A parade of galatheid crabs marching over a bed of mussels at a vent in the Galápagos Rift. (Photo by Robert Hessler, Scripps Institution of Oceanography)

by J. Frederick Grassle

The first news of life at hydrothermal vents arrived in Woods Hole early in 1977 via a news report from the San Francisco Chronicle. The descriptions of giant tube worms and other unusual large animals clearly showed that life at the vents was something qualitatively different from anything known. A number of biologists who had worked together on the sea floor using Alvin, including myself, wanted to see these strange animals for ourselves, and to compare the ecosystems with those found elsewhere in the deep sea. We had used Alvin to conduct experiments on the deep-sea floor, and many of our ideas about deep-sea life had been radically changed as a result of these efforts. Thus, following the discovery of the vents, Howard L. Sanders and Holger W. Jannasch of the Woods Hole Oceanographic Institution, Bob Hessler and Ken Smith of the Scripps Institution of Oceanography, and Ruth Turner of Harvard University suggested that I coordinate the submission of a combined set of study proposals to the National Science Foundation (NSF).

Because deep-sea ecology, invertebrate zoology, and microbiology were well represented in our group, we sought collaborations with other investigators for studies of the physiology, biochemistry, and genetics of the unusual vent animals. Jim Childress at Santa Barbara, and George Somero at Scripps added physiology and biochemistry proposals, while Rich Lutz of Rutgers University, and Don Rhoads and Karl Turekian of Yale University agreed to study the growth of clams and mussels. Large clams, mussels, and tube worms collected at vents were to be kept alive and transferred to pressurized chambers in laboratories at sea for observation and experimental manipulation. Microorganisms

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brought to ambient surface pressure were to be cultured for physiological studies in several land-based laboratories.

**Twenty-Five New Families**

The proposals were accepted by NSF, and many of the major biological discoveries concerning hydrothermal vents were made on the 1979 expedition to the Galápagos spreading center (Oceanus Vol. 22, No. 2, pp. 2-10, and Vol. 27, No. 3). All of the animals at the vents proved to be extremely unusual — they belonged to approximately 25 new families or subfamilies, twice that many new genera, and four times as many new species. The nearest relatives of such species as the several families of limpets are known from the Paleozoic period, more than 250 million years ago. Vent animals only live where there’s a supply of reduced chemical energy from hydrothermally altered seawater. Almost all the species recurred at every vent explored at the Galápagos spreading center, although they were found in different relative proportions.

We concluded that the age of vents and chance events in colonization were less important in determining community composition than relative flux of hydrothermal fluid. The more typical deep-sea fauna does not invade vent habitats, a fact that emphasizes the special adaptations acquired by vent fauna to cope with toxic levels of hydrogen sulfide and other compounds. The number of species at vents is low compared to the number of species occurring at other sites in the deep sea. In addition to communities of living animals, sites marked only by dead shells that dissolve in less than 20 years attest to the ephemeral nature of the vent environment. Vent animals rapidly grow to maturity and produce large numbers of larvae. These tactics are a response to the dynamic nature of vents, and contrast with the slow growth and small number of offspring in typical deep-sea species.

In this way, new vents are colonized before the populations perish with the cessation of hydrothermal flow. Each vent area has its own unique set of species that is found nowhere else, as well as some species that are known from other sites. Distant vent fields are genetically isolated, and colonization by mussels appears to occur episodically from distant sites.

*(continued on page 44)*

At top, a bouquet of tube worms in the Galápagos (Photo by Jack Donnelly, WHOI). Opposite page, clockwise from top: a bed of mussels at a cold seep in the Gulf of Mexico; a giant sea anemone in the Galápagos with Alvin’s temperature probe at right; acorn worms (enteropneusts) in the Galápagos; a dandelion-like siphonophore, kin to the Portuguese man-of-war; a close-up of tube worms.
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Photo by Holger Jannasch, WHOI

Photo by Robert Hessler, Scripps

Photo by J. Frederick Grasle, WHOI

Courtesy of National Geographic Society

Photo by James Childress, UC/Santa Barbara
Chemiosynthetic microorganisms dependent on reduced sulfur compounds were identified as the main primary producers within the vent ecosystem. A major surprise was the discovery of bacteria living on hydrogen sulfide within the tissues of the large animals; the bacteria supply their hosts with food. Physiological, biochemical, and morphological observations in the laboratory were crucial to this discovery. The variety of free-living microorganisms living in hydrothermal plumes and colonizing surfaces was also a major surprise. Other reduced compounds in the vent fluids, such as hydrogen, ammonia, methane, and reduced forms of manganese and iron, supply energy for microbial growth.

Unanswered Questions
There’s still a great deal to be learned about every aspect of these studies. Especially exciting are the somewhat unpredictable discoveries that occur as each new vent field is explored. Inevitably, these cause vent workers to modify the recent hypotheses that until then had seemed to explain most of the previously observed phenomena. Giant “megaplumes,” for example, are now known to spew forth occasionally from sites on the Juan de Fuca Ridge off the American/Northwest Pacific Coast. Do these vent extrusions of hydrothermal fluid provide the chief means for vent species to be transported great distances?

In comparison to other vent fields, the Mid-Atlantic Ridge has yielded a very different fauna, dominated by shrimp (article, pp. 47–52), despite similarities in the chemical composition of vent fluids and the temperature regime. Is this a consequence of the comparative geographic isolation of this region of the Mid-Ocean Ridge system? Or does it reflect the possibility that the Atlantic vent fields may last thousands of years instead of just tens of years? Biologists still haven’t had the opportunity to visit the Atlantic vents, and other surprising phenomena are certain to be discovered.

The time scales of major volcanic, tectonic, and hydrothermal events are unknown. Future biological studies must be closely integrated with the study of these processes at long-term “observatories” on the sea floor. In addition, exploration of new sites by biologists, geologists, and chemists will form a basis for global comparisons of hydrothermal ecosystems. Reduced compounds, such as methane and sulfides, seep from the continental margin at depths to 3,900 meters, and support communities similar to those in vent areas, yet the chemical composition, temperatures, and hydrodynamic regimes are quite different. What are the essential features of the environment that allow these cold seeps to support communities similar to those of hydrothermal vents? Is it simply the source of chemical energy, or is the temporal pattern of flow important?
The World of Vents and Seeps

These varied creatures represent the rich invertebrate life at the vents and seeps on the ocean floor. The sites are indicated by the numbers below and on map, opposite page. Ruth Turner drew the clams and mussels, Austin Williams the shrimp and crabs, Cindy Van Dover the tube worms, and Daniel Desbruyères, Marian Pettibone, Bob Zottolli, and James Blake the polychaetes. Rosemarie Petrecca provided research assistance.

**CLAMS**
- Calyptogena
  - 1, 3, 4, 5, 6, 7, 8, 9, 10, 12, 13, 14

**POLYCHAETE WORMS**
- Alvinella
  - 6
- Ophyrotricha
  - 5, 6, 7
- Paralvinella
  - 5, 6, 7, 10, 11
- Amphisamtha
  - 3, 5, 6, 7, 10
- Branchinotogluma
  - 5, 6, 7, 10
- Euphroline
  - 5, 7

**MUSSELS**
- Bathymodiolus
  - 5, 6
- Mytilid, new genus
  - 2, 3, 4, 11

**TUBE WORMS**
- Escarpia
  - 3, 4, 8
- Lamellibrachia
  - 4, 6, 9
- Oasisia
  - 6
- Ridgeia
  - 10
- Riftia
  - 5, 6, 7
- Tevnia
  - 6

**SHRIMP**
- Alvinocaris
  - 2, 3, 4, 5
- Rimmocaris
  - 2, 11

**CRABS**
- Bythograea
  - 2, 5, 6, 11
- Munidopsis
  - 1, 3, 5, 6, 7, 10, 12

**POGONOPHORAN WORMS**
- Pogonophorans
  - 1, 4

*The animals are not drawn to scale*
Ever since Darwin, evolutionary biologists have been intrigued by oceanic islands, and events occurring on the geologic time scales important to the origin of species. For example, the spacing and temporal sequence of new islands of the Hawaiian chain formed by volcanic eruptions have played a major role in the speciation of the highly diverse terrestrial insect fauna. Deep-sea vents are linearly arranged along the Mid-Ocean Ridge and the pattern of cessation and initiation of flow can be thought of as a template for the evolution of species.

Critical data on the spacing of vents, on the length of time they are habitable, and the age of whole vent fields, as assessed by geological and chemical investigations, are needed to understand the life histories and evolution of vent populations. Water circulation associated with vents provides the means by which the dispersal stages of vent organisms are transported from one vent site to another. This circulation has not been well studied, but is expected to occur on several spatial scales, including local heat-driven convection, mesoscale eddies*, and deep-sea currents. In addition to providing the connecting link between vent populations, this circulation disperses vent productivity to organisms in surrounding deep-sea communities.

Our study of vent communities has greatly extended the range of physical and chemical environments known to support life. There is renewed interest in the animal diversity represented by marine invertebrates. Ecologists have begun to think more broadly about potential sources of energy for both natural and aquacultural systems. Archaebacteria, living anaerobically at high temperatures, are related to the most ancient forms of life. These bacteria are genetically distinct from other organisms, and have been classified as a separate kingdom distinct from plants, animals, and other microorganisms. The existence of these organisms in the high-energy vent environments has led to increased speculation that similar environments may have led to the origin of life. The chemistry of organic compounds, and their interaction with organisms, need to be much better known in a variety of hydrothermal environments to evaluate this possibility.

* Deep-sea vent mesoscale eddies are tens of kilometers in diameter.