

Deep-Sea Hydrothermal Vent Communities

Lauren S. Mullineaux

Communities at deep-sea hydrothermal vents form oases in the desert-like deep sea. They are unique in ways that extend our understanding of the diversity of life, and they challenge ecological paradigms. Deep-sea hydrothermal vents were first described in 1977 in the eastern Pacific. Early biological studies focused on demonstrating that microbial chemoautotrophy supported the food web and on investigating the striking adaptations of species to extreme conditions. Vent communities are tightly constrained by the physical and chemical environment, which sets limits on species' distributions and abundances. Invertebrate species interactions determine community composition within these limits through processes that parallel those observed in coastal habitats, but sometimes in ways that challenge established ecological theory. Volcanic and tectonic activity can be frequent at vents, changing or destroying habitat and eliminating communities. This disturbance makes larval exchange critical for maintenance of populations and diversity in the regional metacommunity. Species distributions are influenced by barriers to larval (and genetic) exchange, but the stochasticity introduced by disturbance makes it difficult to predict the species composition at any particular vent without knowing its history. Exploration of remote areas of mid-ocean ridge and arc/back-arc systems continues to reveal new species, novel physiological and biochemical adaptations, and intriguing communities. We are far from a full understanding of these systems, but as supplies of metals dwindle and prices increase, seafloor mining at hydrothermal vents has become a reality. Predicting the effect of human disturbance on vent communities is a challenge that requires careful application of our present field-based and theoretical understanding of their metacommunity dynamics.

Deep-sea faunas differ in many ways from those in coastal habitats; perhaps none are more unique and fascinating than the chemosynthetically based communities at deep-sea hydrothermal vents. Vent communities were first described in 1979 from the deep eastern Pacific near the Galápagos archipelago, where scientists reported on gutless, mouthless tubeworms up to 3 m in length, along with a variety of other organisms, in association with chemical-rich seafloor hot springs (Corliss et al. 1979). These organisms formed oases of biological production in the mostly food-poor deep sea (**Figure 17.1**). The initial puzzle was how this production was sustained in a system where food was thought to be supplied solely by the remains of surface plankton that escaped consumption as they dropped to the seafloor. Examination of the tubeworms (Cavanaugh et al. 1981), and later of vent clams, mussels, and polychaetes (reviewed in Van Dover 2000), revealed symbiotic bacteria that use reduced chemicals to produce organic carbon. These bacteria and other free-living microbes in the vent system support an ecosystem fueled by chemosynthesis, rather than by the photosynthetic processes that provide the basis for virtually all other marine and terrestrial communities.

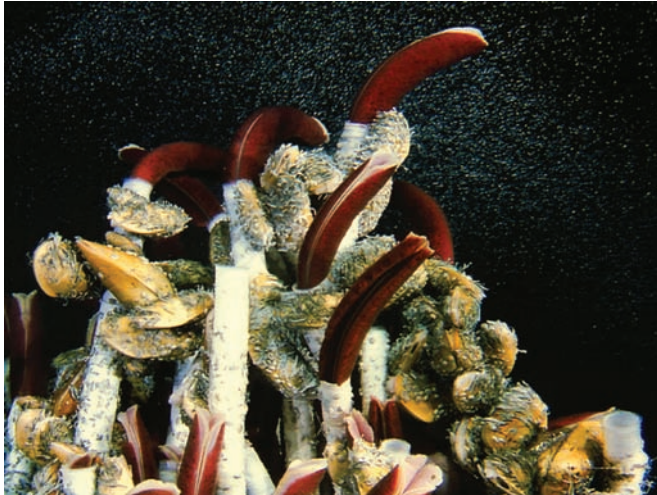


Figure 17.1 Giant siboglinid tubeworms (*Riftia pachyptila*) provide habitat for numerous other species at deep-sea hydrothermal vents in the eastern Pacific. Shown here are the mussel *Bathymodiolus thermophilus*, limpets (bumps on the tubes), and planktonic amphipods swarming in the vent fluids. (Courtesy of the WHOI Alvin group.)

Subsequent expeditions, starting in the eastern Pacific and expanding globally, provided more detail on the unique species, astonishing adaptations, and varied functions in vent communities. Vent communities occur in all ocean basins; over 200 deep-sea vent fields have been visited along mid-ocean spreading centers and subduction zones (**Figure 17.2**), and more are discovered each month. Many vent species have specific adaptations to the high temperatures and caustic chemicals in the vent fluids (Childress and Fisher 1992). Alvinellid polychaetes can survive exposure to fluid temperatures of 60°C and above (reviewed in Fisher et al. 2007). Others, such as the gutless tubeworm *Riftia pachyptila*, have unusually high growth rates (Lutz et al. 1994). The microbes use a variety of different biochemical pathways to fix carbon and respire (Sievert and Vetriani 2012), and they have been investigated as a way of understanding the earliest life on earth (Schulte 2007). The physiological capabilities of vent species have been well reviewed (Childress and Fisher 1992; Fisher et al. 1994), and further information on the first 20 years of ecological research at vents is available in textbook (Van Dover 2000) and handbook (Desbruyères et al. 2006) form. Information on groups not covered herein can be found in recent articles on microbes (Sievert and Vetriani 2012), tiny invertebrates (meiobenthos: Gollner et al. 2010) and eukaryotic protists (Edgcomb et al. 2002).

Deep-sea vents are a seafloor expression of underlying volcanic and tectonic activity, which makes the habitat inherently dynamic. On fast-spreading ridges, vents have been observed to arise and shut down on time scales of decades. The populations living at individual vents must

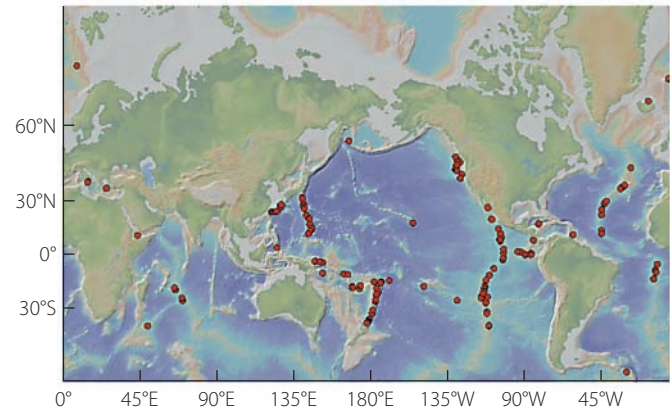


Figure 17.2 Map of known deep (>200 m) hydrothermal vents, which are distributed along mid-ocean ridges, subduction zones, and other volcanically active areas on the seafloor. (Courtesy of Stace Beaulieu.)

be able to disperse in order to persist regionally in the long term. Vent species typically disperse in planktonic larval form, although some highly mobile crustacean species (crabs, shrimps) may migrate between neighboring vents as adults (**Figure 17.3**). Barriers to dispersal, in the form of continents, seafloor topography, or ocean currents, can prevent exchange of organisms between distinct biogeographic provinces and can limit gene flow regionally (Vrijenhoek 2010). When vents were first discovered, ecologists wondered how larvae could disperse far enough and often enough to sustain populations (Lutz et al. 1984). Questions about how vent populations persist in this transient patchy environment continue to be a focus of research.

In the past decade, scientists' understanding of vent communities has become more nuanced, illuminating the uniqueness of these systems and illustrating how they broaden our understanding of basic ecological concepts. After a brief description of vent communities and their inhabitants, this chapter focuses on three emerging themes in vent ecology. The first is the classic question of species interactions along environmental gradients, but the chapter shows that vent communities do not necessarily follow theory developed in coastal systems. The second theme is the influence of disturbance and the critical role of larval dispersal in species distributions, regional diversity, and community resilience. The discussion focuses on the issues of whether larvae travel far enough to disperse between vents and whether vent populations are open or closed. An open population is one that exchanges larvae with other, geographically separated populations in the region; a closed population is one that reseeds only itself (Cowen and Sponaugle 2009). The third theme is metacommunity dynamics. The chapter takes a metapopulation approach to vent communities in order to synthesize studies of succession, diversity, genetic exchange, and bioge-

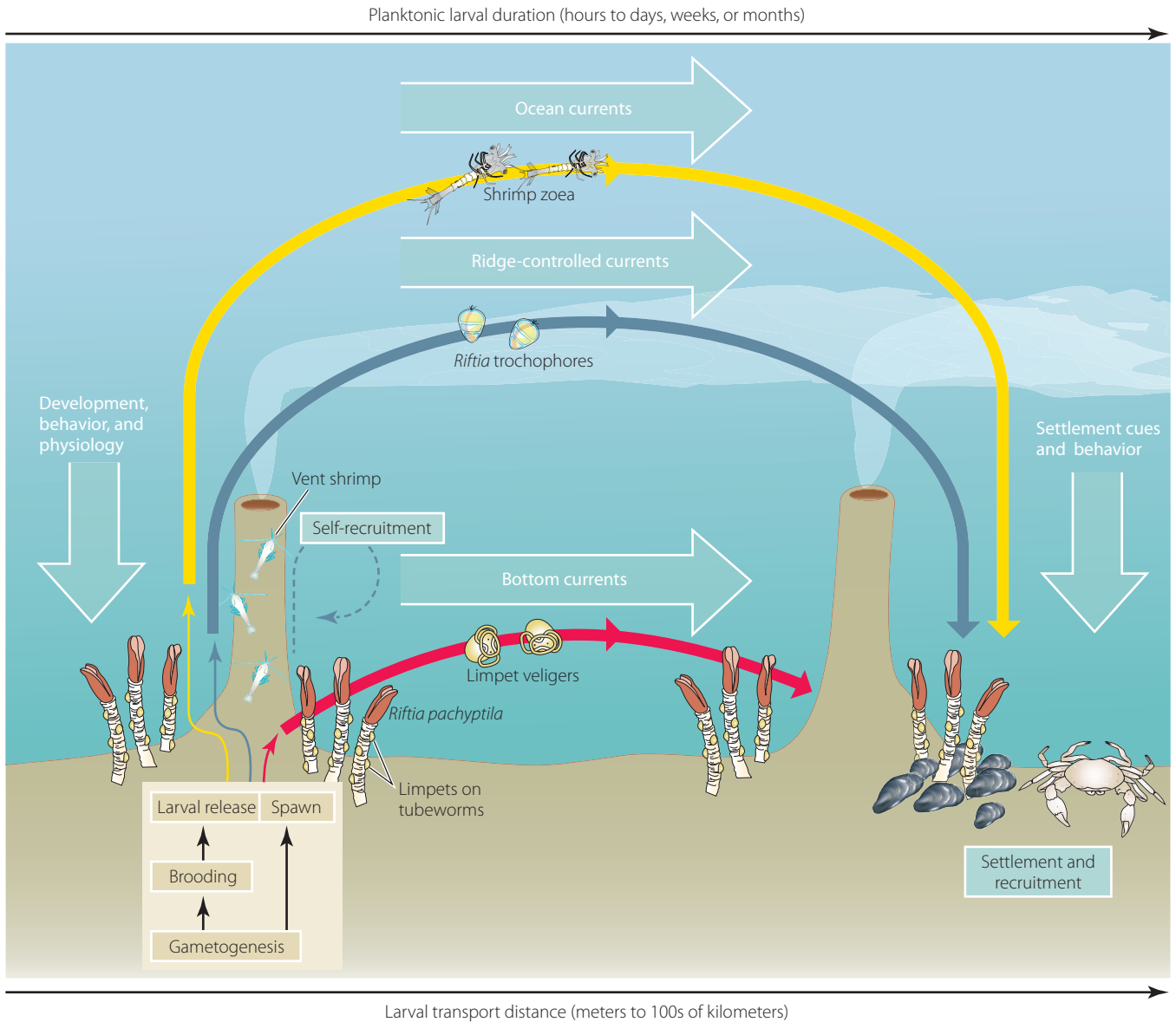


Figure 17.3 Idealized diagram of larval connectivity at hydrothermal vents, showing processes influencing larval production, dispersal, settlement, and recruitment. Expected dispersal pathways of vent species with different life histories are shown with different-colored arrows. Representative species from different vent provinces, with different life histories, are displayed. Larval behavior is important during dispersal, when larvae are transported in currents, and at settlement, when they may respond to cues. (After Adams et al. 2012.)

ography and apply them to issues of human disturbance of vent communities. It should be noted that hydrothermal vents on rocky substrate are not the only habitats that host chemosynthetic communities in the deep ocean. Hydrocarbon seeps, sediment-covered hydrothermal vents, and large masses of organic matter, such as whale carcasses, also support fascinating patchy communities, but they are outside the scope of this study.

Vent Habitat and Inhabitants

Species living at vents are influenced strongly by the physical and chemical environment, which is both extreme and highly variable. Hydrothermal fluids reach temperatures exceeding 400°C (high pressure keeps them from boiling), and possibly as high as 485°C (Connelly et al. 2012). They contain high concentrations of reduced chemicals that are leached as the fluids move upward through heated rock or magma below the seafloor. Source fluids (those undiluted by seawater) typically are anoxic, acidic (pH 2–4), and enriched in hydrogen sulfide (H₂S) and methane (CH₄), which provide energy for microbial production. They also are enriched in iron, zinc, copper, and numerous other transition metals (von Damm 1995) that are toxic to organisms. These conditions are too extreme to support life.

When the fluids exit the seafloor, however, they mix with overlying seawater, creating gradients in temperature and chemical properties where organisms flourish.

Concentrated vent fluids typically enter the benthic habitat as dark, particulate-laden jets, called black smokers, forming mineral chimneys from the precipitation of dissolved compounds as they contact cold, oxygenated seawater. Much of the fluid has already mixed with ambient seawater before it comes into contact with vent animals, either in subsurface chambers, while flowing through porous surface rocks, or while passing through the mineral chimney lattice. These diffuse flows are where most of the animals live. Turbulent mixing generates gradients in temperature from 40°C to less than 2°C, oxygen concentrations from undetectable to ambient, sulfide concentrations up to several hundred micromolar, and pH from 4 to 8 (Johnson et al. 1988; Le Bris et al. 2006). These gradients may extend over tens of meters, but directly at the mixing interface, very steep gradients occur on scales of millimeters to centimeters. In this highly dynamic mixing environment, an organism at a fixed spot can experience the full range of the gradient over a period of seconds as turbulent eddies pass or as tidal currents shift.

An important consequence of mixing between vent and ambient fluids is the coexistence of chemical compounds that usually are not found together. Oxygen and hydrogen sulfide, for instance, coexist only in a transient state before they react with each other and transform. This disequilibrium provides the energy for microbial production, termed chemosynthesis, or more properly, *chemolithoautotrophy* (*chemo* = energy source from chemicals, not light; *litho* = inorganic electron donor; *auto* = inorganic carbon source). Chemolithoautotrophs generate energy by using redox reactions that occur at the interface between oxidized seawater (containing oxygen and other oxidizing compounds) and hydrothermal vent fluids (containing reducing compounds such as hydrogen sulfide and methane).

Primary production by chemolithoautotrophs supports animal communities through grazing, suspension feeding on free-living microbes, or symbioses. The large, habitat-forming foundation species at vents tend to be symbiont hosts: alvinellid polychaetes, siboglinid tubeworms, and clams in the eastern Pacific, large snails in the western Pacific, shrimps in the mid-Atlantic, yeti crabs and peltopsiroid gastropods in the Southern Ocean (Rogers et al. 2012), and amphipods in the Arctic (Pedersen et al. 2010). Bathymodiolid mussels are prominent and widespread, forming extensive beds in Pacific, Atlantic, and Indian Ocean vents, but have not yet been observed in the Southern or Arctic Oceans. Other prominent components of vents are small (~1 cm) but numerous limpets that graze free-living microbes from the substratum, although symbionts are known for at least one limpet species (Bates 2007). Polychaetes function as generalist scavengers and specialist consumers (Govenar 2012). Predators include

crabs (which are often also scavengers), octopods, and fishes. The discovery of vents in the Southern Ocean has added sea stars to this list (Marsh et al. 2012). Some of the highly mobile fishes and octopods are tightly associated with vents; others are visitors from elsewhere in the deep sea.

In order to get food, vent animals must tolerate exposure to vent fluids. Individuals of some vent species grow at astonishingly high temperatures. The polychaetes living directly on black smoker chimneys are routinely exposed to temperatures greater than 40°C and occasionally may experience 80°C and above (Fisher et al. 2007). The palm worm *Paralvinella sulfincola*, for instance, tolerates temperatures up to 55°C (Girguis and Lee 2006). Vent animals thrive in habitats with very low oxygen concentrations, high heavy metal concentrations, and levels of H₂S that are 100 times the concentrations toxic to most fauna (Childress and Fisher 1992); interestingly, these are the very habitats where the highest levels of microbial production occur. The large foundation species that dominate vent biomass are typically symbioses of an invertebrate and microbes. The photogenic siboglinid (formerly vestimentiferan) tubeworm *Riftia pachyptila* (see Figure 17.1) has no mouth or gut, but instead carries endosymbiotic bacteria in a specialized organ called the trophosome. Other large species, such as clams, mussels, and snails, often host symbionts in their gills. Microbes can withstand conditions even more extreme than those tolerated by vent animals. The highest temperature recorded for growth of a vent microbial isolate in culture is 121°C (Kashefi and Lovely 2003), but it is likely that microbes can survive exposure to superheated fluids as high as 250°C (Takai et al. 2004).

Given the strong gradients in vent fluid flux, and the associated gradients in temperature, toxic chemicals, and food, it is no surprise that vent species distributions tend to correspond to the environmental gradients. In well-studied systems on the East Pacific Rise, communities display a striking zonation along the vent fluid flux gradient (**Figure 17.4**; Hessler et al. 1985; Luther et al. 2001; Micheli et al. 2002). Palm worms (alvinellid polychaetes) and associated species inhabit areas of high-temperature flux (>27°C), siboglinid tubeworms occur in vigorous flux (up to 32°C), mussels and clams inhabit regions with moderate flux (up to 12°C), and various suspension feeders, including barnacles and serpulid polychaetes, inhabit weak flux (<4°C). Analogous patterns are seen on the Juan de Fuca Ridge, where an alvinellid species dominates the high-flux habitats, while an assemblage of the tubeworm *Ridgeia piscesae*, a second alvinellid species, and gastropods inhabit lower-flux environments (Sarrazin et al. 1999). In the Lau Basin (western Pacific), the dominant symbiont-bearing species are distributed along a vent flux gradient, sometimes in a bull's-eye pattern, with white hairy snails (*Alviniconcha* spp.) in the highest-

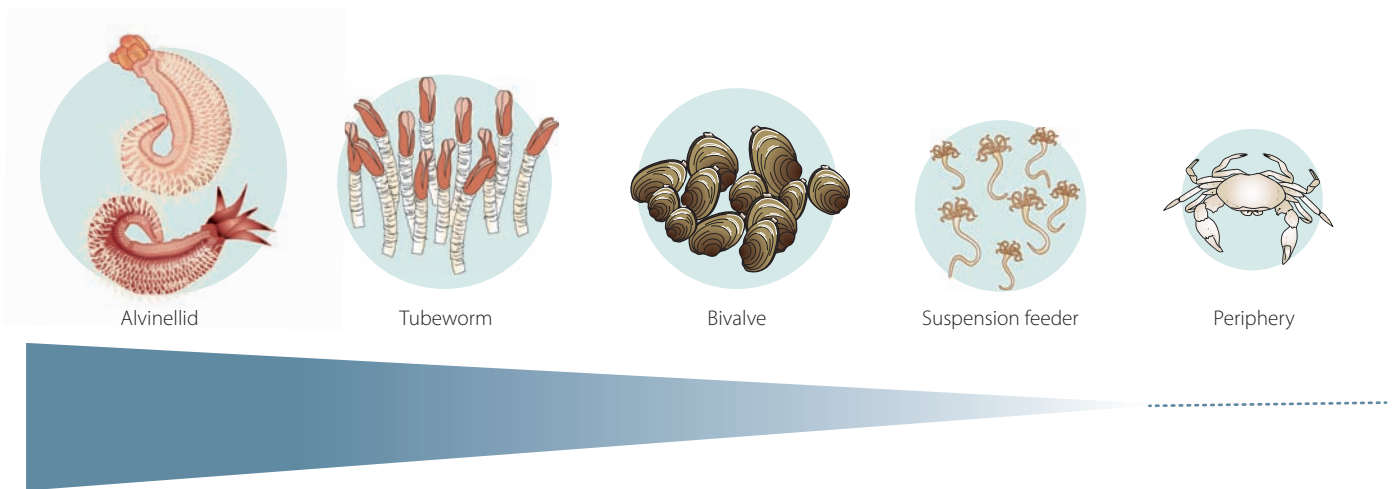


Figure 17.4 Zonation of fauna along a gradient of vent fluid flux in communities from the East Pacific Rise. Zones are named for visually dominant fauna: alvinellids in the superheated chimney environment, tubeworms in fluids up to 32°C, bivalves in fluids at less than

12°C, suspension feeders in fluids at less than 4°C. At the periphery, temperatures are indistinguishable from those of ambient deep sea; this area is populated by vent-associated mobile scavengers and foraminifera. (After Mullineaux et al. 2003; Desbruyères et al. 2006.)

temperature fluxes, the black snail *Ifremeria nautilei* in moderate temperatures, and mussels in the lower temperatures (Podowski et al. 2010). In some unusual western Pacific vents where smoker chimneys are distinctly reddish brown, these dominant molluscs are missing, replaced by low densities of nonsymbiotic shrimps, crabs, polynoid polychaetes, and limpets, possibly in response to high metal concentrations (Mottl et al. 2011). On the Mid-Atlantic Ridge, the high-temperature regions are populated by bresiliid shrimp, followed along the flux gradient by mussels, and then nonsymbiotic grazers and suspension feeders (Cuvelier et al. 2009). In vent fields on the East Scotia Rise (Southern Ocean), assemblages closest to vent sources are dominated by the yeti crab, followed by pelto-spiroid gastropods, stalked barnacles, and a carnivorous anemone (Marsh et al. 2012) at greater distances. Peripheral fauna include predatory and scavenger taxa such as sea stars, pycnogonids, and octopods.

New Insights on Species Interactions

The close association between vent environmental conditions and species distributions led early vent investigators to conclude that physical and chemical conditions control species occurrences along vent fluid gradients, but more recent studies have revealed an important role of biological interactions. Temperature, hydrogen sulfide, pH, and oxygen tend to covary in vent fluids (pH and oxygen inversely with the others), making their individual effects difficult to discern. Careful studies with precisely placed chemical probes (Sarrazin et al. 1999; Luther et al. 2001; Matabos et al. 2008; Nees et al. 2009; Podowski et al. 2010; Mullineaux et al. 2012) have demonstrated a close correspondence between faunal distributions and various environmental

conditions, including temperature, pH, oxygen, hydrogen sulfide, and other toxic compounds. These extreme environmental conditions no doubt limit species distributions by determining how close species can live to vigorous, high-temperature vent effluent. On the other end of the gradient, the lack of sufficient hydrogen sulfide or other reduced chemicals to support chemosynthesis limits the ability of species, particularly those with endosymbionts, to acquire food (Fisher et al. 1994). Within these boundaries, however, the realized abundances and distributions of species are set by biological interactions, as animals eat one another, vie for space and food, and provide habitat or other benefits to one another.

Over the past decade, vent researchers have discovered that predation, competition, and facilitation have strong influences on the distribution of vent species along environmental gradients. Much of this transition in concepts has come about through the use of manipulative field experimentation. The change in perspective parallels the transition of concepts in rocky intertidal communities, which were thought to be controlled by physical processes (wave exposure, desiccation, etc.) until experiments in the 1960s and 1970s (Connell 1961; Dayton 1971; Paine 1977) revealed the strong influence of biological interactions.

What are the roles of species interactions in a physically extreme habitat?

One approach to looking at interactions experimentally is to compare colonization on experimental surfaces whose exposure intervals overlap in duration. When results from a continuous interval are compared with those from two sequential intervals, the differences can reveal competition (abundance or diversity in continuous interval is less than in sequential intervals), facilitation (the reverse), or

tolerance (no difference between continuous and sequential intervals). Such experiments near 9°50' N on the East Pacific Rise showed that competition was prominent in assemblages inhabiting the more populated end of the vent fluid gradient, whereas facilitation occurred in the sparser communities in cooler fluids (Mullineaux et al. 2003). In the high-temperature range of diffuse flows (termed the high-temperature zone), grazing species, dominated by the limpet *Lepetodrilus elevatus*, competed with subsequent colonists, both other grazers and sessile tubicolous species, presumably by disrupting their settlement through bulldozing. This limpet has also been observed dominating communities at vents near 13° N, even on sulfide edifices, where it appears to exclude other gastropod species that are considered better adapted to the "alvinellid" habitat (Matabos et al. 2008). In the lower-temperature zone, tubicolous polychaetes and other suspension feeders appeared to facilitate one another, perhaps through gregarious settlement cues or gardening of microbes. Exclusion of grazers from these experiments showed that predation reduced the populations of the most numerous limpet, *L. elevatus*, in the high-temperature zone, preventing it from excluding congeners and other gastropod grazers (Micheli et al. 2002). Examination of predatory fish guts (Sancho et al. 2005) confirmed that the vent fish *Thermarces cerebrus* specialized on the dominant limpet *L. elevatus*. Reciprocal transplant experiments showed that some vent species can survive and influence subsequent colonization in zones with higher, but not lower, vent fluid flux than where they typically reside (Mullineaux et al. 2009). This asymmetry is consistent with the general observation that biological interactions, in concert with physiological tolerances or nutritional requirements, determine how close to the superheated hydrothermal fluids a particular species will live.

Although many vent species (e.g., tube-forming polychaetes, barnacles) are attached permanently to the substrate as adults, others, such as gastropods, bivalves, crabs, and shrimps, are mobile. In situ experiments have demonstrated that when gastropod species with different habitat distributions are exposed to a temperature gradient, they each move to a temperature range that is at the high end of their natural distribution (Bates et al. 2005). Differences between habitat occupation and temperature preferences by these three species suggest that competition for space, both within and between species, may cause individuals to be displaced into lower-quality (food-limited) habitats toward the periphery of the vents.

Colonization experiments on the Juan de Fuca Ridge (Kelly et al. 2007) also show evidence of biological interactions, but with a surprising difference in the behavior of gastropods. Positive interactions were apparent for two gastropod species, including *Lepetodrilus fucensis*, a member of the globally distributed lepetodrilid group, possibly due to gregarious settlement. Two polychaete species, on

the other hand, showed negative interactions, presumably due to competition for space or food.

General ecological theory, derived from rocky intertidal systems in strong vertical gradients of wave energy and desiccation, suggests that we should expect physical factors to set the upper (extreme-end) limits of distributions and biological interactions to set the lower (non-extreme) ones. That does not appear to be the case at vents, where biological interactions are most prevalent near the extreme boundary, in conditions where high temperatures and toxic chemistry would exclude most non-vent species (although, clearly, the temperature of superheated vent fluids sets the ultimate limit of life at the extreme end of the gradient). At the non-extreme end, food availability appears to be the most likely limiting factor. A striking difference between vents and most other marine habitats is that food availability covaries with physicochemical stress, instead of varying inversely with it. This difference results in situations in which classic paradigms drawn from intertidal systems do not apply.

Larval Dispersal and Exchange in Patchy, Disturbed Habitat

Larval exchange, or ecological connectivity, between vent fields has been a focus of research on vents since their first discovery. It is an important process on both ecological and evolutionary time scales. Over generations, larval exchange allows the population dynamics at one site to influence others in the region. On longer time scales, larval dispersal is the vector of genetic exchange, and it is the mechanism by which barriers, topographic and oceanographic, limit species ranges.

The geologic setting of vents provides the structural and dynamic framework for larval exchange. Vents are typically distributed along the mid-ocean ridges generated by seafloor spreading and the volcanic arcs and back-arcs created by subduction (see Figure 17.2), although they also occur on ridge flanks and hot-spot volcanoes. On ridges, vents tend to occur in fields, with multiple discrete vent effluent sites connected hydraulically below the seafloor. The fields are distributed along ridge segments, which are offset from one another by transform faults. The ridges and ridge segments are roughly linear features, separated by distances from a few kilometers to 1000 km, making dispersal between neighboring vent fields a one-dimensional process. In general, vents occur more densely on fast-spreading ridges, like the East Pacific Rise, than on slow-spreading ones, such as the Mid-Atlantic Ridge, due to magma being closer to the seafloor (Baker and German 2004). The proximity and supply of lava also influence ridge topography. Fast-spreading ridges tend to have shallow, narrow axial valleys, while slow-spreading ridges typically have wide (10 km) and deep (1 km) axial valleys (Fornari and Embley 1995). Mean near-bottom currents are typically aligned along seafloor topography

(Thomson et al. 2009; Lavelle 2012), so transport along ridges is much more likely than exchange between them across large basins.

Although ecological studies have focused on vents on mid-ocean ridges, half of the world's known active vent fields are found in arc and back-arc settings. Dispersal between vents at volcanic arcs becomes a complex issue, as the vents are on separate volcanoes, spread over a wide range of depths. Dispersal from arc to back-arc sites would seem possible, as some are within a few tens of kilometers of one another.

Deep-sea vents are a seafloor expression of underlying volcanic and tectonic activity, so they are inherently dynamic. Larval exchange, therefore, is a function not only of transport, but also of the extinction and rebirth of vents, sometimes in new locations. On ridges that are spreading relatively quickly, like the East Pacific Rise and the Juan de Fuca Ridge, and in active subduction zones (western Pacific), disturbance is common, and its effects on vent communities can be studied directly. Repeat visits to vents on the fast-spreading southern East Pacific Rise suggest that they may be transient over time scales of years (Vrijenhoek 2010), although no eruptions have been observed there directly. In contrast, on slow-spreading ridges such as the Mid-Atlantic Ridge, vents may stay active for hundreds of years (Fornari and Embley 1995) and accrete sulfide deposits in the same location for thousands of years (Petersen et al. 2000).

The populations living at individual vents must be able to disperse in order to persist regionally in the long term. Questions about how they do this continue to be a focus of vigorous research.

Can larvae travel far enough to disperse between vents?

The ability of vent larvae to disperse between vents depends in large part on their larval life span, or planktonic larval duration. Inferences about the feeding and life span of larvae can be made from their morphology. Larvae of some vent species resemble the adults (**Figure 17.5**); others look completely different. Some molluscs, such as archaeogastropod limpets, set a single larval shell and appear to rely solely on lipid stores from the egg to fuel their larval stage (they are lecithotrophic). Others, such as predatory whelks, add to the larval shell as the larvae develop, presumably as they feed in the plankton (Tyler and Young 1999). Although feeding in the plankton (planktotrophy) might seem like an advantage for vent species, the developmental mode of most vent species appears to be phylogenetically constrained to ancestral traits, rather than evolved to facilitate long-distance dispersal (Bouchet and Warén 1994) or other attributes specific to vents. Crabs and shrimps develop through multiple feeding stages and have complex larval life cycles. Bythograeid crabs appear to move off vent sites to spawn, and their larvae return when they reach the ultimate megalopae stage (Epifanio



Figure 17.5 Larvae of vent species, clockwise from upper right: scallop *Bathypecten vulcani*, snail *Phymorhynchus* sp., crab *Bythograea thermydron*, polychaete *Glycera* sp., limpet *Ctenopelta porifera*, limpet *Gorgoleptis emarginatus*. (After Mills et al. 2009; Courtesy of Susan Mills and Stace Beaulieu.)

et al. 1999). Some caridean shrimps rise up into the photic zone to feed on phytoplankton (Dixon et al. 1998; Herring and Dixon 1998). The planktonic duration of feeding larvae is expected to be longer than that of those using lipid stores, but durations of nonfeeding larvae can be quite long in the cold waters of the deep sea (Marsh et al. 2001) due to reduced metabolic rates.

Recent breakthroughs in the ability to culture deep-sea species have led to quantitative information about planktonic larval duration, and to new insights into behavior, in several vent species. Larvae of the giant tubeworm *Riftia pachyptila* have been reared through early developmental stages in high-pressure systems in the laboratory (Marsh et al. 2001); calculations based on their lipid stores and metabolic rates show they can survive for 38 days or longer without feeding. Thermal tolerances of larvae of the palm worm *Alvinella pompejana*, cultured at deep-sea pressure, indicate that they must move away from the high-temperature habitat of the adults in order to develop (Pradillon et al. 2001). Similarly, larvae of the tubeworm *Riftia pachyptila* do not develop normally unless they escape the warm vent fluids of the adult habitat and reach temperatures below 7°C (Brooke and Young 2009).

Larvae of deep-sea species (those living below 1500 m) are unable to survive at surface pressure (e.g., Marsh et al. 2001; Pradillon et al. 2001), with the intriguing excep-

tion of the late-stage megalopa of *Bythograea thermydron*, a vent crab. These larvae are routinely kept alive on board ship and have been maintained in the laboratory at surface pressure for months to assess their swimming behaviors (Epifanio et al. 1999). The megalopae swim at speeds up to 10 cm per second, but only at high temperatures (25°C); swim speed was inversely proportional to temperature. Because swimming speeds are low at ambient deep-sea temperatures, swimming behavior in this species is probably useful for locating suitable habitat within a vent field, but not for swimming between them. No deep-sea vent species has been cultured through its full larval development. Several species living at vents shallower than about 1000 m, however, can be kept successfully in laboratory culture at ambient surface pressure. An aquarium system developed specifically for rearing organisms from chemosynthetic communities has been used to spawn larvae of a variety of species, including crabs, shrimps, squat lobsters, and clams (Miyake et al. 2010). In this system, larvae of some species (e.g., barnacles: Watanabe et al. 2004) have been reared through multiple stages for many months, but none have been cultured through metamorphosis.

Larvae of invertebrates swim slowly, most at speeds of a few millimeters per second (Mileikovsky 1973; Chia et al. 1984), so their horizontal dispersal is determined largely by transport in currents. On mid-ocean ridges, the topography of the ridge itself influences the deep flows. Currents often are intensified near ridges (Thomson et al. 1990; Cannon and Pashinski 1997; Thurnherr et al. 2011), reaching velocities an order of magnitude higher than typical deep abyssal flows. This intensification is attributed to interactions of the topography with local and regional hydrography, reviewed recently for a broad audience (Lavelle 2012) as well as for the more oceanographically adventurous (Thurnherr et al. 2011; Lavelle et al. 2012). Mean flows tend to be oriented along the axis of the ridge, although strong cross-ridge flows occur on tidal time scales. Larval transport calculations, based on a larval life span of 38 days for the tubeworm *Riftia pachyptila*, show that larvae can potentially disperse 100 km or more in a nonfeeding stage (Marsh et al. 2001). This distance is sufficient to allow larvae to move between vent fields on a ridge segment, and potentially between neighboring segments, but only if the currents remain generally along-axis in direction as they cross the transform fault. Such long-distance dispersal, however, may be a rare occurrence, as discussed in the next section.

The observation that low metabolism leads to long planktonic duration, even in a nonfeeding larva, helps explain the seemingly paradoxical early observation that most vent larvae do not feed in the plankton. Some species appear capable of dispersing between vent fields along a ridge segment, but it is unclear whether they can traverse the distance between segments or across an ocean basin. The discovery of chemosynthetic communities on whale carcasses raised the possibility of vent species using the

whales as stepping-stones (Smith et al. 1989). The majority of species colonizing whale falls are not, however, deep-sea hard-substrate vent fauna, and the most recent taxonomic counts show only 11 of roughly 500 vent species also occurring on whale falls (Smith and Baco 2003). Hydrocarbon seeps have also been suggested as connectors between vent communities (Vrijenhoek 2010), but again, only a few species overlap. Metacommunities on whale falls and seeps are fascinating in their own right, but probably do not play a significant role in vent larval connectivity.

Are vent populations open or closed?

The transient nature of vents means that populations at individual sites must be open, at least occasionally, if the species is to persist regionally. Several lines of evidence, however, point to a scenario in which most larvae supplied to a particular vent field have been spawned nearby. Larval abundances tend to be higher near vents than away from them (Mullineaux et al. 2005); although not on small (hundreds of meters) spatial scales (Metaxas 2004; Mullineaux et al. 2013). The locations of nearby source populations and the directions of currents influence larval supply to a vent (Adams and Mullineaux 2008) such that supply is greater when a source population is up-current within tens of kilometers.

On mid-ocean ridges, where most vents are located on ridge crests, often in axial valleys, the valley walls may steer bottom currents and impede transport off the ridge (Mullineaux et al. 2005). Where the walls are sufficiently tall (e.g., 100 m, as at the Juan de Fuca Ridge), and venting sufficiently vigorous, the buoyant vent plumes drive circulation along the ridge axis channeled by the walls (Thomson et al. 2003), enhancing the exchange of larvae along the ridge axis. Topographic influences of axial valley walls are also apparent at the Mid-Atlantic Ridge, where the valley is 1 to 1.5 km deep, and where the currents in the valley are hydraulically controlled by the exit of fluids through a small number of sills (Thurnherr et al. 2008). Models suggest that in shallow valleys, bottom currents, rather than buoyant plumes, drive horizontal transport (Kim et al. 1994; Bailly-Bechet et al. 2008). Even in such shallow valleys, however, cross-axis velocities are reduced relative to those just a few meters above the valley wall (Thurnherr et al. 2011). Hence larvae drifting passively in the valley are less likely to get transported off the axis than those above it, and more likely to be carried along the axis, where they come into contact with neighboring vents.

At mid-ocean ridges, as in other marine habitats, the vertical position of larvae in the water column has an important influence on dispersal when current velocities vary with height above the seafloor. Larvae move vertically by being negatively or positively buoyant, by active swimming, or via vertical flows such as the buoyant plumes formed by hydrothermal fluids. Entrainment in the plume transports large volumes of water, and the larvae they contain, from

vent communities (Jackson et al. 2010), although fewer larvae may be entrained in plumes when bottom currents are strong (Kim and Mullineaux 1998). Typically, larvae are most abundant near the bottom, decreasing in abundance with height above the bottom (Kim et al. 1994; Mullineaux et al. 2005). Those staying very near the bottom, in the axial valley, or in flows otherwise impeded by topography are expected to be transported only short distances in slow flows and not to move off the ridge axis. Elevated abundances of larvae, however, have been observed in the neutrally buoyant plume a few hundred meters above the ridge crest on the Juan de Fuca Ridge (Mullineaux and France 1995). On that ridge, flows near the seafloor typically are slower, and move in different directions, than those above (Cannon and Pashinski 1997). The slower flows are thought to be influenced by bottom topography, and transport in the faster flows was considered a “larval highway” between vents (Mullineaux et al. 1991).

Recent coupled studies of larval ecology and physical oceanography on the East Pacific Rise have led to a more nuanced understanding of interactions between larvae and flow during dispersal. A prominent feature of the flow there is a pair of jets aligned along the ridge flanks, flowing in opposite directions at velocities up to 10 cm per second (**Figure 17.6**). These jets have been predicted by models (Lavelle et al. 2010; Lavelle 2012) and observed in

the field (Thurnherr et al. 2011). Similar flow features have been observed elsewhere (Cannon and Pashinski 1997), and it is likely that ridge-associated jets are a key influence on larval transport at fast-spreading mid-ocean ridges.

A biophysical model showed that these jets have a strong, but nonintuitive, influence on dispersal (McGillucuddy et al. 2010). Recruitment of larvae back onto the ridge crest after a 30-day planktonic larval duration is approximately three times more likely for larvae that rise up to the level of the neutrally buoyant plume (~200 m above bottom) than for those with no vertical displacement that are whisked away in the jets. The decrease in dispersal distance with height above the bottom reflects the less vigorous currents aloft. Thus, contrary to expectations, it appears that larvae rising a few hundred meters above the ridge crest are more likely to recolonize natal habitat than those staying near the seafloor. Even though the number of larvae at this height is small, some species may use this vertical transport as an effective mechanism for repopulating natal or neighboring vents.

Such models are informative, but field observations provide further surprises. A tracer experiment in which a 1200 m long streak of sulfur hexafluoride (a conservative tracer that is detectable at very low concentrations) was released along the axial trough at 9°30' N revealed that a small percentage of tracer had reached vents at 9°50' N af-

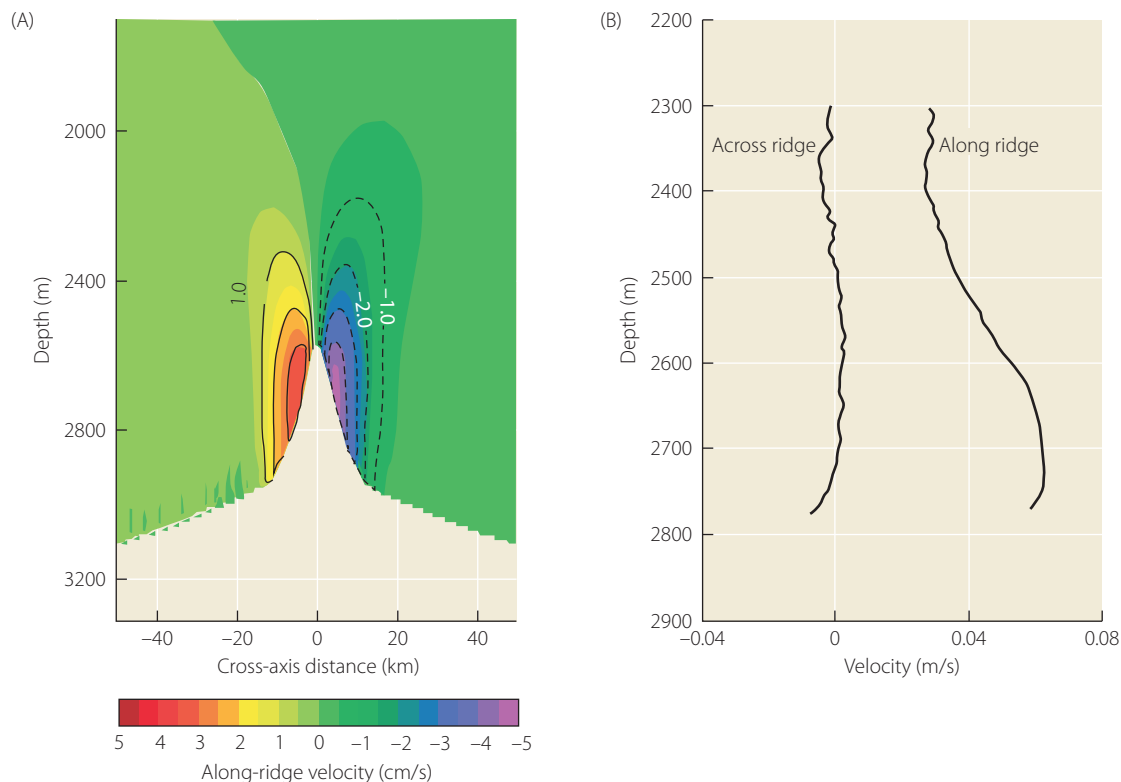


Figure 17.6 (A) Currents along the ridge axis (ridge jets), showing year-long average of meridional (north–south) flow velocity, with positive (northward) values to the west of the ridge. Over short periods, the jet can be wider and velocities greater than these averages.

Values are from Lavelle model of flows near 10° N on the East Pacific Rise. (B) Observed currents across and along the ridge, averaged over a 1-month period from the western ridge flank, about 10 km off axis. (After Lavelle et al. 2012.)

ter approximately 40 days, illustrating that there certainly are pathways for larvae between the two sites on the time scale of larval viability (Jackson et al. 2010). Subsequently, the bulk of the tracer (about 60%) was found to the west of the 9°50' N site and to the south of a group of off-axis seamounts. A numerical reenactment of the experiment (Lavelle et al. 2010) indicates that initially the tracer moved west, where it entered the northward-flowing flank jet and within a week reached the seamounts. Subsequent reversal of regional flow moved the tracer eastward along the north side of the seamounts back toward the ridge. Perhaps the most surprising aspect of this study was the return of tracer to the ridge after it had moved a substantial distance (over 50 km) off axis. The implications for larval transport are that off-axis transport does not necessarily mean loss from the regional vent fields, and that there are multiple dispersal pathways between vents along a ridge segment.

Field observations indicate that the vertical swimming behaviors of vent larvae influence their dispersal. Many species, particularly gastropods, appear to actively remain near the bottom by sinking or swimming downward. On the East Pacific Rise, vertical distributions of larvae of several common gastropod species were significantly skewed toward the seafloor, compared with expected distributions of passive larvae in a biophysical model (Mullineaux et al. 2013). Measurements of swimming behavior of vent larvae at deep-sea pressure are difficult to obtain, but early-stage larvae of vent crustacean and polychaete species have been observed to swim upward in unpressurized tanks (Miyake et al. 2010). Newly hatched larvae of vent gastropods, however, tend to move toward the bottom (Metaxas 2011) when kept in an unpressurized culture vessel, although one species of *Shinkailepas* did initially go up before moving downward. If gastropod larvae display this same downward behavior at deep-sea pressure, they might remain near the seafloor, sheltered from currents by topography, and avoid transport away from their natal habitat. In contrast, species with upward-swimming larvae may rise off the bottom and become exposed to energetic flows associated with the ridge. Thus larval behavior has the potential to create differences between species in ecological and genetic connectivity.

Although geographically limited larval exchange within and between neighboring vent fields may be the norm, a rare long-distance dispersal event can have striking effects on vent communities. Such an event occurred after an eruption in 2006 (Tolstoy et al. 2006) paved over vents near 9°50' N on the East Pacific Rise. The two pioneer gastropod species dominating the new vents were *Lepetodrilus tevnianus*, which had not been common there before, and *Ctenopelta porifera*, which had never been observed before on the ridge segment (Mullineaux et al. 2010). The nearest (and only) known population of *C. porifera* is near 13° N (Desbruyères et al. 2006), more than 300 km away. The appearance of a pioneer species after a disturbance is not uncommon, but usually it is a species found commonly in

disturbed habitat. It is not clear how these larvae survived the voyage, which is longer than most estimates of dispersal potential in deep-sea currents. A possible explanation is transport in mesoscale eddies, which have been proposed as a fast track between ridge segments (Adams and Flierl 2010). In the Pacific, off the coast of Central America, wind-driven eddies extend all the way to the seafloor, transporting vent larvae off the East Pacific Rise (Adams et al. 2011). Most of the time, transport in such eddies would result in loss of the larvae to inhospitable habitat, but occasionally the larvae may be carried long-distance to vent fields hundreds of kilometers away, even across transform faults.

An open question remains: How do larvae find a suitable vent after a long voyage? This question is a tough one to answer because it requires tracking individual larvae in the field or conducting experiments on late-stage larvae in pressurized laboratory conditions. Larvae of many coastal species have sophisticated sensory systems, and it is quite likely that larvae of vent species are able to detect and respond to a vent-related settlement cue. The cue might be chemical (H₂S), physical (temperature), hydrodynamic (turbulence), acoustic (noise from black smoker vents), or biological (biofilms or suspended microbes), and it would be most effective if it were unique to vents and could be detected from outside a vent field. No such cues are known for vent species, but culturing methods are improving, and it may simply be a matter of time before a cue is discovered.

Colonization and Succession

Deep-sea hydrothermal vents experience major eruptive disturbances that eradicate the resident faunal communities and alter the physical and chemical environment. On fast-spreading ridges these eruptions occur frequently, years to decades apart. Faunal successional changes after an eruptive disturbance, and associated fluid environmental conditions, are well described from the East Pacific Rise (Shank et al. 1998) and the Juan de Fuca Ridge (Tunnicliffe et al. 1997; Marcus et al. 2009). Faunal changes after an eruption often correlate with changes in vent fluid flux and composition. Vent fluid sulfide concentrations tend to decrease in the months to years following an eruption, and vent fluid flux decreases, leading to lower microbial production and reduced toxicity levels. As the habitat changes, certain species may be excluded (e.g., because H₂S levels are too low to support their symbionts), while other species (e.g., whose sulfide tolerances are low) may invade. Biological interactions, however, play an important role in these changes.

As foundation species (tubeworms, mussels, etc.) get established, they provide essential habitat for myriad smaller grazing and scavenging species (Govenar et al. 2005). Initial colonists facilitate settlement of subsequent species through modification of the substrate, as shown in colonization experiments in which the tubeworm *Tevnia*

jerichonana preceded the larger tubeworm *Riftia pachyptila* even when the colonization surfaces were placed in established clumps of *R. pachyptila* (Mullineaux et al. 2000). This facilitation may be a direct effect, through a surface-bound chemical settlement cue, or an indirect effect, by influencing microbial biofilms (Sievert and Vetriani 2012). The nature of the interactions may be species specific and density-dependent. Pioneer gastropods at Juan de Fuca vents appear to facilitate subsequent settlers (Kelly et al. 2007), whereas those on the East Pacific Rise exclude others once they reach high densities (Mullineaux et al. 2003).

If succession at vents follows a deterministic trajectory set by species' responses to decreasing temperature and sulfide levels, then responses of the community to future disturbances should be predictable based on environmental conditions. If, however, succession is influenced by the availability of particular pioneer colonists at the time of the disturbance, then initial conditions need to be considered. The occurrence of alternative successional trajectories has been documented for terrestrial and, more recently, coastal marine systems (McCook 1994; Sousa 2001). In these systems, initial conditions, such as the availability of propagules and the presence of predators and competitors at the time of disturbance, are especially important. These conditions may "canalize" succession and lead to quite different outcomes (Berlow 1997). Determining whether this process occurs at deep-sea vents is important in order to predict how vent communities will respond to future natural and human disturbance. On the East Pacific Rise, monitoring after a 1991 eruption showed that the siboglinid tubeworm *Tevnia jerichonana* is a pioneer colonist, followed in succession by the larger, faster-growing tubeworm *Riftia pachyptila* and then the mussel *Bathymodiolus thermophilus* (Shank et al. 1998).

The catastrophic seafloor eruption near 9°50' N on the East Pacific Rise in 2006 provided an opportunity to test whether succession is deterministic or may progress to alternative stable states depending on initial colonization conditions. Initial colonists included the pioneer tubeworm *Tevnia jerichonana*, as they did after the prior eruption, but there were also some surprises, most notably the appearance of the gastropods *Lepetodrilus tevnianus* and *Ctenopelta porifera* (Mullineaux et al. 2010), neither of which had been prominent after the 1991 eruption. Two years after the 2006 eruption, *C. porifera* had declined in relative abundance, possibly in response to decreasing H₂S levels, but *L. tevnianus* continued to dominate (Mullineaux et al. 2012). Four years after the eruption, visual observations showed that the tubeworm *Riftia pachyptila* had become established and that juvenile mussels were appearing. When compared with that after the 1991 eruption, the succession of foundation species (tubeworms and mussels) appeared to be delayed, even though habitat chemistry became similar to the pre-eruption state more quickly. The question of whether *L. tevnianus* has persisted, excluding the suite of related limpets that dominated prior to the

eruption and leading to an alternative community state, remains to be answered on future expeditions.

Recovery of vent communities after eruptions on the Juan de Fuca Ridge is rapid, with species composition developing to resemble the pre-eruption state within 2 to 3 years. Two separate eruptions have been examined, one on the CoAxial Segment in 1993 (Tunnicliffe et al. 1997) and a second on Axial Seamount in 1998 (Marcus et al. 2009). After the eruption at the CoAxial Segment, the first recruits were the familiar symbiont-bearing siboglinid tubeworm *Ridgeia piscesae* and alvinellid polychaetes. In 2 years, roughly one-third of the regional species pool had become established, although some of the individual vents had gone extinct. Community development after the 1998 eruption on Axial Seamount was qualitatively similar, although the tubeworm *R. piscesae* took up to 3 years to establish aggregations; before that, communities were dominated by grazing polychaetes. In 3 years, most of the pre-eruption species had reestablished. These successional trajectories corresponded to both biological events (establishment of tubeworm clusters) and abiotic factors (H₂S and temperature, which varied with vent fluid flux), resulting in two different mature communities, one dominated by limpets at lower flux and the other by alvinellids at higher flux. As on the East Pacific Rise, the rapid postdisturbance recolonization of the Juan de Fuca vents occurred in locations that were within tens of kilometers of active, undisturbed, vent communities.

Little is known about succession of species on high-temperature smokers because the proximity to 300°C fluids makes this habitat very difficult to work in. Studies have not been initiated after eruptions, but manipulative experiments have monitored the recolonization of palm worms (genus *Alvinella*) and associated species and the development of the tube and mineral habitat after disturbance. When mature communities are nearby (i.e., on the same sulfide edifice), pioneer colonists tend to be juvenile or nonreproductive alvinellids (Pradillon et al. 2005). The associated community recovers quickly (within 5 months), mostly by local immigration rather than larval settlement (Pradillon et al. 2009). The alvinellid habitat on sulfide chimneys is dynamic on time scales even shorter than those of the surrounding diffuse-flow habitat because the polychaetes' tubes and mineral aggregations change local fluid conditions over weeks to months, requiring the foundation species *Alvinella* and associated fauna to move along the chimney.

Metacommunity Dynamics

Many questions about the distribution, abundance, and dynamics of vent communities require looking at a broader perspective than individual vents or populations. The transient nature of vents, and the connection of their patchy communities by larval dispersal, makes them well suited to a metapopulation approach. A metapopulation

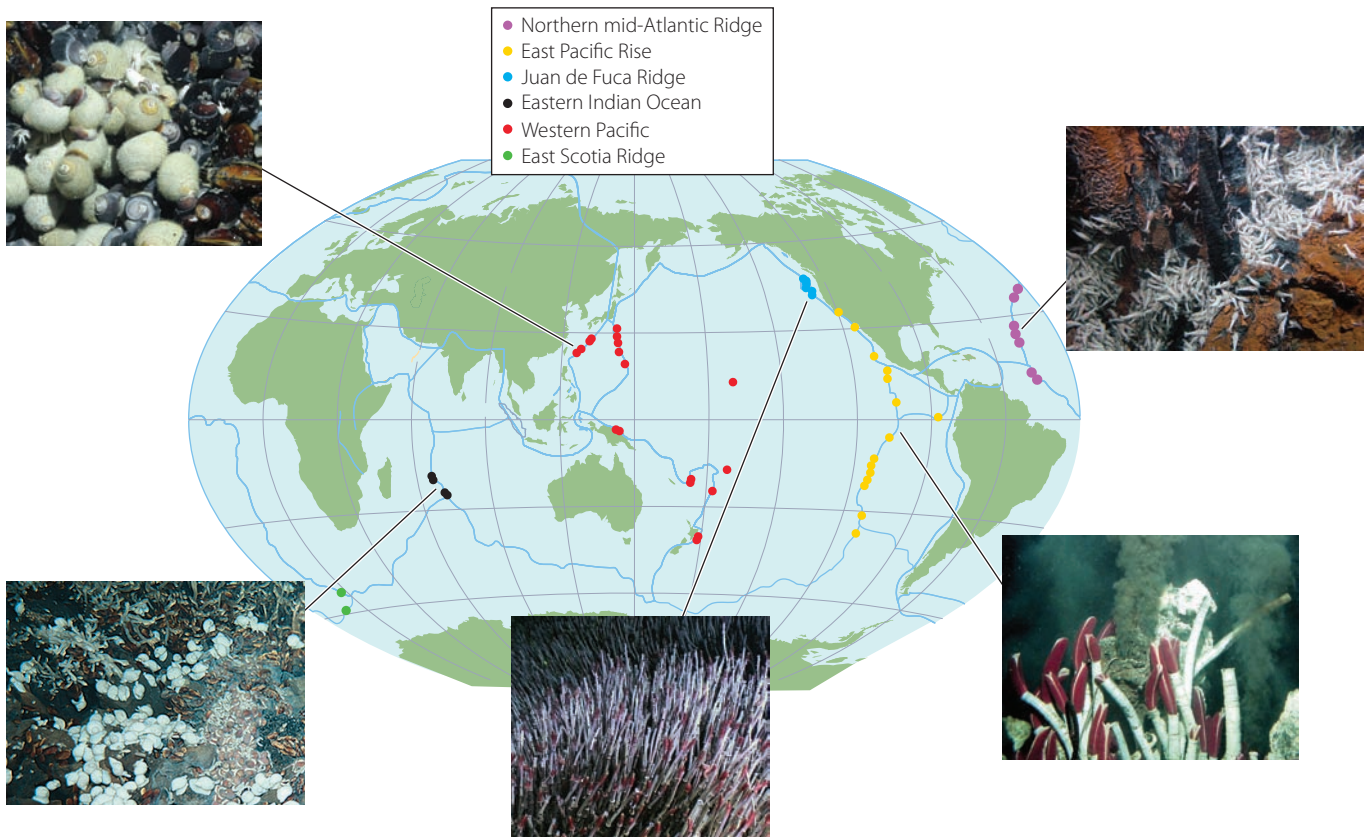
is a group of geographically separated populations, each of which is subject to extinction and connected to the others by migration (larval dispersal in the case of vents), so that the dynamics in one population can potentially affect dynamics in others (Hanski 1999). A metacommunity is an expansion of the metapopulation concept to include multiple species and their interactions (Leibold et al. 2004). Metapopulation theory is used on ecological time scales to address questions of population dynamics and persistence, and on evolutionary time scales to explore questions of genetic exchange and evolution. The kinds of questions asked include how the balance between larval retention and dispersal shapes patterns of species diversity and distributions (Holyoak et al. 2005), and how barriers to exchange influence genetic differentiation and species ranges (Vrijenhoek 2010).

In order to understand vent species diversity and distributions in a metapopulation context, it helps to have a sense of global species distributions and potential barriers to dispersal. Vent faunas form discrete biogeographic provinces (Figure 17.7), each of which has a characteristic fauna (Van Dover et al. 2002; Bachraty et al. 2009; Moalic et al. 2012; Rogers et al. 2012). The main provinces host a large “mas-cot” species or group of species that define them visually. The East Pacific Rise hosts the giant tubeworm *Riftia pachyptila* and two related tubeworm species. To the north, the Juan de Fuca Ridge supports a smaller tubeworm, *Ridgeia*

piscisae. Western Pacific vents are characterized by large, symbiont-bearing snails (Desbruyères et al. 2006). Interestingly, many western Pacific sites support dense populations of flatfishes, which are not found elsewhere at vents (Tunnicliffe et al. 2010). Vent chimneys on the northern Mid-Atlantic Ridge are covered by several different species of bresiliid shrimp, except in a few sites where mussels dominate (Desbruyères et al. 2000). Indian Ocean vents host shrimps and snails (Hashimoto et al. 2001; Van Dover et al. 2001; Nakamura et al. 2012) and align in some analyses with vents in the southwestern Pacific.

As new vent sites are discovered, biogeographic analyses are revealing more structure (for example, separating the southern from northern East Pacific Rise; Bachraty et

Figure 17.7 Biogeographic provinces of vent fauna, showing distinct regions and their visually defining species (clockwise from upper right): northern Mid-Atlantic Ridge, with shrimp (*Rimicaris exoculata*); East Pacific Rise, with giant tubeworms (*Riftia pachyptila*); Juan de Fuca Ridge, in the northeastern Pacific, with bushy tubeworms (*Ridgeia piscisae*); eastern Indian Ocean, with a mix of gastropods, stalked barnacles, and shrimps; western Pacific, with large snails (*Alviniconcha* spp.) and *Ifremeria nautili*. Newly discovered communities on East Scotia Ridge (see Figure 17.8) may represent an additional distinct province. (Mid-Atlantic Ridge photo © Missao Sehama; East Pacific Rise photo courtesy of Woods Hole Oceanographic Institution; Juan de Fuca Ridge photo courtesy of Neptune Canada; Indian Ocean photo courtesy of K. Nakamura; western Pacific photo courtesy of Chuck Fisher.)



al. 2009) and adding new provinces in previously unexplored regions. A recently discovered vent community in the Southern Ocean (East Scotia Ridge) is quite different from those at any other sites and appears to represent a new province (Rogers et al. 2012). It is dominated by a new species of crab (the yeti crab), stalked barnacles, and anemones (Figure 17.8), and it is missing such vent regulars such as siboglinid tubeworms, bathymodiolid mussels, and alvinocarid shrimps. Vents have been discovered on the southern Mid-Atlantic Ridge (German et al. 2008); a description of the fauna has not yet been published, but visual assessments suggest that it is similar to communities at North Atlantic vents (Perez et al. 2012). The discovery of active vents in the Arctic Ocean (Pedersen et al. 2010) revealed communities dominated by siboglinid tubeworms; these vents may also represent a new province.

Formal metapopulation theory was first used at vents to resolve an apparent paradox: the lack of genetic differentiation along the northern East Pacific Rise in populations of the palm worm *Alvinella pompejana*, which is inferred to have limited dispersal potential (Jollivet et al. 1999). In this model, vents expire and reopen at different locations, causing individual populations to experience extinction and population genetic structure to become homogeneous despite limited dispersal. Extinction and recolonization are well known to affect genetic divergence among populations and are likely to have a strong effect at vents (Shea

et al. 2008). General metapopulation models that include extinction and recolonization (Slatkin 1977; Whitlock and McCauley 1990) show that the character of dispersal, interacting with habitat dynamics, determines the extent of genetic divergence between populations. If individuals recolonizing newly reopened sites disperse from multiple other sites in the metapopulation, rather than from a single site, genetic divergence will be decreased. This process may explain the low population divergence that has been observed over broad geographic regions in many vent taxa (Vrijenhoek 2010). Interestingly, estimates of genetic similarity in metapopulations along ridges are often inconsistent with expectations from inferred planktonic larval duration. This discrepancy may be due to oversimplification in larval dispersal estimates, which typically do not include temperature-dependent metabolic rates or vertical swimming behaviors. Similar disconnects between larval duration and realized connectivity are found in non-vent and shallow marine habitats (e.g., Weersing and Toonen 2009). It appears that an ability to feed in the plankton does not necessarily extend dispersal distance.

Interpretations of genetic patterns in a metapopulation context have revealed distinct barriers to dispersal that apply across multiple species and others that impede only selected species. These investigations offer insight into the life history characteristics that result in widespread exchange and the processes that result in biogeographic boundaries. The eastern Pacific offers a good example because it has been sampled extensively for numerous vent species. Within this region, the Galápagos Rift is separated from the rest of the East Pacific Rise by the Galápagos triple junction (see Figure 17.7). Most species investigated, including the tubeworm *Riftia pachyptila*, show distinct

Figure 17.8 Vent fauna from the Southern Ocean. (A) Dense aggregation of anomuran yeti crabs (a newly discovered species of genus *Kiwa*) and stalked barnacles (cf. *Vulcanolepas*) crowding a vent on the East Scotia Ridge at a depth of 2400 m. (B) Close-up of yeti crab *Kiwa hirsuta* from the Pacific–Antarctic Ridge. (A courtesy of Alex Rogers; B © IFREMER/A. Fifis.)



genetic differences between Galápagos and East Pacific Rise populations (France et al. 1992; Hurtado et al. 2004), with the exception of the mussel *Bathymodiolus thermophilus* (Craddock et al. 1995). The Galápagos triple junction also separates the northern from the southern East Pacific Rise, creating a presumed barrier to dispersal. The palm worm *Alvinella pompejana*, the tubeworm *Tevnia jerichonana*, and limpets *Lepetodrilus ovalis* and *Eulepetopsis vitrea* are genetically different across this barrier (Won et al. 2003; Hurtado et al. 2004; Plouviez et al. 2009), whereas *R. pachyptila* and *B. thermophilus* are not. The Easter Microplate creates a distinct break in the southern East Pacific Rise, separating genetically distinct populations of *Bathymodiolus* mussels, which may be distinct species (Won et al. 2003), and sister species of bythograeid crabs (Guinot et al. 2002; Guinot and Hurtado 2003) as well as the tubeworms *R. pachyptila* and *T. jerichonana*. Populations of the polychaetes *Alvinella pompejana* and *Branchiopolynoe symmytilida* are not genetically differentiated across this boundary. Interestingly, the mussels and crabs with planktotrophic larvae are isolated across this boundary, whereas polychaetes with lecithotrophic larvae are not. These results indicate that larval connectivity across potential barriers is species-specific and is not necessarily well predicted by inferred larval dispersal potential.

Metacommunity studies are useful for interpreting diversity differences among the vent communities of the various provinces. Within a province, vent communities differ in species occurrence, but tend to have a subset of the province's species pool, without geographic clines (Juniper et al. 1990; Van Dover and Hessler 1990). Thus diversity can be compared at the province level. Diversity is high on the East Pacific Rise, reduced in the northeastern Pacific, and low in the Atlantic (Bachraty et al. 2009). Juniper and Tunnicliffe (1997) suggest that a combination of regional age, disturbance rate, habitat heterogeneity, and habitat area is responsible for these patterns. The Atlantic basin is relatively young compared with the Pacific, and the vents are more stable and widely spaced. These characteristics would all contribute to low diversity relative to the Pacific, where the regional species pool has long been in existence, the vents are disturbed more frequently (mitigating competitive exclusion), and the vent habitat is larger (more vents). Other researchers have found similar patterns in the diversity of invertebrates associated with mussel beds (Turnipseed et al. 2003) and with tubeworm clumps (Tsurumi and Tunnicliffe 2003), but have offered different explanations. Turnipseed and colleagues (2003) 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. Tsurumi (2003) suggests that diversity at northeastern Pacific vents is limited by frequent disturbance and habitat transience.

Neubert and colleagues (2006) evaluated these alternatives by varying disturbance rate, habitat area, and colonization rate in a metapopulation model. The model results

showed, as expected, that diversity is elevated where suitable vent habitat is plentiful. A notable result was that diversity depended on the relative rates of colonization and disturbance, or of vent recovery and disturbance, rather than factors such as vent spacing or colonization rate alone. Thus, when vent ecologists explain reduced diversity as a consequence of frequent disturbance or of wide vent spacing, they may be invoking the same process, a reduction in the ratio of colonization to disturbance. It is important to note that facilitative interactions between species became important in the model when habitat was sparse and colonization rates low, indicating that diversity patterns cannot be predicted using only vent dynamics or species' colonization abilities.

As true metacommunities, hydrothermal vent systems can be investigated within any of the main theoretical frameworks used to understand processes underlying observed patterns in species distributions and diversity (patch dynamics, species sorting, source–sink dynamics, and neutral models: Leibold et al. 2004). Empirical data are available to inform colonization–competitive ability trade-offs, including successional patterns (patch dynamics), species responses to environmental heterogeneity (species sorting), and interactions between dispersal and habitat quality (source–sink dynamics). The strong links between species occurrence and vent environmental conditions argue against using a neutral model, in which species are assigned equal competitive and dispersal capabilities, although such an approach might provide a valuable null model for comparison. These approaches are particularly valuable for predicting the responses of vent communities to perturbations, either natural or anthropogenic.

Conservation of Vent Communities

Vent communities are subject to natural eruptive and tectonic disturbance; this disturbance can occur on time scales comparable to species' generation times in regions of high tectonic and volcanic activity. Since their discovery by humans, vents have been subject to other disturbances, including harvesting and manipulation by researchers, and even visits by tourists. Early on, researchers recognized the need to self-regulate, especially in international waters, in order to avoid loss of biodiversity and disruption of one another's projects, so an international effort was made to institute a code of conduct (Mullineaux et al. 1998) and to regulate activities through protected areas (Devey et al. 2007). More recently, mining of deep-sea vent deposits has become economically feasible, raising questions about its effect on vent community diversity and persistence. The platitude that vent species are well adapted to disturbance has been used to counter the concerns of vent researchers and conservation ecologists, but a critical examination is warranted.

Industry has taken a renewed interest in mining hydrothermal vents in order to extract precious metals (copper, zinc, silver, gold), and rare-earth elements needed for

high-tech manufacturing (Hoagland et al. 2010). In 1997 Papua New Guinea was the first nation to grant exploration licenses for mining vents at depths greater than 1000 m in the Manus Basin; other nations have followed suit elsewhere (the International Seabed Authority maintains an up-to-date list of exploration contracts and licenses). Scientists have responded to this development with a call for objective evaluation of impacts through such organizations as the International Seabed Authority (www.isa.org.jm), the U.N. Convention on Biological Diversity and its offshoot, the Global Ocean Biodiversity Initiative (www.gobi.org), and the International Network for Scientific Investigation of Deep-Sea Ecosystems (INDEEP, www.indeep-project.org, the deep-sea successor to the Census of Marine Life program). They highlight the potential for mining operations to irreversibly destroy habitat, reduce benthic primary productivity, and decrease regional biodiversity (Van Dover 2011), as well as eliminate species whose ecological roles, biochemical capabilities, and potential for ecosystem services might never be uncovered. Efforts are also under way through various nongovernmental organizations and individual institutions to critically evaluate the effects of mining of deep-sea vents and to establish criteria for establishing marine protected areas. In all of these responses, scientists emphasize the critical need for surveying vent communities before they are mined and for understanding two main aspects of the at-risk communities: (1) their resilience to disturbance and (2) their connectivity to other locations. These attributes are interrelated and inform efforts to design management strategies, particularly the locations and sizes of marine protected areas (MPAs). The kinds of data that inform these efforts are precisely the ones presented in this chapter on species' environmental tolerances, larval dispersal capabilities, genetic connectivity, source-sink dynamics, and resilience and diversity in metapopulations.

Although the quick recolonization times observed after eruptions at vents in the eastern Pacific indicate that those particular vent communities are resilient, those observations may not be generalizable to vent metapopulations elsewhere. These rapid recoveries were made on fast-spreading ridges where vents are spaced relatively closely (~50 km or less), and source populations for colonists were nearby. The type of pioneer species that is effective in this region through rapid local dispersal may not be effective where vents are more widely separated. Most of the regions presently targeted for mining are on ridges whose spreading rate is medium, slow, or very slow, where vents are widely separated and can be very long lived. Biological exploration in these regions has been limited, so little is known about the distribution of species, and nothing is known about larval connectivity or the resilience of communities. Furthermore, mining activities have important disturbance consequences that differ from those of volcanic eruptions. Both mining and volcanic eruptions change the vent benthic substrate and topography, but mining is

likely to leave behind sediment and rubble (Steiner 2009), whereas natural eruptions form pillow lava mounds and sheet flows (Chadwick et al. 2001). This substrate change may alter how quickly (if ever) mined vents can be recolonized by vent species, and will ultimately determine whether mining activities result in changes in regional vent community persistence and diversity.

Unlike natural eruptive disturbance, mining can be regulated, and monitoring can be designed with full knowledge of the extent of the planned disruption. In metapopulations with identified source populations and known larval connectivity, the choice of where mining occurs can minimize negative impacts. Strategies developed for sustainable use of marine resources in coastal environments, including creation of marine reserves (Sanchirico and Wilen 2001; Treml et al. 2008), can be adapted to inform efforts at deep-sea vents. Marine protected areas have been designated at some vents within nations' economic zones or extended continental shelves, including the Endeavour vents on Juan de Fuca Ridge, the Lucky Strike, Menez Gwen, and Rainbow vents on the Mid-Atlantic Ridge, vents in the Mariana arc (western Pacific) as part of the Marianas Trench Marine National Monument, and the Guaymas Basin vents in the eastern Pacific. Designation of protected areas in the high seas, where most vents are located, is a complicated process because of the need for international cooperation, but the designation in 2010 of the Charlie-Gibbs Marine Protected Area in international waters of the northern Atlantic shows it can be done.

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