Biodiversity and Biogeography of Hydrothermal Vent Species

Thirty Years of Discovery and Investigations

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The discovery of hydrothermal vents and the unique, often endemic fauna that inhabit them represents one of the most extraordinary scientific discoveries of the latter twentieth century. Not surprisingly, after just 30 years of study of these remarkable—and extremely remote—systems, advances in understanding the animals and microbial communities living around hydrothermal vents seem to occur with every fresh expedition to the seafloor. On average, two new species are described each month—a rate of discovery that has been sustained over the past 25–30 years (Van Dover et al., 2002; Fisher et al., this issue). Furthermore, the physical, geological, and geochemical features of each part of the ridge system and its associated hydrothermal-vent structures appear to dictate which novel biological species can live where. Only 10 percent of the ridge system has been explored for hydrothermal activity to date (Baker and German, 2004), yet we find different diversity patterns in that small fraction. While it is well known that species composition varies along discrete segments of the global ridge system, this "biogeographic puzzle" has more pieces missing than pieces in place (Figure 1, Table 1).

In this paper, we start with a general picture of the global ridge system and hydrothermal environments, then continue with a description of known biodiversity—including physiological adaptations—and species distribution, which leads into a discussion of the factors that might drive observed biogeography patterns. We conclude with a look toward the future, describing the main efforts being made to fill the gaps in our knowledge of vent biogeography.

On the Seafloor, Different Species Thrive in Different Regions

Soon after animal communities were discovered around seafloor hydrothermal vents in 1977, scientists found that vents in various regions are populated by distinct animal species. Scientists have been sorting clues to explain how seafloor populations are related and how they evolved and diverged over Earth's history. Scientists today recognize distinct assemblages of animal species in six major seafloor regions (colored dots) along the system of volcanic mountains and deep-sea trenches that form the borders of Earth's tectonic plates. But unexplored ocean regions remain critical missing pieces for assembling the full evolutionary puzzle.

Northeast Pacific vent communities are dominated by "bushes" of skinny tubeworms called Ridgea piscesae.
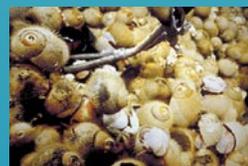
Western Pacific vent communities are dominated by barnacles and limpets, as well as hairy gastropods, shown above.

Missing Pieces
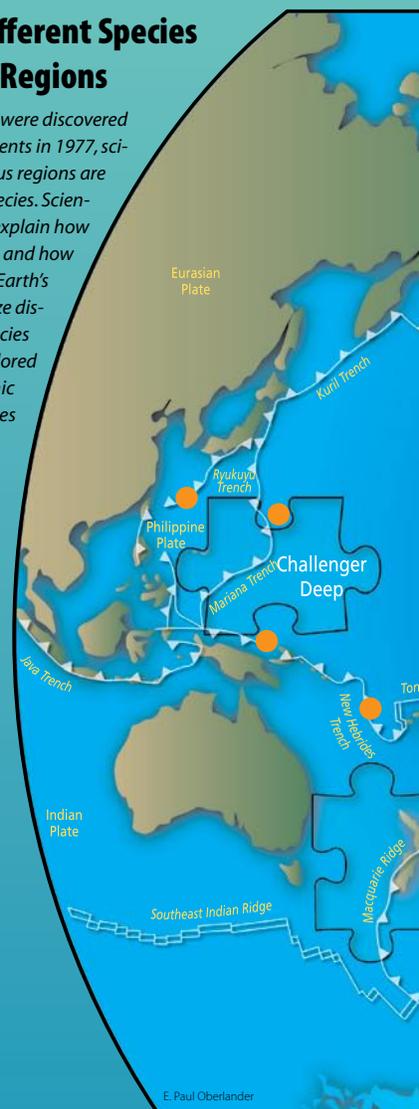
Challenger Deep
Unusual life forms may have evolved under conditions of extreme pressure in this 11,000-meter-deep trench, the deepest part of the world's oceans.

Map labels:
Gakkel Ridge
Arctic Ocean
Aleutian Trench
Juan de Fuca Ridge
North American Plate
Reykjanes Ridge
Eurasian Plate
Mendocino Triple Junction
Cayman Trough
Caribbean
Cocos Plate
Galápagos Triple Junction
Pacific Plate
East Pacific Rise
Nazca Plate
Peru - Chile Trench
South American Plate
South Atlantic
Mid - Atlantic Ridge
Arabian Plate
Sheba Ridge
Carlsberg Ridge
Central Indian Ridge
African Plate
Indian Ocean Triple Junction
Easter Island Triple Junction
Southeast Indian Ridge
Kermadec Trench
Tonga Trench
New Zealand
Chile Rise
Southwest Indian Ridge
Antarctic Plate
Drake Passage
Southern Ocean
East Scotia Rise
Bouvet Triple Junction
Pacific - Antarctic Ridge
Endurance

Ridges / Fracture Zones   Subduction Zones

Shallow Atlantic vents (800-1700-meter depths) support dense clusters of mussels on black smoker chimneys.

Deep Atlantic vent communities (2500-3650-meter depths) are dominated by swarms of shrimp called Rimicaris exoculata.

Central Indian vent communities are populated by Western Pacific-type fauna, but also have North Atlantic-type shrimp species.

Eastern Pacific vent communities are dominated by tall, fat tubeworms called Riftia pachyptila.

New Zealand
This region has a full spectrum of habitats supporting seafloor life (hydrothermal vents, cold seeps, whale carcasses, and wood from shipwrecks and trees) in close proximity. How have species evolved in these diverse settings?

Chile Rise
This region has a variety of chemosynthetic habitats and geological features in close proximity. How do seafloor populations diverge or converge at this triple junction on the "highway" of mid-ocean ridges?

Southern Ocean
The Drake Passage may act as a key link or bottleneck for larval dispersal between the Atlantic and Pacific. Whale carcasses and shipwrecks (such as Shackleton's Endurance) may offer refuges or stepping-stones between vents.

South Atlantic
Powerful currents and huge seafloor chasms (fracture zones) may act as barriers blocking the dispersal of vent larvae and disconnecting vent populations in the North and South Atlantic.

Caribbean
In this region, methane seeping from the seafloor also supports animal communities. Did animals migrate between "cold seeps" and nearby hot vents over evolutionary history?

Arctic Ocean
The Arctic Ocean has never had deep connections with other major oceans. It may harbor fundamentally different vent animals that evolved in isolation over the past 25 million years.

ABIOTIC SETUP OF THE VENT HABITAT: PHYSICAL, GEOLOGICAL, AND GEOCHEMICAL PROPERTIES

Today, satellite technology provides a clear visualization of the globe-encircling mid-ocean ridge. It is here, at seafloor-spreading centers, that lava wells up from Earth's interior to generate fresh oceanic crust (see Langmuir and Forsyth, this issue). While a small proportion of these volcanic systems are found in back-arc basins close to subduction zones (see Martinez et al., this issue), the vast majority of all Earth's mid-ocean ridges form a single, continuous, globe-encircling volcanic chain that is roughly 60,000 km in length. Mid-ocean ridges typically lie at around 2000- to 5000-m depth and therefore represent environments that experience high pressures, complete darkness, and ambient temperatures of only ~ 2°C.

Spreading rates for mid-ocean ridges—the speed at which two tectonic plates are being pulled apart from each other—vary across the whole system. Ridges can be classified according to their spreading rates into ultra-slow spreading (< 20 mm yr^{-1}) such as the Arctic Gakkel Ridge (see Snow and Edmonds, this issue), slow spreading (20–50 mm yr^{-1}) such as the Mid-Atlantic Ridge, intermediate spreading (50–90 mm yr^{-1}) such as the Central Indian Ridge, and fast (90–130 mm yr^{-1}) to superfast (130–170 mm yr^{-1}) spreading such as the East Pacific Rise. Spreading rates are important in shaping ridge morphology (MacDonald et al., 1991) and, as a consequence, the hydrodynamics of the habitat. At slow-spreading rates, the walls of the ridge axis are separated by a deep (1–3 km) and wide (5–15 km) rift valley that constrains dispersing hydrothermal plumes. Some of the largest and longest-lived hydrothermal vents discovered thus far occur along the slow-spreading Mid-Atlantic Ridge. In contrast, fast-spreading centers exhibit shallow and narrow (order of tens of meters) summit calderas where hydrothermal plumes are not constrained. Along the fastest sections of the East Pacific Rise, vent sites are so geographically close that they can form a continuum along the ridge axis. These topographic and physical characteristics have the potential to affect the patterns of faunal distribution (see below). The western Pacific Ocean seafloor is characterized by a complex system of back-arc basins and volcanic arcs with active hydrothermal venting. These back-arc basins are isolated spreading centers that have been active for less than 10 million years—a short geological time compared to the ages of mid-ocean ridges (Hessler and Lonsdale, 1991). Their iso-

Table 1. Dominant fauna of main proposed biogeographical provinces.

Biogeographical Province and Depth	Dominating Fauna
Azores (shallow north Atlantic, 800-1700 m)	Bathymodiolid mussels, amphipods, and caridean shrimp
Mid-Atlantic Ridge between Azores Triple Junction and Equator (deep north Atlantic 2500-3650 m)	Caridean shrimp—mainly *Rimicaris exoculata*—and bathymodiolid mussels
South Mid-Atlantic Ridge	Caridean shrimp, bathymodiolid mussels, and clams
East Pacific Rise and Galápagos Rift	Vestimentiferan tubeworms—mainly *Riftia pachyptila*—and bathymodiolid mussels, vesicomyid clams, alvinellid polychaetes, amphipods, and crabs
Northeast Pacific	Vestimentiferan tubeworms excluding Riftiidae, polychaetes, and gastropods
Western Pacific	Barnacles, limpets, bathymodiolid mussels, "hairy" gastropod, vesicomyid clams, and shrimp
Central Indian Ridge	Caridean shrimp *Rimicaris kairei*, and mussels, "scaly" gastropods, and anemones

lation—both from one another and from mid-ocean ridges—and their relatively short active geological ages make back arcs particularly interesting habitats for biogeographic and gene-flow analyses (Desbruyères et al., 2007; see below).

Hydrothermal circulation occurs at mid-ocean ridges when dense, cold seawater percolates downward through fractured oceanic crust near the ridge crest (Figure 2). The vent fluid is geothermally heated close to the magma chamber that feeds the ridge, reaching temperatures that can exceed 400°C. The fluid is also chemically modified, losing all dissolved oxygen and accumulating high concentrations of dissolved reduced gases such as methane and hydrogen sulfide). They are also strongly acidic (pH 2–3) compared to the near-neutral character (~ pH 8) of the deep oceans and are rich in numerous metals—dominantly iron, manganese, copper, and zinc, but also

precious metals such as silver, gold, and platinum, as well as those often thought of as highly toxic to life (e.g., cadmium, mercury, arsenic and lead). The buoyant, superheated fluid is expelled into the water column through polymetallic sulfide chimneys or "black smokers" that can tower tens of meters above the seafloor (Figure 3). While approximately half of all hydrothermal fluids are currently believed to be discharged from the seafloor in this spectacular black-smoker form, about an equal amount mixes with cold seawater and percolates down into the highly fractured seafloor as more dilute warm waters. The latter have precipitated their mineral load but, importantly, still contain high concentrations of dissolved methane and hydrogen sulfide, which are emitted from the seabed in this "diffuse-flow" form, typically at temperatures that are measured in tens of degrees Celsius (further detailed information on hydro-

thermal vent chemistry and functioning, and associated mineral deposits, can be found in an article by Tivey in this issue). It is these vent fluids that provide the necessary energy, in the form of reduced chemicals, for the development of the lush faunal communities found at vents. The hydrothermal trophic web is based in the production of chemoautotrophic

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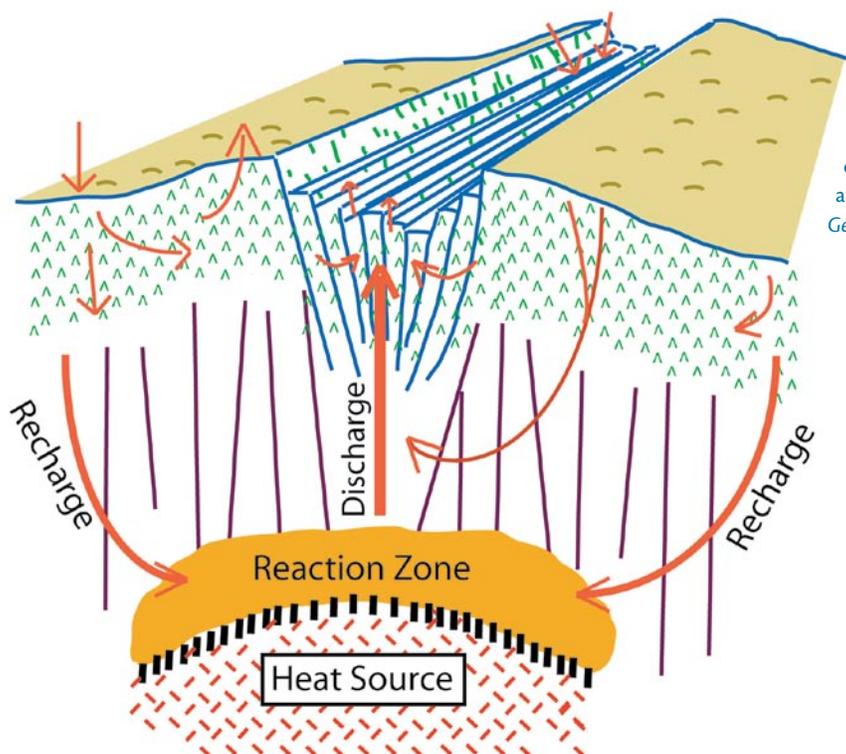
Figure 2. Schematic illustration of hydrothermal fluid circulation beneath the seafloor at mid-ocean ridge crests. *From German and Von Damm (2004)*

Recharge

Discharge

Recharge

Reaction Zone

Heat Source

microbes (Cavanaugh, 1983; Jannasch, 1984) that use reduced compounds from the vent fluids to fix carbon dioxide from seawater. The microbes are found free-living as well as in highly successful symbiosis with many of the macroinvertebrates inhabiting the vent habitat and they are responsible for the very high production at hydrothermal vents.

BIOGEOGRAPHY OF HYDROTHERMAL VENTS: A KNOWLEDGE PUZZLE UNDER CONSTRUCTION
Biodiversity and Adaptations

A sound knowledge of an ecosystem's species composition is essential for any subsequent biogeographic investigations and to understand the factors driving distribution patterns. The dawn of bio-diversity studies in hydrothermal vents takes us back to nine black-and-white photographs of large white bivalves on black basalt, taken by the Deep-Tow Camera System on May 29, 1976, on the Galápagos Spreading Center (Lonsdale, 1977). A year later, during *Alvin* dives revisiting the region, geologist Jack Corliss gave astonishing accounts of the first observations of giant tubeworms later described as *Riftia pachyptila* (Corliss et al., 1979) and thick beds of mussels assembled around seafloor openings emitting diffuse vent fluids. Only 30 years have passed since those initial discoveries; we now know of more than 550 vent species and their composition and distribution at more than 100 vent sites along the global mid-ocean ridge system (Desbruyères et al., 2006).

Figure 3. Black smoker from the North Mid-Atlantic Ridge. *Photo credit: Deutsche-Ridge Schwerpunkt Program and the MARUM-Quest ROV*

The first impression when looking at a vent field is the profusion of life, with high densities and biomass of exotic animals (Figure 4). This bounty explains why hydrothermal vents are often referred to as "oases of the deep." While biomass is extremely high relative to the surrounding deep sea, biodiversity at vents is low, especially in relation to the high biodiversity of non-chemosynthetic, deep-sea benthos (Grassle and Maciolek, 1992). This relationship is true for all groups, from meio- and macrofauna found on oceanic basalt and sediments highly modified by hydrothermal fluid to macro- and megafauna living on mussel beds or tubeworm fields (Van Dover, 2000). The low diversity and high densities of individuals in vent communities is typical of habitats with high energy availability and environmental conditions with high or low values within their range, such as very wide temperature ranges or high levels of toxic chemicals. The most speciose phyla found at hydrothermal vents are the arthropods, followed by the molluscs and the annelids. However, our knowledge of the diversity and distribution of vent species is still limited to an extremely small section of the global ridge system, and every new detailed survey and investigation, both on newly discovered sites and on well-explored ones, brings new species and ecologies to be identified and described, as well as new insight to the phylogeography of vent species.

One major characteristic of vent biological communities is the high degree (~ 85 percent) of species endemism, with many species showing important physiological, morphological, and ecological adaptations to particular environ-

Figure 4. The giant tubeworm *Riftia pachyptila,* the mussel *Bathymodiolus,* and crabs from East Pacific Rise vents. *Image courtesy of Richard A. Lutz*

mental factors. Arguably, one of the most remarkable vent animals is the giant tubeworm *Riftia pachyptila* from the Galápagos Rift and East Pacific Rise. This worm and related species were first described as a new phylum, Vestimentifera, but have now been moved to the family Siboglinidae in the Phylum Annelida, Class Polychaeta (Halanych, 2005). *Riftia pachyptila* lack a mouth and a digestive system, and depend completely for growth and reproduction on organic matter produced by their endosymbiotic chemosynthetic bacteria. These bacteria are found densely packed in an organ that spans the interior of the animal's body, called the trophosome. The tubeworm absorbs hydrogen sulfide, carbon dioxide, and oxygen through its well-irrigated plume and transports them to the trophosome via the vascular system along with modified hemoglobin, which transports unbound or available sulfide.

A different fascinating polychaete from the East Pacific Rise is the Pompeii worm, *Alvinella pompejana.* This polychaete lives inside organic tubes that it builds on the exterior walls of active chimneys in close proximity to venting fluid; in contrast to the *Riftia habitat,* the chemistry of this fluid is dominated by iron-bound complexes with hydrogen sulfide (Luther et al., 2001). The maximum temperature tolerated by this species is a continuing subject of debate, with values ranging between 10°C and 80°C (Gaill and Hunt, 1991; Cary et al., 1998).

In the crustaceans, a remarkable example of sensory adaptation is found on the caridean shrimp *Rimicaris exoculata* from the Mid-Atlantic Ridge. These shrimp live in massive, dense, and dynamic aggregations (3000 per liter; Gebruk et al., 2000) on the chimney walls, feeding on symbiotic bacteria cultivated within their enlarged gill chambers, on their external carapace, and on ingested mineral particles. The "eyes" of *R. exoculata* are considered to have evolved into a broad ocular plate that forms part of the shrimp's dorsal surface. The plate's novel photoreceptors apparently do not form a distinct image; instead, these "eyes" are highly sensitive to dim light, perhaps an adaptation for detecting radiation from the orifices of hot black smokers and for allowing the shrimp to orient to the chimney walls (Van Dover et al., 1989).

Examples of metabolic, morphological, sensory, and symbiotic adaptations are abundant at the vent habitat, and exploration of new sites still results in the discovery of striking animals, such as the "scaly foot gastropod" recently found on

the Central Indian Ridge (Figure 5). This gastropod, still awaiting description, harbors thiotrophic (sulfurous) bacteria in a greatly enlarged esophageal gland and has an operculum modified into several hundred aligned scales covered by thick layers of iron sulfides, whose purpose is unknown (Warén et al., 2003).

Known Distribution Patterns of Vent Species

Although we have only explored a very limited proportion of the active hydrothermal vents that potentially exist worldwide, the description of the fauna from the vent sites that we do know is already sufficient to demonstrate that different faunal communities characterize different ocean basins/hydrothermal regions (Figure 1). Biogeography is the science that documents and explains spatial patterns of biodiversity. The present distribution of a species represents (1) the historical events acting on geological time scales, or vicariance, that have shaped its geographical range, and (2) the dispersal potential of the species determined by its life-history patterns, topography, and hydrography, and acting on ecological time scales (Tunnicliffe et al., 1996). A number of physicochemical properties of hydrothermal vent habitats (described above) make these systems interesting for biogeographical studies (Tunnicliffe et al., 1991, 1998): (1) the species are constrained to specific, linear habitats, (2) vent habitats are globally distributed, (3) they are discrete and ephemeral environments, (4) there is a high degree of endemism, (5) there are phylogeographic relationships with other reducing environments, such as cold seeps on continental margins or whale falls, and (6) identifying faunal provinces and their boundaries allows us to rapidly characterize a mechanism responsible for creating and/or maintaining the province. Our present knowledge of hydrothermal vent biology identifies six distinct biogeographical domains characterized by specific faunal assemblages: (1) the Azores shallow Atlantic vent communities (80–1700 m), (2) the fauna of the deep Mid-Atlantic Ridge vents between the Azores Triple Junction and the Equator, (3) the East Pacific Rise communities found from 30°N to the Easter Micro-Plate, (4) the Northeast Pacific vent communities of the Explorer, Juan de Fuca, and Gorda Ridges, (5) the western Pacific back-arc basin communities, and (6) the vent fauna of the Central Indian Ocean (Figure 1, Table 1) (Van Dover et al., 2002; Shank, 2004).

Speciation Through Vicariance

The processes affecting biogeographic patterns over geological time scales include vicariant events, where the movement of oceanic plates plays a defining role. Vicariance is, for example, used to explain the formation and boundary of the Northeast Pacific and East Pacific Rise biogeographic provinces during the Mid-Tertiary (~ 28 million years ago [Ma]). Subduction of the Farallon Plate under the North American Plate caused the split of the Farallon-Pacific Ridge, resulting in the separation of the Gorda-Juan de Fuca-Explorer Ridge system, to the north, from the East Pacific Rise, to the south (Tunnicliffe et al., 1996). Subsequent biological isolation permit-

Figure 5. The "scaly foot gastropod" from the Indian Ocean ridge. *Image courtesy of Charles Fisher*

ted divergent evolution of the fauna on the now-bisected ridges, resulting in an absence of the tubeworm *Riftia pachyptila*, the clam *Calyptogena magnifica*, and the polychaete *Alvinella* spp. from Northeast Pacific vent sites, and the proliferation of vestimentiferan tubeworms on the East Pacific Rise.

Another example of a major vicariant event is the closure of the Isthmus of Panama 5 Ma and the resulting isolation of Pacific marine fauna from the Atlantic Ocean. Although there was a major deep-ocean gateway in this region prior to the closure, there were no ridge connections. However, comparisons of cold-seep fauna from the Gulf of Mexico, the Oregon margin, and the California margin indicate close taxonomic similarities, suggesting a dispersal pathway for seep species between the Pacific and Atlantic Oceans via the (now-closed) Isthmus of Panama (Tunnicliffe et al., 1996). The only existing ridge connection between the Pacific and the Atlantic was through a complex mid-ocean ridge and subduction system between South America and Antarctica, which, in the Tertiary, could have served as a dispersal pathway between the two ocean basins (Tunnicliffe et al., 1996). A similar analysis of vent fauna at the genus level indicates a relatively close connection between the western Pacific back-arc and Central Indian Ridge vent faunas as described by Desbruyères et al., 2007. These authors suggest a potential past dispersal pathway via the Southeast Indian Ridge, Macquarie Ridge Complex (south of New Zealand), and Kermadec Arc (north of New Zealand) that would explain these similarities. The connection via the Pacific-Antarctic ridges and Macquarie Ridge has also been sug-

gested as a potential dispersal route for vent siboglinid polychaetes between the Southwest Pacific back-arc basin and the East Pacific Rise fauna (Tunnicliffe and Fowler, 1996; Kojima et al., 2003).

> With every new discovery and investigation of known sites and communities, our knowledge and understanding of the diversity and functioning of these remote and exuberant ecosystems increases, helping us understand the processes driving the deep sea and the global biosphere.

Distribution Patterns and Ecological Processes

While tectonic dynamics affect biogeography at the geological time scale, a number of ecological and biological factors play major roles in the distribution of species, acting within the life span of the animal. These processes are related to the life-history patterns of the species and environmental factors. Marine invertebrates ensure gene flow, dispersal, and colonization through their larval phase. The microscopic larvae of invertebrates are transported passively in the water column, and are affected by a number of factors, both biotic (e.g., metabolic capacity, larval anatomy, behavior, swimming capabilities, and mortality rate) and abiotic (e.g., deep-water currents, geological barriers, distance between sites, and chemical suitability of habitats) (Cowen et al., 2000; Mullineaux et al., 2005). The life-history traits of marine invertebrates are very diverse, ranging from species that produce a high

number of small eggs to species that produce a lower number of larger eggs (Ramirez-Llodra, 2002). Typically, larvae hatching from smaller eggs develop during a planktonic phase in which they feed in the water column, allowing longer dispersal times but also increasing mortality risks. In contrast, larvae hatching from larger eggs exhibit abbreviated, lecithotrophic development, usually feeding only on the energetic reserves provided in the egg. These nonfeeding larvae have, in general, lower dispersal potentials but higher survival probability. However, recent studies show that the low temperature of bathyal and abyssal waters can result in long metabolic life spans for larvae of vent species such as *Riftia pachyptila*, allowing for long dispersal distances (Marsh et al., 2001). Furthermore, studies show that the embryos of the vent polychaete *Alvinella pompejana* can achieve long dispersal times through developmental arrest when dispersing in cold abyssal waters, only completing their development upon encountering warm water (Pradillon et al., 2001). In hydrothermal vent species, there are examples of all life-history patterns and larval types, but the relatively

limited data on reproduction of vent species indicates that lecithotrophic larval development is dominant (Tyler and Young, 1999; Young, 2003). It is the interactions between the life-history traits of a species and the physical, chemical, and geological environmental factors of the larval and juvenile habitat that shape the dispersal and colonization of a species; at the same time, ridge spreading rates, deep-ocean currents, major fracture zones, and other bathymetric features can all also play important roles in driving biogeographic patterns.

The effect of ridge spreading rate on larval dispersal is, potentially, directly related to the distance between active vent sites, their life span, and the geomorphology of the ridge valley (see, e.g., Baker and German, 2004). On slow-spreading ridges such as the Mid-Atlantic Ridge, where the time-averaged magmatic budget is relatively low, vent sites may be fewer and longer lived. Consequently, the distance between potentially suitable recruitment areas may be greater, and, certainly, the presence of large fracture zones interspersed with numerous smaller-scale ($\geq$ 10 km) offsets every few tens of kilometers along axis creates potential physical barriers to larval dispersal. Also, the valleys of slow-spreading ridges have steep walls that retain the hydrothermal plume within the valley, potentially limiting across-axis dispersal. In contrast, magmatically more robust, fast-spreading ridges such as the East Pacific Rise harbor vent sites that may be closer in space and are certainly less likely to be offset from one another along axis. The absence of multiple ridge-crossing fractures, in particular, creates a virtual continuum of poten-

tially favorable settlement habitats along the ridge axis that act as stepping stones for genetic communication among populations (or gene flow) through dispersal and successful colonization. Furthermore, hydrothermal plumes are not retained within the shallow walls of the axial East Pacific Rise summit graben, allowing for across-axis plume movement and potentially greater larval dispersal (Van Dover et al., 2002).

Large fracture zones and other topographic features (e.g., seamount chains, depressions) can play important roles in the gene flow of vent species; the research community is currently addressing their effects. A recent study on genetic differentiation of five vent annelids—*Riftia pachyptila*, *Tevnia jerichonana*, *Oasisia alvinae*, *Alvinella pompejana*, and *Branchypolynoe symmytilida*—in eastern Pacific vents revealed barriers to dispersal affecting one or several of these species (Hurtado et al., 2004). The 6000-m depression at Hess Deep between the East Pacific Rise and Galápagos Rift could limit gene flow of *Alvniella pompejana* (Hurtado et al., 2004) and of the amphipod *Ventiella sulfuris* (France et al., 1992), while the 240-km Rivera Fracture Zone on the northern East Pacific Rise may be a barrier to dispersal for *O. alvinae*, *T. jerichonana*, and *B. symmytilida* (Hurtado et al., 2004) as well as for *V. sulfuris* (France et al., 1992).

Another controlling factor of biogeographic patterns may be ridges in hydrographic isolation. An example of a potential topographic barrier to gene flow is found in the Arctic, where the ultraslow-spreading ridges of the Norwegian Sea and Arctic Basin are isolated from the Atlantic ridge system

by the Iceland hotspot and its off-axis trace, which generates a shallow-water sill extending across the full breadth of the North Atlantic Ocean. Recent geochemical studies indicate the existence of abundant active vents on the Gakkel Ridge (Edmonds et al., 2003), but these habitats and potential associated fauna have not yet been directly observed. A biological investigation of the Gakkel Ridge during the International Polar Year (2007–2008) will provide crucial data for understanding the evolution of fauna that may have thrived in isolation for the past ~ 28 million years.

In the equatorial region of the Mid-Atlantic Ridge, the 60-million-year-old Chain and Romanche Fracture Zones represent formidable geological features (4-km high and 935 km of ridge offset) that greatly affect both the linearity of the ridge system and large-scale ocean circulation in this region. It has been suggested that these major facture zones result in a geological barrier to the dispersal of vent species along the Mid-Atlantic Ridge axis, isolating certain species north and south of the equator, while others, such as the shrimp *Rimicaris exoculata* whose high pelagic larval and juvenile dispersal capacity allows it to exploit phytodetritus in the water column, may not be affected (Shank et al., 1998). These hypotheses are being tested by current research programs (see below).

Along with their potential as barriers to north-south, along-axis gene flow, the Mid-Atlantic Ridge fracture zones may serve as a conduit for larval transport through deep-water currents from west to east in the Atlantic Ocean. The North Atlantic Deep Water (NADW) flows south along the east

coasts of North and South America as far as the equator before being deflected east and crossing the Mid-Atlantic Ridge through the fracture zones (Messias et al., 1999). These fracture zones could be pathways for migrants between chemosynthetic sites in the Gulf of Mexico to similar habitats in the Gulf of Guinea. Moreover, recent physical studies indicate the presence of massive currents or deep-water jets in these regions (Schmid et al., 2005) that could increase the velocity of larval transport between the two sides of the Mid-Atlantic Ridge and enhance the possibility of successful communication among populations. It is known, for example, that the seep-dwelling caridean shrimp *Alvinocaris muricola* inhabits both Gulf of Mexico and Gulf of Guinea cold seeps (Ramirez-Llodra and Segonzac, 2006); in addition, the siboglinid tubeworm *Escarpia southwardae* has recently been described at the Gulf of Guinea seeps, with morphological and genetic characteristics that indicate a close taxonomic relationship with *E. laminata* from the Gulf of Mexico seeps (Andersen et al., 2004). While these findings may suggest a certain degree of gene flow across the Mid-Atlantic Ridge, data are still very limited. Further molecular and larval ecology studies are needed in order to fully understand dispersal pathways of vent species, and particular attention should be paid to the effect of larval retention by local hydrodynamics (Marsh et al., 2001; Mullineaux et al., 2005) and the decrease in larval concentration by diffusion and mortality (Cowen et al., 2000). In the southern oceans, the Circumpolar Current has been suggested as a pathway that may link species from the southern East Pacific Rise, the East Scotia Rise near Antarctica, the southern Mid-Atlantic Ridge, and the Southwest Indian Ridge (Figure 1) (Van Dover et al., 2002; Hurtado et al., 2004).

Finally, depth may also play a significant role in biogeographic patterns, as suggested by Desbruyères et al. (2001) for the differences found near the Azores Triple Junction, where depth decreases from 2400 m at Rainbow to 850 m at Menez Gwen. This depth variation causes changes in fluid toxicity and suspended mineral particles, accompanied by an impoverishment of vent endemic species at shallower depths and an increase in non-vent bathyal species. These authors also suggest that the existence of several biogeographic islands in this region is driven by depth.

LOOKING TOWARD THE FUTURE

Thirty years after the discovery of hydrothermal vents, the investigation of vent habitats and their associated fauna is still in a critical exploratory and discovery phase. Every new systematic survey of a ridge section uncovers new vent sites and their biological communities, often yielding species new to science and sometimes new physiological or morphological adaptations. The latest discoveries span from pole to pole and around the globe, including the detection of hydrothermal plume signals in both the Arctic (Edmonds et al., 2003) and Antarctic regions (German et al., 2000; Klinkhammer et al., 2001), the discovery of new hydrothermal sites along the Central Indian Ridge (Van Dover et al., 2001), and the first investigations of vent sites on the Mid-Atlantic Ridge south of the equator (German et al., 2005; Shank, 2006). The geological, geochemical, physical, and biological investigations of these regions will provide essential information toward completing the biogeographical puzzle of vent biogeography (Figure 1), increasing our knowledge of species diversity and distribution, and providing the necessary clues to understand what factors drive and shape vent communities and species distribution.

To address the gaps in our knowledge of biogeography in deep-water chemosynthetic ecosystems (including hydrothermal vents, cold seeps, whale falls, and regions of low oxygen and other reducing habitats), the international scientific community is joining efforts in the framework of the ChEss program (www.noc.soton.ac.uk/chess). ChEss is one of the 14 field projects of the Census of Marine Life (www.coml.org), a 10-year global initiative to describe the diversity, abundance, and distribution of life in the oceans. Within this context, the main goal of ChEss is to describe the biogeography of species from deep-water chemosynthetic ecosystems and understand the forces driving them (Tyler et al., 2003). To achieve this goal, ChEss has selected a number of priority study areas based on our present knowledge of biogeography (Figure 1). These include: (1) the Atlantic Equatorial Belt, to address scientific questions of gene flow across and along the Mid-Atlantic Ridge equatorial fracture zones; (2) the Southeast Pacific region off Chile, a unique site where the Chile Ridge is subducting beneath the South American Plate and where we find all known chemosynthetic habitat types in close proximity;

(3) the New Zealand region, where vents, seeps, whale falls, and other reducing ecosystems are also found in close proximity; and (4) the polar regions, with development of field programs along the potentially isolated Gakkel Ridge and in the Antarctic. Large-scale national and international collaborations and sharing of human and infrastructure resources are making such research programs possible, greatly facilitated by coordination of international programs such as ChEss and InterRidge (www.interridge.org).

The exploration, investigation, and sampling of remote, dynamic, and topographically complex ecosystems such as hydrothermal vents also requires continuing development of state-of-the-art technologies for fieldwork and laboratory analyses. For example, to continue exploration at ever-higher latitudes, robotic vehicles are increasingly important—both remotely operated vehicles and autonomous underwater vehicles (AUVs). Indeed, with so much of the global mid-ocean ridge yet to be investigated, AUVs that can operated independently of a mother ship are increasingly recognized as one technology, in particular, that will be vital to push back the barriers to our knowledge (see, e.g., Yoerger et al., this issue).

CONCLUSION

Exploration and investigation of new sites at key locations is essential to fill in important gaps in the biogeographical puzzle of hydrothermal vents. The existence of such ecosystems was completely unexpected 30 years ago, but their discovery has changed the way we understand both Earth and the life upon it. With every new discovery and investigation of known sites and communities, our knowledge and understanding of the diversity and functioning of these remote and exuberant ecosystems increases, helping us understand the processes driving the deep sea and the global biosphere. Continuing exploration of hydrothermal vents will no doubt lead to the description of new species, a better understanding of geological and geochemical processes affecting their biology (and vice versa), and the understanding of the phylogenetic links between vent species and other faunal communities. As an important societal benefit, this research will also undoubtedly continue to provide potentially interesting sources of active molecules for the biotechnological and biomedical industries.

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