981 (Hirudinea)
Branchinotogluma grasslei Pettibone 1985 (Polychaeta)
Branchinotogluma hessleri Pettibone 1985 (Polychaeta)
Branchinotogluma sandersi Pettibone 1985 (Polychaeta)
Ceuthoecetes aliger Humes and Dojiri 1980 (Copepoda)
Copidognathus papillatus Krantz 1982 (Acarina)
Dahlella caldariensis Hessler 1984 (Leptostraca)
Laubieriellus grasslei Maciolek 1981 (Polychaeta)
Lepidonotopodium riftense Pettibone 1984 (Polychaeta)
Lepidonotopodium williamsae Pettibone 1984 (Polychaeta)
Opisthotrochopodus alvinus Pettibone 1985 (Polychaeta)
Paralvinella grasslei Desbruyeres and Laubier 1982 (Polychaeta)
Prionospio sandersi Maciolek 1981 (Polychaeta)
Xandaros acanthodes Maciolek 1981 (Polychaeta)
21°N
Branchiplicatus cupreus Pettibone 1985 (Polychaeta)
Eunice pulvinopalpata Fauchald 1982 (Polychaeta)
Isaacscalanus paucisetus Fleminger 1983 (Copepoda)
Lepidonotopodium fimbriatum Pettibone 1983 (Polychaeta)
Melanodrymia aurantiaca Hickman 1984 (Gastropoda)
Neolepas zevinae Newman 1979 (Cirripedia)
13°N
Thermaloniscus cotylophorus Bourdon 1983 (Isopoda)

Soft Sediments at Vents

Soft-sediment communities in the deep sea include many species, even in collections covering a small surface area. In the mounds region of the Galápagos Rift, the species diversity at the areas away from mounds is typical of what may be seen in deep-sea sediments (Fig. 3), despite a very slow hydrothermal circulation (~1 cm per year away from the mounds) (*12*). Close to the mounds where there are mineral deposits and much greater hydrothermal circulation (20 to 30 cm per year), the diversity is lower. Near vents on the East Pacific Rise the only sediments are the mineral fallout from black smokers. Communities in these sediments also have low diversity. The only one of these sites with an obvious flux of sulfide through sediments supporting microbial growth is in the Guaymas Basin. Here microbial mats cover the sediment surface (Fig. 4), and dense populations of a few species of bivalves and polychaetes are supported. Some of the hydrothermally influenced patches of sediment in the Guaymas Basin are permeated by petroleum hydrocarbons, and in the most extreme situation only one species, a polychaete, *Ophryotrocha* n.sp., survives.

Feeding

Two hypotheses have been advanced to account for the source of primary production available to vent animals (*13*). According to one hypothesis, chemosynthetic microorganisms provide food for the dense concentration of large animals; according to the other, the heat-driven circulation causes bottom currents that transport photosynthetically derived suspended food from peripheral regions (*13*). This large convection cell resulting from the rising plume of warm water might concentrate particles settling from the surface.

The second hypothesis can be eliminated from consideration as providing a significant source of food for *Riftia*, *Neomphalus* limpets, and *Calyptogena*. Large adult specimens of these animals are frequently found so far down in the vents that lateral advection could not supply particles of food. The presence of symbiotic chemosynthetic bacteria in *Riftia*, *Calyptogena*, and mussels indicates that microorganisms could provide most of the food for these animals (*14*). Vent mussels and clams are capable of feeding on suspended particles, but most of these particles appear to originate in the hydrothermal fluid. The particles emanating from the vents are much richer in nitrogen and lipid compounds than particles collected in peripheral areas (*15*). Mussels can survive away from the main supply of hydrothermal fluid, but those individuals transplanted from a central to a peripheral vent area showed minimal growth and experienced a loss of body weight over a 9-month period (*16*). In the main vent area the biomass of mussels may exceed 10 kg per square meter (*2*). Convection cells may be important in recirculating particulates emanating from the vents. Peripheral species such as enteropneusts and siphonophores may benefit from this material and its associated plankton, supplemented by photosynthetically derived particles. However, analysis of stable isotopes of carbon, nitrogen, and sulfur in the tissues of *Riftia*, *Calyptogena*, mussels (no sulfur analyses), and the crab *Bythograea* indicated a local source (chemosynthetic organisms) rather than a pelagic source for these elements (*17*).

At least part of the time, the crabs and some of the amphipods are scavengers. Although attracted to bait, the crabs have been observed to scrape the microbial growth from the surface of *Riftia* tubes and to prey on *Riftia* and small mussels (*15, 19*). Serpulids and enteropneusts feed on suspended particles, whereas the anemones and siphonophores may rely more on zooplankton. Examination of the gut contents of these species has revealed no identifiable organisms (*20*).

Pompeii worms, *Alvinella pompejana*, form ball-like structures around vents with temperatures up to 250°C. The animals themselves may be found at 20° to 40°C (*3, 21*). External microorganisms live in close association with dendritic branches of the posterior parapodia and are likely to supply a major portion of the food supply (*3, 21*). The tentacles on the head can be used either for suspension feeding or for feeding on surface deposits.

A zoarcid fish from vents at 13°N and 21°N is a predator. The pink bythytid fish at the Galápagos (possibly the genus *Diplacanthopoma*) is most frequently seen head down in the vents (*22*). It has not been captured, but it may feed directly on microorganisms in the hydrothermal fluid.

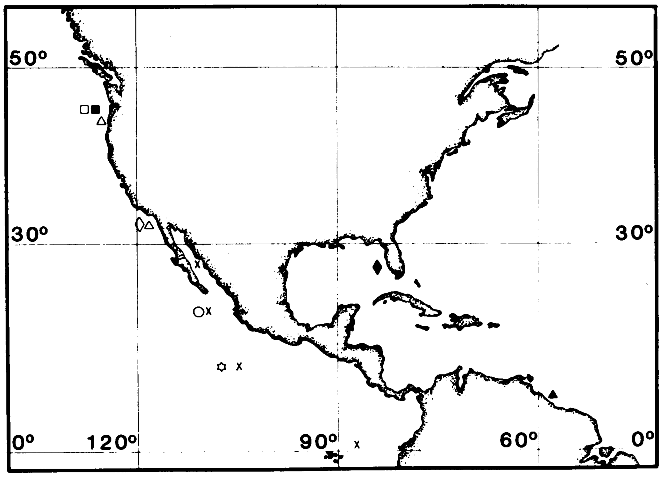

Fig. 1 (left). Photo showing the giant tube worm *Riftia*, mussels, and the crab *Bythograea* at the Rose Garden hydrothermal vent on the Galápagos Rift at a depth of 2500 m. Fig. 2 (right). Distribution of vestimentiferan species (*10*). Each symbol represents a morphological type, and the shading indicates species.

Rates

Each vent community persists for only several years to several decades. The best evidence in support of this idea is the finding of only dead shells at some sites (*5*). Since *Calyptogena* shells need less than 15 years to dissolve, the vents where these shells have been found must have shut down within that period (*7*, *23*). Estimates of heat loss at the 350°C vents indicate a life-span of less than 10 years (*24*). At one 13°N site, hydrothermal activity and vent temperatures declined from 1982 to 1984, resulting in death of *Riftia* and *Alvinella* (*6*). Radiochemical dating techniques, based on the use of naturally occurring members of the ^{238}U and ^{232}Th decay series in the growth horizons of *Calyptogena* shells, indicate ages from 3 to 30 years (*25*). A direct measure of growth was obtained from mussels marked with a file on the growing margin and recovered after a little more than 9 months. The growth rate was ~1 cm per year; thus the oldest mussels were 19 ± 7 years of age (*18*). For most vent species, reproductive success requires that new vent fields be colonized. Under these circumstances one would expect that there would be strong selection for rapid growth, the ability to produce many offspring, and an efficient means of dispersal. Recent studies, based on the use of very accurate rates of shell dissolution to estimate the age of clams, indicated a growth rate of ~3 cm per year up to a size of 11.5 cm and less than 1 cm per year from this size to 20 cm (*26*). Female clams 9 to 10 cm long have reached maturity and have produced ripe ova when 12 to 14 cm in length. Female mussels begin to ripen at an average length of 6.6 cm and become fully ripe when ~9 cm in length (*26*). The growth rate of the third large species, *Riftia*, is not known. Thus the life-spans for the clams and mussels are approximately the same as the life-spans of active vents, but the times to maturity are on the order of 4 to 6 years.

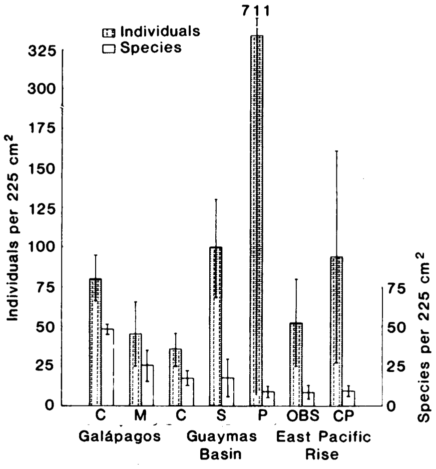

Fig. 3. Species and individuals per 225-cm^2 box core at soft-sediment hydrothermal areas. Abbreviations: C, control samples; M, mounds; S, hydrogen sulfide; P, petroleum; OBS, ocean bottom seismograph site; and CP, collapsed pit site.

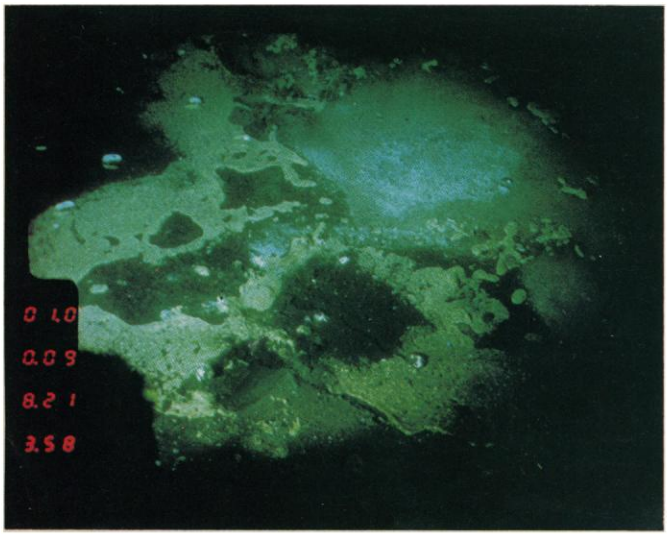

Fig. 4. Microbial mats on the sediment surface in the Guaymas Basin.

The need to produce many larvae in order to colonize new vents may be a sufficient reason for large body size, if there is an adequate food supply. The presence of bacterial symbionts might also contribute to the large body size of *Riftia*, clams, and mussels (*27*). Large volumes of tissue in these animals are given over to food-producing symbionts. Some of the best known shallow-water invertebrates with photosynthetic symbionts, such as giant clams (*Tridacna*) and some hermatypic corals (considering the entire colony as an individual), also reach a large maximum size. The many exceptions, such as the threadlike deep-sea Pogonophora and marine oligochaete worms, have evolved no substantial external skeletal supports. The thick tube of *Riftia* contrasts with the much thinner tubes and smaller size of its vestimentiferan relatives.

The rates of metabolism, growth, and fecundity are low in deep-sea organisms living away from vents. With the exception of the flora in the guts of some deep-sea species, the rates of microbial activity are also low and oxygen uptake by soft-sediment benthic communities is two to three orders of magnitude less than that of shallow-water communities. One small deep-sea clam requires ~50 years to reach maturity and lives for ~100 years (*28*). The most rapidly growing deep-sea soft-sediment clam grows to maturity in 2 years and produces a few hundred eggs at any one time (deep-sea bivalves may produce as few as two eggs at a time) (*29*). The bivalves with the most opportunistic life histories in the deep sea are the wood borers, which reach maturity in a few months and produce thousands of eggs at one spawning (*30*). Wood is an ephemeral habitat for these animals; to survive they must continually colonize new pieces of wood. In this sense, they face problems similar to those faced by vent animals, although the absolute time scale is different. The community living in wood may be of interest in the study of the evolution of vent bivalves, since the closest relative of the Guaymas Basin vent mussel (*Idasola*) is associated with wood elsewhere in the deep sea (*31*).

Microbial turnover at vents contrasts sharply with corresponding rates at similar depths elsewhere in the deep sea (*32*). The four large vent animals (*Riftia*, *Bythograea*, *Calyptogena*, and the mussel) have metabolic rates that are similar to those of their shallow-water relatives and that are orders of magnitude higher than those of their relatives in other parts of the deep sea (*16*, *33*). Studies of vents have laid to rest the idea that constraints of pressure and temperature alone limit the activities of deep-sea organisms. Microorganisms and the food chains that depend on them have evolved in response to the rich supply of reduced compounds available for chemosynthesis. A further constraint is that the animals must continually colonize new vents tens and occasionally hundreds of kilometers away. Despite differences in faunal composition and at least partial isolation of vent fields, these communities have had a long evolutionary history. Fossil vent worm tubes have been identified in Cretaceous sulfide ores (*34*), and the nearest relative of the archeogastropod limpets date from the Paleozoic, over 200 million years ago (*9*). The cooccurrence of a clam, a mussel, and a vestimentiferan worm at widely separated sites in the Pacific and Atlantic represents either an unusual distribution from a single lineage or, even more remarkably, cases of parallel evolution.

References and Notes

1. J. Brooks *et al.*, *Eos* **66**, 106 (1985); Canadian American Seamount Expedition, *Nature (London)* **313**, 212 (1985); C. Paull *et al.*, *Science* **226**, 965 (1984).
2. R. Hessler and W. Smithey, in *Hydrothermal Processes at Seafloor Spreading Centers*, P. A. Rona *et al.*, Eds. (Plenum, New York, 1983), pp. 735–770.
3. Galápagos Biology Expedition Participants, *Oceanus* **22**, 1 (1979); K. Crane and R. Ballard, *J. Geophys. Res.* **85**, 1443 (1980); J. F. Grassle in *Hydrothermal Processes at Seafloor Spreading Centers*, P. A. Rona *et al.*, Eds. (Plenum, New York, 1983), pp. 665–676.
4. D. Desbruyeres, P. Crassous, J. Grassle, A. Khripounoff, D. Reyes, M. Rio, M. Van Praet, *C. R. Acad. Sci.* **295**, 489 (1982).
5. R. Ballard, J. Francheteau, T. Juteau, C. Rangan, W. Normark, *Earth Planet. Sci. Lett.* **55**, 1 (1981); R. Ballard, T. H. van Andel, R. Holcomb, *J. Geophys. Res.* **87**, 1149 (1982); R. Ballard, R. Hekinian, J. Francheteau, *Earth Planet. Sci. Lett.* **69**, 176 (1984).
6. L. Laubier and D. Desbruyeres, *La Recherche* **161**, 1506 (1984).
7. R. Turner and R. Lutz, *Oceanus* **27**, 54 (1984); Florida Escarpment Cruise Participants, *ibid.*, p. 32.
8. J. Grassle, personal communication.
9. J. McLean, *Bull. Biol. Soc. Wash.*, in press.
10. M. Jones, *Oceanus* **27**, 47 (1984).
11. D. Desbruyeres and L. Laubier, *Oceanol. Acta* **3**, 267 (1980); *Proc. Biol. Soc. Wash.* **95**, 484 (1982); V. Tunnicliffe, *Eos* **64**, 1017 (1983); personal communication.
12. J. F. Grassle *et al.*, *Bull. Biol. Soc. Wash.*, in press.
13. J. Enright *et al.*, *Nature (London)* **289**, 219 (1981); P. Lonsdale, *Deep-Sea Res.* **24**, 857 (1977).
14. C. M. Cavanaugh *et al.*, *Science* **213**, 340 (1981); *Nature (London)* **302**, 58 (1983); H. Felbeck, *Science* **213**, 336 (1981); *Nature (London)* **293**, 291 (1981).
15. P. Comita and R. Gagosian, *Nature (London)* **307**, 450 (1984).
16. K. L. Smith, *Ecology* **66**, 1067 (1985).
17. G. H. Rau, *Nature (London)* **289**, 484 (1981); ——— and J. I. Hedges, *Science* **203**, 648 (1979); G. H. Rau, *ibid.* **213**, 338 (1981); B. Fry, H. Gest, J. Hayes, *Nature (London)* **306**, 51 (1983).
18. D. Rhoads *et al.*, *J. Mar. Res.* **40**, 503 (1982).
19. A. Williams, *Proc. Biol. Soc. Wash.* **93**, 443 (1980).
20. P. Pugh, *Philos. Trans. R. Soc. London* **301**, 165 (1983); K. Woodwick and T. Sensenbaugh, *Proc. Biol. Soc. Wash.*, in press.
21. RISE Project Group, *Science* **207**, 1421 (1980); F. Gaill *et al.*, *C. R. Acad. Sci.* **298**, 553 (1984); *ibid.*, p. 331.
22. D. Cohen and R. Haedrich, *Deep-Sea Res.* **30**, 371 (1983).
23. R. Lutz, L. Fritz, D. Rhoads, *Eos* **64**, 1017 (1983).
24. K. Macdonald *et al.*, *Earth Planet. Sci. Lett.* **48**, 1 (1980).
25. K. Turekian, J. K. Cochran, Y. Nozaki, *Nature (London)* **280**, 385 (1979); K. K. Turekian and J. K. Cochran, *Science* **214**, 909 (1981); ———, J. Bennett, *Nature (London)* **303**, 55 (1983).
26. C. Berg, *Bull. Biol. Soc. Wash.*, in press.
27. Observations made by K. Turekian.
28. K. Turekian *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **72**, 2829 (1975).
29. J. F. Grassle and L. Morse-Porteous, unpublished data; H. Sanders and J. Allen, *Bull. Mus. Comp. Zool. Harv. Univ.* **145**, 237 (1973).
30. R. D. Turner, *Science* **180**, 1377 (1973).
31. ———, personal communication.
32. H. Jannasch and C. Taylor, *Annu. Rev. Microbiol.* **38**, 487 (1984).
33. J. Childress and T. Mickel, *Eos* **64**, 1018 (1983); J. Childress and R. Mickel, *Mar. Biol. Lett.* **3**, 73 (1982); T. Mickel and J. Childress, *Biol. Bull. (Woods Hole, Mass.)* **162**, 70 (1982).
34. R. M. Haymon, R. A. Koski, C. Sinclair, *Science* **223**, 1407 (1984).
35. I thank the crew of DSRV *Alvin* and S. Brown-Leger, L. Morse-Porteous, R. Petrecca, and I. Williams for technical assistance; I thank J. P. Grassle, L. Morse-Porteous, and J. M. Peterson for invaluable comments and assistance in the preparation of the manuscript. The work was supported by grants OCE7810458, OCE7810459, OCE8115251, and OCE8311201 from the National Science Foundation. This is contribution No. 5963 of the Woods Hole Oceanographic Institution, 71 of the Galápagos Rift Biology Expedition, and 50 of the Oasis Expedition.

Geomicrobiology of Deep-Sea Hydrothermal Vents

Holger W. Jannasch and Michael J. Mottl

Deep-sea hydrothermal vents were discovered in the 1970's after an extensive search along the Galápagos Rift (*1*, *2*), a part of the globe-encircling system of sea-floor spreading axes. During the past 7 years, more hydrothermal vent fields have been located along the East Pacific Rise. They fall into two main groups: (i) warm vent fields with maximum exit temperatures of 5° to 23°C and flow rates of 0.5 to 2 cm sec^{-1} and (ii) hot vent fields with maximum exit temperatures of 270° to 380°C and flow rates of 1 to 2 m sec^{-1}. Hot vent fields commonly include warm- and intermediate-temperature vents ($\leq$300°C) ("white smokers") as well as high-temperature vents (350° $\pm$ 2°C) ("black smokers"). A highly efficient microbial utilization of geothermal energy is apparent at these sites—rich animal populations were found to be clustered around these vents in the virtual absence of a photosynthetic food source (*3*–*5*).

Microorganisms, mainly bacteria, are efficient geochemical agents. As prokaryotic organisms, they lack a membrane-bound nucleus and thereby the complex genetic apparatus of the higher, eukaryotic organisms. At the same time, bacteria retain a much wider metabolic diversity than is found in plants and animals. Because of the resulting biochemical versatility of natural microbial populations and the smallness, general resistance, and dispersibility of bacterial cells, these organisms are able to exist in more extreme environments than the higher organisms. Therefore, the occurrence of certain microorganisms at deep-sea vents was predictable; however, their ability to make it possible for higher forms of life to thrive with an unusual efficiency on inorganic sources of energy in the absence of light was entirely unexpected.

Chemosynthesis

The most significant microbial process taking place at the deep-sea vents is "bacterial chemosynthesis." The term was coined by Pfeffer in 1897 (*6*) in obvious contrast to the then well-known photosynthesis. Both processes involve the biosynthesis of organic carbon compounds from CO_2, with the source of energy being either chemical oxidations or light, respectively. More specifically,

---

Holger W. Jannasch is a senior scientist in the Biology Department and Michael J. Mottl is an associate scientist in the Chemistry Department at Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.