CHAPTER 9

A Metapopulation Approach to Interpreting Diversity at Deep-Sea Hydrothermal Vents

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I. INTRODUCTION

Hydrothermal vent communities inhabit the deep sea in locations where volcanic activity causes hot, chemical-rich fluids to exit the seafloor. These surprisingly productive systems were first discovered in 1977 during a research expedition to the Galapagos Rift in the eastern Pacific ocean. Investigators found giant clams, more than 25 cm in length, and red-plumed tubeworms with 3-m-long tubes. The abundance, size, and novelty of organisms astonished biologists, and challenged the prevailing view of the deep sea as a sparsely populated desert inhabited mostly by small individuals. Subsequent investigation has revealed that the vent habitat is patchy and transient, making the ecosystem well suited to a metapopulation framework. Our goal in this chapter is to provide an introduction to the natural history of vent ecosystems in the deep sea (>1 km water depth) and to give an example of how metapopulation models can be used to address one class of questions about species diversity patterns at vents. We frequently use

Marine Metapopulations, Jacob P. Kritzer and Peter F. Sale

vents along the East Pacific Rise as examples because they are the systems most familiar to us.

The discovery of productive communities at vents perplexed biologists because the flux of photosynthetically-derived food particles from the sea surface was considered insufficient to support them. However, early studies revealed the prevalence of microbial chemoautotrophy and suggested that it might supplant photosynthesis as the basis of the food web. Microbes use reduced chemicals such as hydrogen sulfide and methane in the vent fluids as their energy source for fixing organic carbon (reviewed in Karl, 1995). Many of the microbes are free-living, either as plankton or on the seafloor, but some exist in close associations with metazoans. A prominent example is the symbiotic association between vestimentiferan tubeworms and bacteria. The tubeworms have no mouth or gut, and use instead an internal organ called a trophosome filled with chemoautotrophic bacteria. The bacteria are so numerous that they can comprise 15% of the body weight of the tubeworm (Fisher et al., 1988). Other species (e.g., mollusks) have bacteria associated with their gills, and some crustaceans and polychaetes support epizootic bacteria on their outer surfaces.

Vent fluids provide the reduced chemicals needed for chemoautotrophy, but they can exit the seafloor at extreme temperatures (>400°C) and with high concentrations of trace metals (Cu, Co, Zn, Pb) that are potentially toxic to many organisms (Childress and Fisher, 1992). In cases where undiluted fluids exit the seafloor, they immediately mix with oxygenated seawater, precipitating dark ferric sulfides, giving the vents the name *black smokers*. Some of the precipitates form directly on the seafloor and develop into large chimneys. In other cases, where hydrothermal fluids have mixed with ambient (2 to 4°C) seawater in the subsurface, they leak out of cracks and crevices at temperatures of a few degrees or tens of degrees above ambient. Diffuse venting usually is clear, but has been called *shimmering water* because the elevated temperatures, and consequent density anomalies, refract light used by observers. Areas of diffuse venting often are associated with high-temperature smokers and a decrease in temperature with distance from the main conduits. Because vent fluids are heated, they are lighter than seawater and may rise to levels of hundreds of meters above the seafloor before they entrain enough seawater to become neutrally buoyant. These plumes have been important in locating new vents, because they are geographically more extensive, and therefore easier to find, than the vent orifices.

The majority of invertebrates inhabiting deep-sea vents can live only in vent habitats. More than 440 species have been observed at vents, most of which are endemic species (Tunnicliffe et al., 1998). New species still are being described at a rapid rate (Fig. 9-1). Taxonomic groups that are common in the deep sea, such as polychaetes, mollusks, and crustaceans, are also common at vents, but in very different forms (see review in Van Dover, 2000). Vestimentiferan tubeworms are among the best known of Pacific vent species because of their large

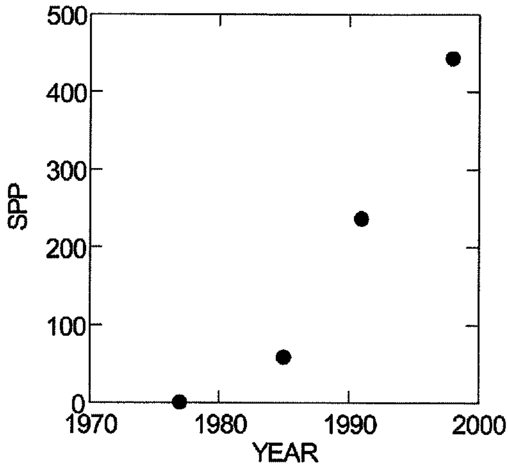

FIGURE 9-1. Number of vent species described since the discovery of vent ecosystems. Total vent species described at the time of publication of major reviews by Newman (1985), Tunnicliffe (1991) and Tunnicliffe et al. (1998).

size, bright-red plumes, and unusual morphology (Fig. 9-2A). Originally thought to be a new phylum, these tubeworms are now considered to be highly specialized polychaetes in the family Siboglinidae (Rouse, 2001). They live in the diffuse flows at temperatures as high as 30°C. Other polychaetes in the family Alvinellidae (e.g., Pompeii worms) inhabit smoker chimneys in the Pacific and are exposed regularly to temperatures of 40°C (Desbruyères et al., 1998) and perhaps higher. Numerous smaller polychaete species live in the interstices of tubes, shells, and rock, functioning as scavengers, predators, and suspension feeders. Small tube-building polychaetes in the family Serpulidae (feather-duster worms) form extensive fields outside the boundaries of detectable venting (Fig. 9-2B), capturing bacteria and organic particles as they drift away from the vents. The giant clams of the eastern Pacific have red hemoglobin-filled tissues to capture hydrogen sulfide from vent fluids. Their gills are greatly modified to support endosymbiotic bacteria rather than suspension feed, and they insert their foot directly into the vent fluids to absorb sufficient hydrogen sulfide for their endosymbionts. Mussels occur in the diffuse fluids at many vents (Fig. 9-2C), sometimes forming beds 50 cm thick and extending many tens of meters. Juvenile mussels feed on suspended matter, but older individuals appear to get most of their nutrition from bacteria in their gills. Grazing limpets are very common, covering not only the basaltic surfaces, but also the tubes and shells of other

FIGURE 9-2. Hydrothermal vent fauna on East Pacific Rise: (A) thicket of vestimentiferan tubeworms providing habitat for bythograeid crabs and fish; (B) field of suspension-feeding serpulid polychaetes; (C) vent mussels (with yellowish periostracum covering shell) and galatheid crabs. (see color plate)

sessile invertebrates. They appear to subsist on benthic bacteria, just as related shallow-water species graze on benthic algae. A large predatory snail species occurs in the eastern Pacific, but its role in structuring the communities is unknown. Galatheid and bythograeid crabs function as scavengers and, when given the opportunity, predators. Other mobile predators include fish and octopods, some of which are endemic to vents, and others that are foraging opportunistically. Vent faunas in biogeographic provinces other than the eastern Pacific differ substantially in species composition; processes potentially responsible for this variation are discussed in Section IV.

Vents have now been located at volcanically active sites in all ocean basins (Fig. 9-3). Marine volcanic activity is concentrated along mountain ranges that form as a consequence of seafloor spreading at the boundaries of tectonic plates. Along these midocean ridges, magma rises up to the surface of the Earth's crust, heating fluids within the crustal rocks and episodically erupting onto the seafloor. The ridges are linear features, and constrain the distribution of most venting to the narrow margins of crustal plates. Exceptions are found in volcanically active back-arc and fore-arc basins (e.g., Lau basin in the western Pacific), where subduction of the Earth's crust generates volcanism, and on seamounts such as Loihi, which appears destined to become the southernmost island of Hawaii. Vents and their associated communities occur as discrete patches, separated from each other by areas of seafloor that are not exposed to hydrothermal fluids. An individual vent may comprise an isolated black smoker, an area of diffuse flow, or a combination of focused and diffuse venting. Vents may be separated by less than 1 km, forming clusters along an active segment of a ridge (e.g., near 9°N along the East Pacific Rise; Fig. 9-4), but these clusters are often separated from each other by hundreds to thousands of kilometers. Although our understanding of the spatial scales of vent distributions is limited by the resolution and extent of geological mapping (i.e., the absence of vents in many regions may be the result of lack of surveys), it is clear that vents are patchy, and this patchiness occurs over a wide range of spatial scales.

Like terrestrial volcanic and hydrothermal systems, deep-sea vents are transient. The life spans of vents and their spacing along a ridge both depend on the magmatic, tectonic, and hydrologic processes that result in release of hydrothermal fluids (reviewed in Fornari and Embley, 1995). The fluids enter the seafloor as ambient seawater, seeping downward into the crustal rocks. They are heated by magma (either directly by contact or indirectly through thermal conduction) and interact with the rocks, gaining some chemicals and losing others. Eventually, the hot, buoyant fluids seep back up through the crust. Conduits up to the seafloor may be formed abruptly through volcanic eruptions or by tectonic cracking and diking events. These conduits may close or become rerouted as a result of tectonic shifts, geochemical clogging (e.g., mineral precipitation as temperatures cool), lava flows, or basaltic-pillow collapses and rockfalls (Haymon et al., 1993).

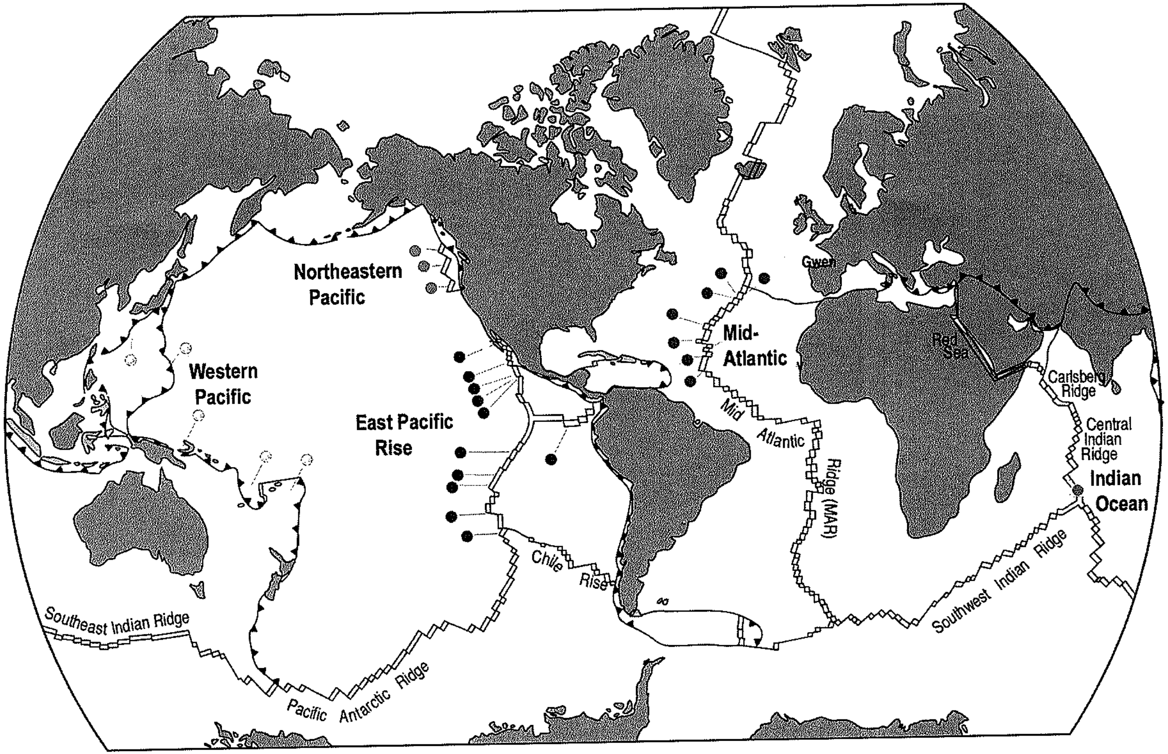

FIGURE 9-3. Global distribution of known hydrothermal vent communities on mid-ocean ridges and back-arc spreading centers. Biogeographic provinces are distinguished by color: Western Pacific (lightest gray); Northeastern Pacific (gray); East Pacific Rise (black); Mid-Atlantic Ridge (dark gray, including 3 northernmost vents near Azores); and Indian Ocean (light gray). Map redrawn from Van Dover et al. (2002).

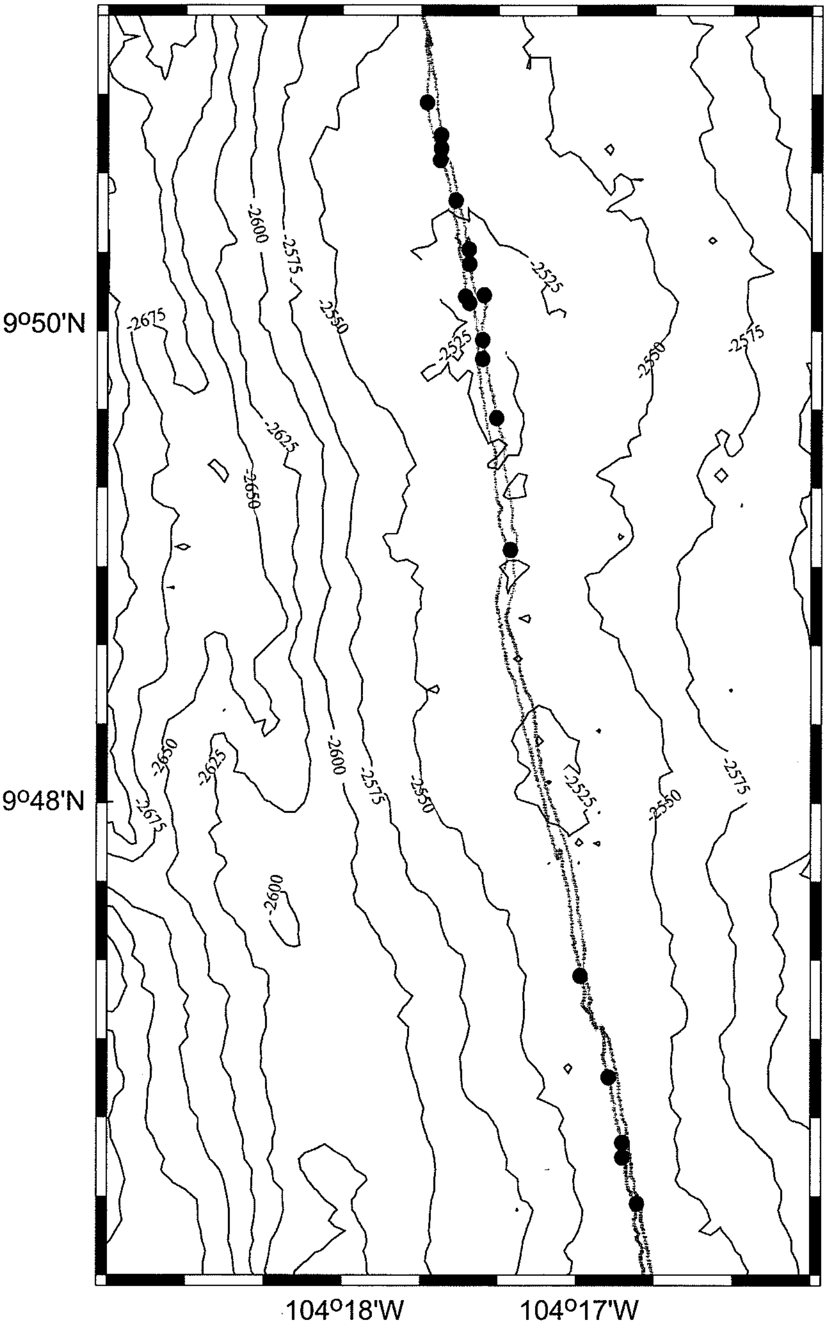

FIGURE 9-4. Spacing of hydrothermal vents (black circles) in vent clusters located near 9°50′N and 9°47′N on the East Pacific Rise. From K. von Damm, unpublished data.

II. VENT SYSTEMS AS METAPOPULATIONS

The study of vent ecology is well suited to a metapopulation approach because of the patchy distributions and transient nature of the habitat, and the endemism of component species. Relatively little is known about the life histories of species, dynamics of populations, or structure of communities, due to their recent discovery and remote locations. Although this lack of information could be considered a drawback, it does mean that theory can contribute substantially to explaining patterns, identifying important parameters and processes, and guiding future empirical research. In this section we summarize information on the spatial and temporal scales of physical and ecological processes that are relevant to metapopulation modeling of vent ecosystems.

A. DYNAMICS AND DISTRIBUTION OF VENT HABITAT

The dynamics of venting on the deep seafloor vary among ridge systems with different spreading rates. Vent habitats on the Mid-Atlantic Ridge (a slow-spreading ridge) are sparse, and known vents are separated by as much as a thousand kilometers (Fig. 9-3). Dating studies at one vent, TAG, show that venting has occurred over 10,000 years at this location (Lalou et al., 1993). During that time, however, the venting appears to have ceased and restarted on timescales of hundreds of years. The ridge crest is relatively broad on the Mid-Atlantic Ridge, and the valley walls can be 50 m high or more. The observed vent communities have been discovered over a wide range of depths (850–3500 m), and in a variety of geological, topographic, and oceanographic settings (Van Dover, 1995). Chemical composition of the vent fluids varies, depending on the geological setting, and likely influences the composition of colonizing species (Desbruyères et al., 2001). In contrast, vents on the East Pacific Rise (a fast-spreading ridge) are separated by a few hundred kilometers at most, and often occur in clusters (Haymon et al., 1991). The vents have life spans as short as years to decades (Haymon et al., 1993; MacDonald et al., 1980). Geologists do not fully understand the processes that control the spacing and transience of vents, but the rate and character of magma delivery to the crust appear to be associated with the spreading rate of a ridge and the dynamics of its venting.

B. DISPERSAL AND COLONIZATION

Given the patchiness and transience of the vent environment, it is clear that migration is essential for vent species to maintain their populations and geographic ranges. Because adults of most vent species are attached or have minimal migratory capabilities, it also seems likely that vent species disperse through the water via larval stages. However, the dispersal mechanisms and their population consequences have not been easy to predict. For instance, Lutz et al. (1980) predicted that most vent species should have larvae that feed in the water to disperse long distances, but an examination of egg sizes and larval shell types did not support the idea. Subsequent studies showed that reproduction and larval type of vent species were highly constrained by phylogenetic affinity (reviewed in Tyler and Young, 1999). In other words, species retained the life history attributes of their shallow-water ancestors, even if they weren't optimal for the vent environment.

To disperse successfully, a larva must have a sufficiently long life span to survive the transport interval between neighboring vent habitats, and must be able to locate a suitable habitat for settlement. Because larvae of most vent species are small (Berg and Van Dover, 1987) and appear to be relatively weak swimmers, dispersal rates and trajectories are strongly influenced by oceanic circulation. Circulation in the vicinity of mid-ocean ridges is controlled by topography, hydrography, Coriolis effects, turbulent mixing, and regional forcing. Near the ridge, channeling or blocking by topography may intensify flow parallel to the ridge. Coriolis effects (from the Earth's rotation) also contribute to flow along topography or to gyres and eddies in the water column (Cummins and Foreman, 1998). Tidal and longer period oscillations are often prominent at ridge sites (Lavelle and Cannon, 2001), and these can drive substantial vertical flows up and down the ridge flanks, as well as contribute to localized mean flows parallel to the ridge. In general, currents that parallel the ridge axis are expected to facilitate larval exchange among vent communities.

A direct estimate of larval life span has been obtained for only one species, the vent tubeworm *Riftia pachyptila*. Physiological studies of cultured larvae revealed that the larvae can live on the order of 30 to 40 days without feeding (Marsh et al., 2001). If the larvae are transported as passive, neutrally buoyant particles, they have the potential to disperse distances up to 100 km in typical currents near 9 to 10°N along the East Pacific Rise (Mullineaux et al., 2002). However, the ridge at this latitude experiences sustained periods of cross-axis flow, which might sweep larvae off the ridge and away from suitable habitat. Currents near East Pacific Rise vents at 13°N are aligned along the ridge axis for much longer intervals than at 9°N (Chevaldonné et al., 1997), and *Riftia* larvae appear capable of dispersing up to 200 km along the ridge (Mullineaux et al., 2002). In both regions of the East Pacific Rise, vent spacing is on the order of tens of kilometers, suggesting that larvae should be able to disperse effectively between neighboring vents. A similar approach was used to estimate dispersal potential of alvinellid polychaetes on the East Pacific Rise (Chevaldonné et al., 1997). Larval life spans of the alvinellids, as inferred from egg size and life histories of related shallow species, were quite short and allowed dispersal distances on the order of tens of kilometers. These species appear to have sufficiently long larval life spans to disperse between neighboring vents on the East Pacific Rise, but not to survive transport across ocean basins (e.g., between the East Pacific Rise and western Pacific vents) or between disjunct ridge systems (e.g., East Pacific Rise to northeastern Pacific ridge system). Because larval life span has been measured for *Riftia* only, the question of how long-distance transport influences vent ecology remains open.

Other potential topographic and oceanographic barriers to dispersal include the transform faults that separate ridges into segments (e.g., MacDonald, 1982; Fig. 9-3) and provide deep passages between abyssal basins. Although detailed oceanographic observations from discontinuities in ridges are sparse, examples from the Atlantic suggest that the flows across the ridges are often persistent and strong (Ledwell et al., 2000; Mercier and Speer, 1998). Larvae caught in these flows would likely be lost from that ridge system permanently, because no mechanism for return is known.

However, retention of larvae may occur on a local scale near a source vent. The buoyant hydrothermal plume sets up a circulation cell as a consequence of the Coriolis effect (e.g., Helfrich and Speer, 1995), which could retain particles and larvae near their source populations. The circulation cell is expected to extend roughly 1 km from the vent, with focused upward velocities at the center, diffuse downward velocities at the perimeter, and inward velocities along the bottom (Fig. 9-5). Any larvae that sank, swam downward, or had a positive tropic response to vent fluids would tend to accumulate near the vent. Such a retention mechanism would inhibit dispersal, but potentially enhance settlement back into the local population (Mullineaux and France, 1995).

Population genetic studies are useful for inferring dispersal and have constrained the spatial scales over which colonists appear to be exchanged. Most species of tubeworms and mollusks show evidence of extensive gene flow on the 100 km scale typical of a ridge segment, Craddock et al., 1997; Vrijenhoek, 1997; Won et al., 2003), but punctuated by population bottlenecks that might be the result of frequent extinctions. Surprisingly, there is little evidence for "isolation by distance" for any species except on large (thousands of kilometers) scales or across topographic barriers. Along the East Pacific Rise, neighboring populations of the polychaete *Alvinella pompejana* vary genetically, but show no increase in variation with separation distance (Jollivet et al., 1995). Populations of the amphipod *Ventiella sulfuris* are genetically similar at vents within a ridge segment, but substantially different between the East Pacific Rise and the Galapagos spreading center (France et al., 1992). These results indicate that larvae disperse extensively within segments of a mid-ocean ridge, but not across transform faults and other large topographic discontinuities in the ridge system (Tunnicliffe et al., 1998). The lack of documentation for the expected "isolation by distance" pattern has led researchers to speculate that vent larvae exist as a well-mixed, ever-present pool of potential colonists (Van Dover, 2000; Vrijenhoek, 1997). Although this

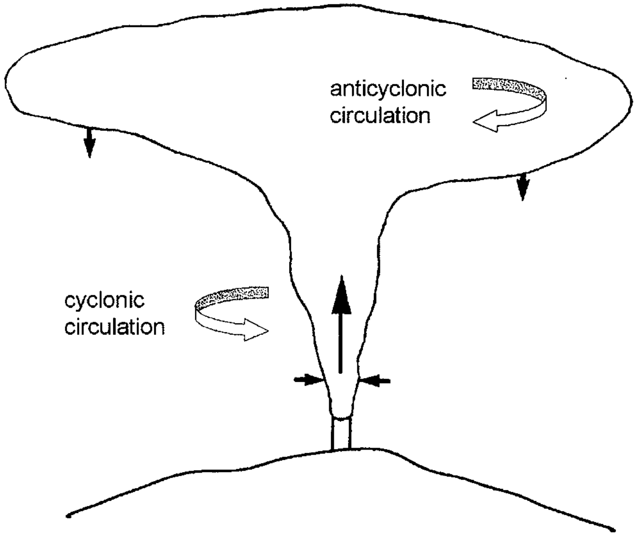

FIGURE 9-5. Diagram of flow in a buoyant hydrothermal vent plume, showing anticyclonic circulation at the neutrally buoyant level and cyclonic circulation below. Redrawn from Helfrich and Speer (1995).

may be a valid generalization on evolutionary timescales, sampling in the water column has demonstrated that abundance and species composition of vent larvae, like their shallow relatives, are highly variable on ecological timescales (Mullineaux et al., 2001).

The dynamic nature of vent habitats will likely influence dispersal success and population genetic structure. Theoretical considerations indicate that introducing variation of vent positions into a metapopulation model (to simulate shifting of hydrothermal activity along a ridge axis) can prevent gene flow and genetic drift from reaching equilibrium (Jollivet et al., 1999). When vent spacing was allowed to vary temporally in simulations, individual populations rarely experienced the prolonged isolation that led to extinction. Similarly, variance in vent positions facilitated gene flow and allowed population genetic structure to become homogeneous in a metapopulation that would have experienced genetic isolation if the vent positions had been static.

Despite potential dispersal barriers, many vent species colonize new habitat rapidly (Micheli et al., 2002; Shank et al., 1998; Tunnicliffe et al., 1997), indicating that they are prompt and efficient dispersers. The expected consequences of unimpeded dispersal and subsequent genetic exchange would be to homogenize species composition and genetic structure across vents on a ridge. However, these studies all were conducted in fields of active venting, where a new habitat was typically within 10 km of established vent communities. In contrast, at Loihi seamount, an isolated vent south of Hawaii, only a few individual metazoan colonists have been detected during the past 10 years, and no vent-endemic populations appear to have become established (Grigg, 1997). It is not clear whether the cause of sparse recruitment is unsuitable habitat or restricted supply of colonists.

III. SPECIES INTERACTIONS

Until recently, vent communities have been assumed to be structured by the extreme physical and chemical features of their environment (Luther et al., 2001; Sarrazin et al., 1999), but in situ, manipulative studies have revealed an important role of species interactions. Facilitation, competition, and predation influence the patterns of zonation, succession, and species composition at vents (Levesque et al., 2003; Micheli et al., 2002; Mullineaux et al., 2003). The physicochemical environment clearly sets the extreme limits of species' occurrences at vents, but interactions with other species influence their distributions within these limits.

Succession is particularly apparent and important in systems in which episodic disturbances induce large changes in availability of primary substratum or food. On ridges, the catastrophic perturbations that create new vents or obliterate existing ones occur on timescales comparable to the species' generation times, making disturbance and primary succession dominant characteristics of the ecosystem. The physical and chemical nature of the habitat continues to be dynamic after eruptions (Butterfield et al., 1997; von Damm, 2000), and changes in the flux and composition of hydrothermal fluids affect chemoautotrophic-based production. The responses of colonizing species at deep-sea vents to these perturbations, either directly through physiological tolerances and nutritional requirements or indirectly through biological interactions, are largely unknown.

Previous studies of invertebrate colonization at hydrothermal vents have documented a distinct and consistent successional sequence over the life span of vents on the East Pacific Rise (Fustec et al., 1987; Hessler et al., 1988). The initial visibly dominant sessile metazoan in sites with moderate-temperature fluids (i.e., <30°C, not high-temperature black smokers) appears to be the small vestimentiferan tubeworm *Tevnia jerichonana* (Shank et al., 1998). This species then is replaced by the larger tubeworm *Riftia pachyptila*, usually over a period of less than one year. Later in the sequence, the mussel *Bathymodiolus thermophilus* colonizes and may, in some cases, displace the tubeworms (Hessler et al., 1988). Time–series observations show that this sequence can correspond to a change in the temperature and chemistry of vent fluids (Shank et al., 1998), although Hessler et al. (1988) and Mullineaux et al. (2000) document species succession under conditions of constant venting and conclude that biological interactions also play a role. Johnson et al. (1994) noted that mussels colonized tubeworm clumps and diverted the hydrothermal fluids away from the tubeworm plumes with their shells. They suggested that this reduction in the supply of hydrogen sulfide to the tubeworms' uptake organs essentially starved them and led to their death. Mullineaux et al. (2000) found that *Riftia* larvae settled onto experimental surfaces only if *Tevnia* was present, whereas *Tevnia* was able to settle alone. The colonization patterns did not correspond to gradients in the physicochemical environment, nor did they reflect larval availability, so it is possible that *Riftia* colonists were facilitated by the smaller pioneer species. The mechanism for facilitation is unknown, although it does not appear to be mediated by the tube material alone (i.e., *Riftia* does not settle preferentially in response to *Tevnia* tubes; Hunt et al., 2004) and does not appear to be obligate. Most likely, the facilitation involves the establishment of a critical microbial flora or release of a chemical settlement cue.

In situ manipulative studies of succession and predation at hydrothermal vents have investigated interactions between other vent species at the East Pacific Rise, including the predatory fish, scavenging crabs, grazing limpets, and suspension-feeding polychaetes. Using caging studies to exclude the predators/scavengers, and bait studies to investigate prey choice, Micheli et al. (2002) found that fish preyed selectively on limpets. When predators were excluded, limpet populations increased, and they excluded most sessile, tube-building, species. Mullineaux et al. (2003) used sequential colonization studies to demonstrate that early colonists at vents had an important influence on later arrivals, and in setting the structure of adult communities. When sessile, tube-building, species settled in areas with low food supply, they facilitated settlement of other sessile colonists. When mobile limpets or sessile tube builders settled in areas of high food supply, they inhibited colonization by all other species, whether mobile or sessile. Fish mediated these interactions by preying selectively on limpets above a threshold size (Sancho et al., 2005). These results demonstrate that species interactions are mediated by predators and alter the structure of communities through mechanisms that vary along gradients of vent fluid flux.

IV. BIOGEOGRAPHY AND DIVERSITY

The species composition of vent faunas varies among geographically disjunct ridges, and each ridge system can be characterized by a few distinct species. As new vents are discovered in unexplored regions, new biogeographic provinces. each with a distinctive fauna, are erected. Among these are the: East Pacific Rise, Northeastern Pacific, Mid-Atlantic Ridge, Central Indian Ocean, and Western Pacific (Fig. 9-3). The northeastern Pacific fauna shares many species and genera with the East Pacific Rise, but has lower species diversity and lacks notable groups, such as endemic decapods (Tunnicliffe et al., 1998). For instance, one species of vestimentiferan tubeworm, *Ridgeia piscesae*, occurs in the northeastern Pacific, in contrast to the three related species found on the East Pacific Rise. Tunnicliffe (1988) suggests that a vicariant event (the subduction of an extensive ancestral north–south ridge by the North American plate) isolated a subsample of eastern Pacific species onto the northern fragment of the ridge. At western Pacific vents, large, symbiont-bearing gastropods dominate many communities (Hessler and Lonsdale, 1991), although bivalves and tubeworms also occur (Kojima, 2002). Vent chimneys at Atlantic vents are covered by several different species of bresiliid shrimp, except in a few sites where shrimp are absent or rare and bivalves dominate (Desbruyères et al., 2000). Indian Ocean vents have only recently been explored. Their inhabitants appear to be related to western Pacific species (Hashimoto et al., 2001; Van Dover et al., 2001), with the exception of a prominent shrimp related to species in the Atlantic.

Along a ridge, individual vents may differ in species occurrence or relative abundances, but clines in species composition or distinct faunistic boundaries have not been observed (e.g., Juniper et al., 1990; Van Dover and Hessler, 1990). These differences between neighboring vents may be the result of environmental variation (e.g. in hydrothermal fluid flux rates or water chemistry) or stochastic events (Hessler et al., 1985); or of water depth, habitat disturbance, or character of water column particulates (Desbruyères et al., 2001). In addition, composition of vent faunas may be influenced by initial colonists or may change dramatically over time (Shank et al., 1998), leading to a mosaic of patches at different stages of succession.

Diversity patterns at hydrothermal vents are difficult to interpret because different regions have been sampled with varying effort and different techniques. Nevertheless, a comparison of species numbers between biogeographic provinces gives a qualitative perspective. As a starting point, diversity at vents is considered to be low compared with most other deep-sea and shallow-water habitats (Jollivet, 1996; Juniper and Tunnicliffe, 1997). Among vents, diversity on the East Pacific Rise is high and perhaps comparable with the western Pacific, whereas diversity at the northeastern Pacific vents is reduced. The lowest number of species is found at the mid Atlantic vents. Juniper and Tunnicliffe (1997) suggested that a combination of regional age, disturbance, habitat heterogeneity, and habitat area were responsible for these observed patterns. For instance, the Atlantic basin is relatively young compared to the Pacific, and the vents are stable, widely spaced, and homogeneous with respect to habitat type. These characteristics all would contribute to low diversity relative to the Pacific, where the regional species pool has long been in existence, the vents are disturbed frequently enough to mitigate competitive exclusion, the vent habitat area is larger (i.e., vents are more densely spaced), and habitat type varies between vents.

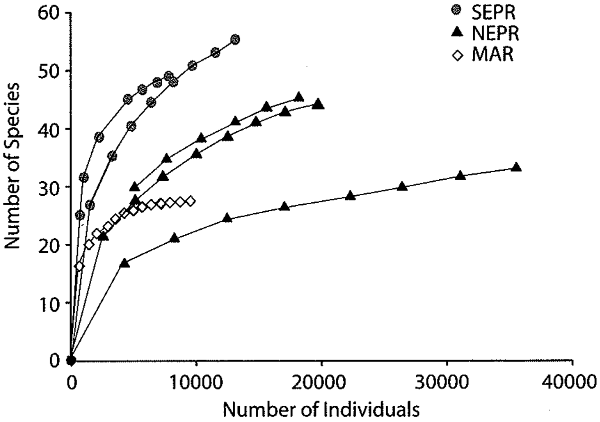

FIGURE 9-6. Comparison of diversity in the vent communities on the Mid-Atlantic Ridge (MAR) and East Pacific Rise (southern = SEPR; northern = NEPR), using sample-based species-effort curves. Each point is a mean diversity value based on 100 randomization operations (without replacement) for each curve. Redrawn from Turnipseed et al. (2003).

Recent studies have approached diversity through more quantitative means, by restricting sampling to invertebrates associated with mussel beds (Turnipseed et al., 2003; Van Dover and Trask, 2000) or vestimentiferan tubeworm clumps (Tsurumi and Tunnicliffe, 2003). Replicate sampling of known volumes or areal coverage allows these investigators to plot species–effort curves and evaluate the effect of sampling on species numbers. Turnipseed et al. (2003) found that diversity in vent mussel beds was lowest in the mid Atlantic and higher at the southern East Pacific Rise than the northern East Pacific Rise (Fig. 9-6). They suggest that the wide spacing of vents in the mid Atlantic limits species dispersal and contributes to extinction of populations at individual vent fields, leading to lowered diversity. They argue that this process is more important in reducing diversity than short vent life spans, as has been suggested by population geneticists (Craddock et al., 1995; Sibuet and Olu, 1998). In contrast, Tsurumi (2003) suggests that diversity at northeastern Pacific vents is limited by frequent disturbance and habitat transience.

V. METAPOPULATION MODELS FOR VENT FAUNAL DIVERSITY

Metapopulation modeling approaches are well suited to investigation of species diversity patterns (van Woesik, 2000; Wilson, 1992). As an example of such an approach, we address the question of why local species diversity differs among geographically separate ridge systems (e.g., eastern Pacific and mid Atlantic). Although some of these patterns have been explained in terms of evolutionary processes and vicariance events (e.g., Tunnicliffe, 1988), we want to investigate whether ecological-scale processes constitute feasible alternatives. Our ultimate objectives are to explore the hypotheses raised by vent researchers to explain diversity patterns. Are they the result of (1) disturbance, as suggested by Craddock et al. (1995); (2) habitat area or heterogeneity, as suggested by Juniper and Tunnicliffe (1997); or (3) habitat separation, as suggested by Turnipseed et al. (2003)? Or alternatively, might the differences in diversity be due to species interactions? To begin evaluating these hypotheses, we develop a model that incorporates the dynamics of vent habitat, species' colonization ability, and facilitation as an example of species' interactions. Complementary examples of the use of metapopulation approaches to address community patterns are presented in chapters on coral reefs (Mumby and Dytham) and general community structure (Karlson) in this book.

For simplicity we start with a spatially implicit model and make no effort to include the various scales of vent spacing observed in nature. As a consequence, we will not be able to study the implications of spatiotemporal correlation in vent activity. We could use a spatially explicit model to address this issue, but that is outside the scope of this study. Also for simplicity, we include facilitation, but not exclusion (competition or predation), in our evaluation of species interactions. Exclusion appears to be a fundamental part of successional sequences at vents and elsewhere, and will be a component of future modeling efforts on this topic.

For our theoretical analyses, we use metapopulation community models (or *metacommunity models*; Wilson, 1992) that describe species as collections of spatially discrete populations connected by dispersal. These models take the form of *patch-occupancy models* (Caswell and Cohen, 1991; Levins, 1970) that describe species as occupying a set of discrete habitat patches (i.e., vents). The *state* of a patch is a list of the species that are present in it. Patch-occupancy models keep track of the proportion of the patches that are in each state. An important assumption of these models is that species can disperse, with equal ease, between any two patches. This assumption allows us to write the models as (relatively) simple systems of differential equations.

Our models are different than most in two ways. First, most metapopulation and metacommunity models assume a static configuration of habitat types (but see Hanski, 1999; Nee and May, 1992). Many marine habitats, however, are known to vary over time. Alterations in hydrothermal fluid flux at deep-sea vents can cause those habitats to switch from suitable to uninhabitable (or vice versa) on timescales as short as the generation times of inhabitants. Our models explicitly include these "vent dynamics."

Second, most metacommunity models account for a very small number of species. The reason is called the *curse of dimensionality*. In a model for *m* species that allows any number of these species to occupy a single patch, the number of states is 2^m; the number of possible transitions is 2^{2m}. With 20 species there would be more than one million states and 10^{12} transitions. The curse is that it becomes impossible to specify the rules for these transitions even for species pools of modest size. Theorists have tried to reduce the state space in a number of ways. In some models, patches are the size of a single individual, so that only one species can occupy a patch at a time. In other models, inferior competitors are eliminated from patches immediately upon the arrival of a superior competitor. Most often, theoreticians avoid the curse by simply keeping the number of species small; one- and two-species models are the most frequently studied. Our models, however, allow for many species by introducing a hierarchy that allows us to specify transition rules in an economical way.

A. A NULL MODEL

To begin, imagine a habitat composed of many discrete vent sites (patches) that are identical in every way, except that at any given time, some of them will be dormant and, hence, uninhabitable. Imagine that all the vents are equidistant from each other. Imagine that the active vents can support an arbitrary number of species, and that dormant vents become active and active vents become dormant at fixed rates. Finally, populate this imaginary dynamic landscape with identical species that do not interact in any way.

This imaginary vent community is, of course, highly contrived. It ignores the obvious fact that real species are different in their reproductive output, longevity, and dispersal abilities. It ignores the fact that some species do compete with each other whereas others facilitate each other's growth. It ignores the facts that real vent habitats are spatially heterogeneous, that some vents are closer to each other than others, and that vents can typically support only a limited number of species at one time. But it is exactly because of these contrivances that this imaginary vent ecosystem is so useful. Because it leaves out almost every interesting biological interaction, we can use it to derive baseline statistics against which we can compare the results of models that incorporate biological processes that we care about.

We constructed a mathematical model of the imaginary vent ecosystem just described, a so-called *null model*, using the following recipe. First, identify every species in the community with a number between 1 and m; m is then the size of the species pool. Let N be the total number of vents (both active and dormant). Let S_X be the number of dormant vents, S_i be the number of vents at which species i is present, and $\bar{S}_i$ be the number of active vents at which species i is absent. Assume that dormant vents become active at the rate R, and active vents become dormant at the rate D. Because the vent sites are assumed to be equidistant from each other, we will assume that a vent without species i will be colonized by species *i* at a rate that is proportional to the total number of patches that species *i* currently occupies. We call the constant of proportionality the *colonization rate*, *C*, and assume that *C* decreases with the distance between patches. Then, for each $i = 1, 2, \ldots, m$, we have

$$\frac{dS_x}{dT} = D(N - S_x) - RS_x \tag{1a}$$

$$\frac{d\bar{S}_i}{dT} = RS_x - \frac{C}{N}S_i\bar{S}_i - D\bar{S}_i \tag{1b}$$

$$\frac{dS_i}{dT} = \frac{C}{N}S_i\bar{S}_i - DS_i. \tag{1c}$$

In this model, and in the facilitation model that we describe in the next section, species only go extinct when an occupied vent becomes dormant. This assumption is not as bad an approximation as it might appear at first, because the timescale of vent dynamics is approximately the same as the generation time of the species that inhabit them.

For a given species, model (1) has two equilibrium states. At the first, species *i* is eliminated from every vent:

$$S_x = \frac{N}{(R/D)+1}, \quad \bar{S}_i = \frac{N(R/D)}{(R/D)+1}, \quad S_i = 0. \tag{2}$$

At the second equilibrium,

$$S_x = \frac{N}{(R/D)+1}, \quad \bar{S}_i = \frac{N}{(C/D)}, \quad S_i = \left[\frac{(R/D)}{(R/D)+1} - \frac{1}{(C/D)}\right]N; \tag{3}$$

species *i* persists if $S_i > 0$.

Note that the equilibrium levels of the states are always proportional to the total number of vents (*N*). This suggests that we need only keep track of the fractions,

$$s_x = \frac{S_x}{N}, \quad \bar{s}_i = \frac{\bar{S}_i}{N}, \quad s_i = \frac{S_i}{N}, \tag{4}$$

rather than the numbers S_x, $\bar{S}_i$, or S_i. Also note that while model (1) contains three parameters (*D*, *R*, *C*) in addition to *N*, these parameters always appear in the two ratios *R/D* and *C/D*. Thus, at least as far as the equilibria are concerned, the important values are activation and colonization rates relative to the dormancy rate, not the values of the rates themselves. This suggests that we should measure time in units of 1/*D*, the average length of time that a vent remains active. Using

$$t = TD, \quad r = \frac{R}{D}, \quad \text{and} \quad c = \frac{C}{D}, \tag{5}$$

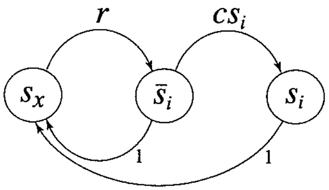

FIGURE 9-7. A graphical representation of the null model (6). Arrows indicate potential transitions among the three states: s_x (dormant), $\bar{s}_i$ (active but uninhabited by species i), and s_i (inhabited by species i). Per capita rates for each transition are indicated next to the arrows.

along with the change of variables (4) in model (1) gives the dimensionless model

$$\frac{ds_x}{dt} = 1 - s_x - rs_x \tag{6a}$$

$$\frac{d\bar{s}_i}{dt} = rs_x - cs_i\bar{s}_i - \bar{s}_i \tag{6b}$$

$$\frac{ds_i}{dt} = cs_i\bar{s}_i - s_i. \tag{6c}$$

The dynamics of this system are summarized in Figure 9-7.

Equation (6a), for ds_x/dt, is decoupled from the rest of system (6) because it represents geological rather than biological processes. Whenever $ds_x/dt = 0$, and hence $s_x = 1/(1 + r)$, we say that the vent system is in "geological equilibrium." In geological equilibrium, the fraction of vents that are active is

$$f = 1 - s_x = \frac{r}{1+r}. \tag{7}$$

It is often more convenient to think of f rather than r when trying to interpret the results of our model.

When, in addition to being in geological equilibrium, $d\bar{s}_i/dt = 0$ and $ds_i/dt = 0$, we say that the system is in "biogeological equilibrium." In the dimensionless parameters, the geological equilibrium (2) is

$$s_x = 1 - f, \quad \bar{s}_i = f, \quad s_i = 0, \tag{8}$$

and the biogeological equilibrium (3) is

$$s_x = 1 - f, \tag{9a}$$

$$\bar{s}_i = \frac{1}{c} \equiv \bar{s}, \tag{9b}$$

$$s_i = f - \frac{1}{c} \equiv s \tag{9c}$$

respectively. Species will only persist in the vent system (i.e. $s > 0$) if

$$cf > 1. \tag{10}$$

The quantity cf is the expected number of new vents that would be colonized by a population at a single inhabited vent over the active period of that vent when the system is in geological equilibrium and all other active vents are uninhabited.[1] Inequality (10) can be interpreted as saying that in order for a species to survive, a single-vent population must be able to colonize at least one other vent before its vent becomes dormant.

1. Diversity Indices

To compare diversity between regions, we introduce indices of diversity at both the local (individual vent) and regional (vent system) scales. A measure of local diversity, α, is the expected number of species at a single active vent. For the null model,

$$\alpha = \frac{ms}{\bar{s}+s} = m\left(1-\frac{1}{cf}\right). \tag{11}$$

Figure 9-8 shows how α changes as a function of c and f for a regional pool consisting of 25 species. Not surprisingly, α increases with both the amount of suitable habitat and the colonization rate.

One measure of regional diversity is simply the expected number of species that the entire vent system can support, α_{reg}. Under the null model, if one species can persist, all species can persist, so

$$\alpha_{\text{reg}} = \begin{cases} m, & \text{if } cf > 1 \\ 0, & \text{otherwise.} \end{cases} \tag{12}$$

A second regional diversity measure, H, is based on the relative proportions of the various species in the system. Let p_i be the relative proportion of species i. Then, setting $p_i \ln p_i = 0$ whenever $p_i = 0$, we define

$$H = -\sum_{i=1}^{m} p_i \ln p_i. \tag{13}$$

For a fixed species pool size, H is maximized when every species is equally likely. This is exactly the case in the null model where

$$p_i = \frac{s_i}{\sum_{i=1}^{m} s_i} = \frac{s}{ms} = \frac{1}{m}, \tag{14}$$

and hence $H = \ln m$.

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[1] It is the analog of the basic reproductive number R_0 in epidemiology.

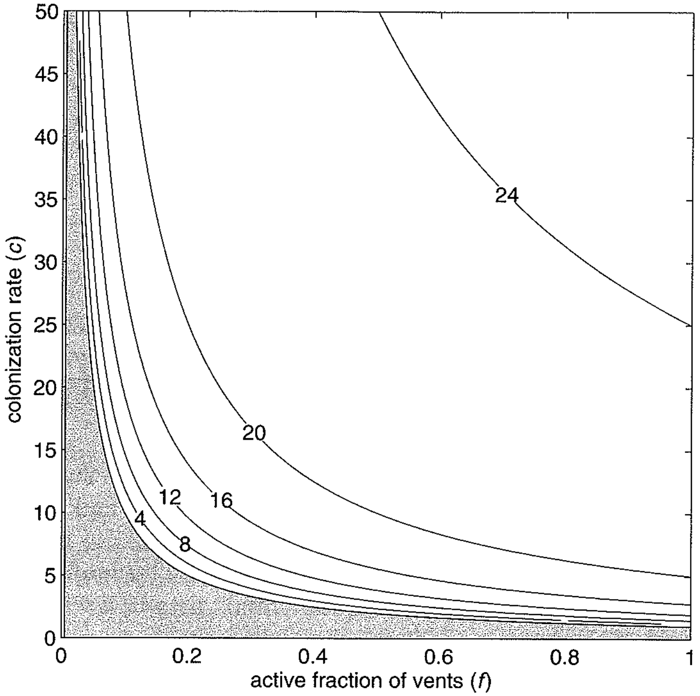

FIGURE 9-8. Contours of local diversity, as measured by the expected number of species in any patch (α), when the species pool contains $m = 25$ species and community dynamics are governed by the null model (6). In the grey area, all species are extinct.

B. FACILITATION

As mentioned in Section III, succession is a well-documented process at hydrothermal vents, and facilitation appears to play a prominent role in the successional sequence. Early species in the sequence accelerate the colonization of later arrivals, and in some cases their presence may be required for later species to become established. Here, we examine how diversity indices introduced earlier in equations (11) through (13) change from their values under the null model when we introduce obligate facilitation.

To begin, we must first specify a successional hierarchy. Without loss of generality, we number the species such that species i must be present at the vent before species $i + 1$ can colonize. Next, it helps to define a new set of state variables. We keep s_x for the fraction of all vents that are dormant, but now we

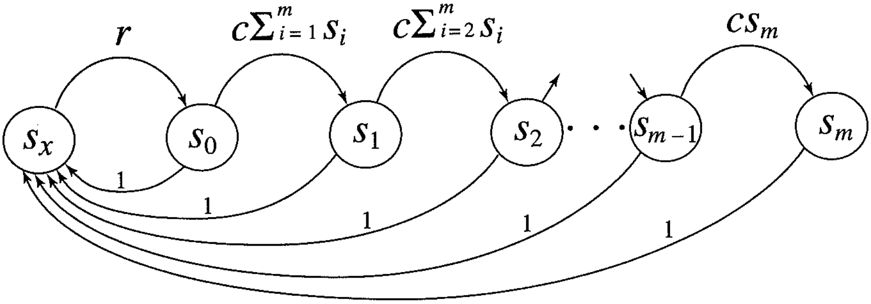

FIGURE 9-9. A graphical representation of the facilitation model (15). Arrows indicate potential transitions among the $m + 2$ states: s_x (dormant), s_0 (active but uninhabited), and s_i (inhabited by species 1 through i). Per capita rates for each transition are indicated next to the arrows.

introduce s_0 as the fraction of all vents that are active but uninhabited. A vent inhabited by species i will also have every species of lower rank. A vent with species 1 through i is in state s_i.

Incorporating this into the null model gives us the facilitation model

$$\frac{ds_x}{dt} = \sum_{j=0}^{m} s_j - rs_x \tag{15a}$$

$$\frac{ds_0}{dt} = rs_x - \left(c\sum_{j=1}^{m} s_j\right) s_0 - s_0 \tag{15b}$$

$$\frac{ds_i}{dt} = \left(c\sum_{j=i}^{m} s_j\right) s_{i-1} - \left(c\sum_{j=i+1}^{m} s_j\right) s_i - s_i, \quad \text{for } 1 \le i \le m-1, \tag{15c}$$

$$\frac{ds_m}{dt} = cs_m s_{m-1} - s_m. \tag{15d}$$

Here again, we have rescaled the variables as in (5), so that time is measured in average vent active periods. A diagram of all the states and transitions is shown in Figure 9-9.

The facilitation model (15) has the same geological equilibrium as the null model (c.f., Equation 8), but now there are m biogeological equilibria. For each j, $1 \le j \le m$, there is an equilibrium at

$$\hat{s}_x = 1 - f, \tag{16a}$$

$$\hat{s}_0 = 1/c, \tag{16b}$$

$$\hat{s}_i = \begin{cases} 1/c, & \text{for } 1 \le i \le j-1, \\ f - (j/c), & \text{for } i = j, \\ 0, & \text{for } i > j. \end{cases} \tag{16c}$$

For a given set of parameters, some of these equilibria have negative values. None of these is relevant. Among the rest, only the equilibrium with the largest number of species is stable. This number is determined by the values of f and c. To have $\hat{s}_k > 0$, we must have $k < fc$.

From the equilibrium values we can calculate ϕ_i, the fraction of active vents that are inhabited by species i:

$$\phi_i = \frac{1}{f}\sum_{j=i}^{m}\hat{s}_j = \begin{cases} 1-[i/(fc)], & \text{for } i \le fc, \\ 0, & \text{for } i > fc. \end{cases} \tag{17}$$

The species frequency decreases as species rank in the hierarchy increases. This contrasts with the species distribution under the null model, which is even.

The expected number of species inhabiting a single active vent is

$$\alpha = \frac{1}{f}\sum_{i=0}^{m} i\hat{s}_i. \tag{18}$$

Contours of α as a function of f and c are shown in Figure 9-10A. As in the null model, local diversity increases with both these parameters. In Figure 9-10B, we have plotted local diversity in the facilitation model relative to its value in the null model. For small values of f and c, facilitation dramatically reduces local diversity. The reduction is less when f and c are both large. Figure 9-10B suggests that it is when suitable habitat is "sparse" (i.e. most vents are dormant [low f] and they are difficult to colonize [low c]) that we should expect facilitative interactions to have a larger effect on local diversity.

For the facilitation model, the regional species richness α_{reg} is the largest integer not exceeding either fc or m. Thus, in contrast to the null model, there is an upper limit to the number of species that the vent system can support in addition to the species pool size, and this number grows in proportion to both f and c. To calculate H, our measure of regional diversity, we use

$$p_i = \frac{\phi_i}{\sum_{i=1}^{m}\phi_i} \tag{19}$$

in formula (13). Patterns in regional diversity are similar to local diversity (Fig. 9-11). Again, it is when suitable habitat is sparse that facilitation has its largest effect.

VI. SUMMARY

Hydrothermal vent communities are apt examples of metacommunities: a group of interacting species inhabiting a set of habitat patches that are connected via

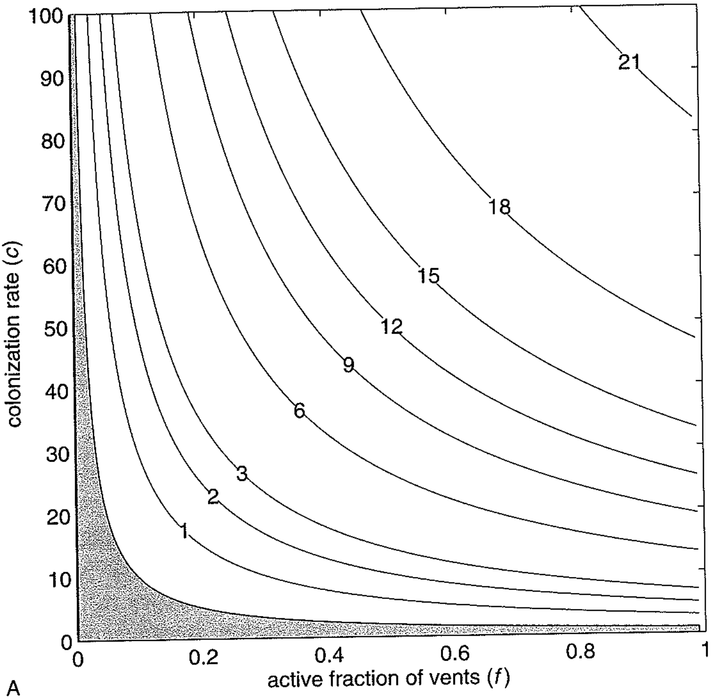

FIGURE 9-10A. Contours of local diversity, as measured by the expected number of species in any patch (α), when the species pool contains $m = 25$ species and community dynamics are governed by the facilitation model (15).

dispersal and subject to local extinction. Every year we learn more about the geology and chemistry that control the location, amount, and quality of this unique habitat. At the same time, we are compiling more information about the abundance and distribution of the species that are endemic to vent systems. As it stands, however, there are few well-documented geographic patterns in the biodiversity of vent species. Furthermore, too little is known about their life histories to justify very detailed models. In this chapter we have analyzed two simple metacommunity models to try to determine whether the hypotheses that have been advanced to describe the few patterns that have been documented are consonant with mathematical reasoning.

As it turns out, the metapopulation models we studied support one shared intuition of vent researchers about the effects of vent dynamics: all else being equal, diversity is elevated where suitable vent habitat is plentiful. As pointed out earlier, researchers have also propounded a variety of causes for the observed

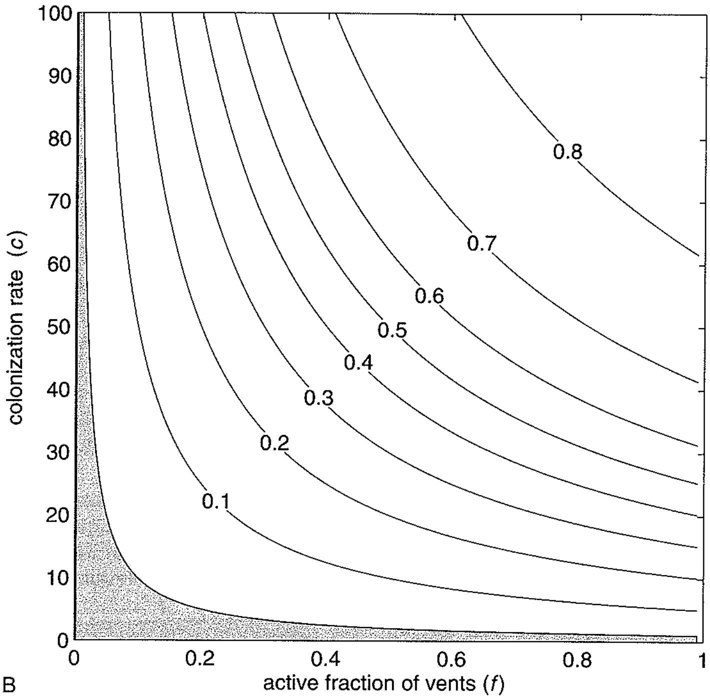

FIGURE 9-10B. Local diversity as measured relative to the null model. In the grey areas, all species are extinct.

differences in faunal diversity between vent systems, and between vent habitats and other benthic habitats. Diversity differences have been attributed to, for example, differences in the extent of barriers to dispersal (and hence to colonization), differences in the spacing of suitable habitat patches, and differences in rates of habitat disturbance. When translated into a mathematical model like the ones we have described in this chapter, these differences would appear as differences in the parameters C, R, and D. An important result of our analysis is that it is the ratios C/D and R/D that are the relevant quantities for determining diversity statistics, rather than the rates C, R, and D themselves. As a result, what may at first appear to be alternative explanations for diversity patterns may in fact be different aspects of the same explanation.

Our analysis also raises the possibility that species interactions, particularly obligate facilitative interactions, become important when habitat is sparse and difficult to colonize. These interactions may result in diversity patterns that cannot be predicted using only considerations of vent dynamics or species' colonization abilities. We are only beginning to understand how vent species

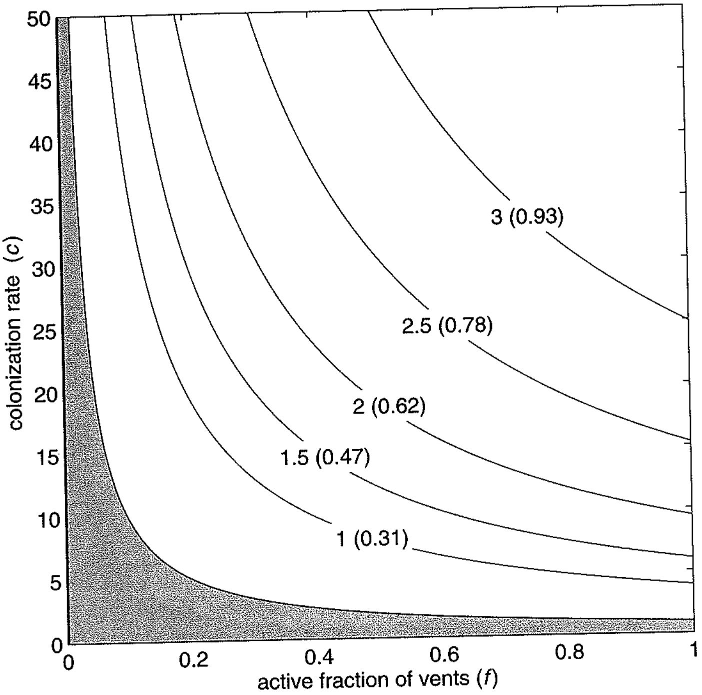

FIGURE 9-11. Contours of regional diversity, as measured by H, when the species pool contains $m = 25$ species and community dynamics are governed by the facilitation model (15). Numbers in parentheses give the ratio of H to its value under the null model. In the grey areas, all species are extinct.

actually interact. Further experiments to establish the nature of these interactions are crucial if we ever hope to determine whether these interactions actually do influence biodiversity.

There is also a need for more theoretical work. In her review of the ecology of Mid-Atlantic Ridge vents, Van Dover (1995) called for a "rigorous theoretical analysis of the consequences of [vent dynamics] . . . for comparative community structure." (277) We join her in that call, and hope that the simple null and facilitation models we have described here will provide a useful framework for further analysis. Along these lines, there are a number of elaborations of our models that we think should be addressed in future research. Among the most interesting to us are the incorporation of exclusion processes other than vent closure (e.g., competition or predation), an allowance for nonobligate facilitation, and the possibility of spatiotemporal correlation in vent dynamics. This last elaboration will require development of spatially explicit versions of our models.

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FIGURE 9-2. Hydrothermal vent fauna on East Pacific Rise: (A) thicket of vestimentiferan tubeworms providing habitat for bythograeid crabs and fish; (B) field of suspension-feeding serpulid polychaetes; (C) vent mussels (with yellowish periostracum covering shell) and galatheid crabs.