Chapter 13
Shaping Vent and Seep Communities: Habitat Provision and Modification by Foundation Species

Breea Govenar

Contents

13.1 Introduction

Ecologists strive to identify mechanisms that determine the structure or composition of biological communities. Until the past decade, the role of positive species interactions in regulating community structure had been relatively overlooked, compared to negative species interactions, such as competition and predation. While mutualism and commensalism have long been recognized as critically important in pairwise species interactions, the impact of facilitation and habitat provision or modification on community dynamics and species diversity has received increased attention only more recently (Bertness and Callaway 1994; Hacker and Gaines 1997).

B. Govenar (✉)
Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA
e-mail: bgovenar@whoi.edu

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Part of the reason for the oversight is that positive species interactions are more prevalent in habitats with harsh environmental conditions (Bertness et al. 1999; Crain and Bertness 2006) and are more often detectable at regional scales (Bertness and Leonard 1997; van de Koppel et al. 2006). Communities may be structured by facilitation cascades, where foundation species create the habitat or modify the environment that facilitates the settlement of other species, which subsequently interact with one another (Bruno 2000; Altieri et al 2007). Foundation species are large or spatially dominant organisms that create or provide habitats, colonized by other species (Bruno and Bertness 2001; for review).

The definition of foundation species overlaps with the definitions of ecosystem engineers and keystone species. However, each classification is unique and has a different emphasis for explaining the cause of variation in biological communities. Ecosystem engineers are broadly defined as organisms that modify, maintain, create, or destroy habitats (Jones et al. 1994; Wright and Jones 2004, 2006). The primary role of ecosystem engineers is the alteration of the availability of resources, such as water, light, and nutrients. The effect of ecosystem engineers on the associated biological community may be either large or small, and either positive or negative (Jones et al. 1997; Wright et al. 2002; Wright and Jones 2004). Beavers are common examples that modify the local environment by building dams that change the hydrology of the watershed at regional scales and create additional habitats that are colonized by different species, resulting in greater local and regional species diversity than rivers and streams without beaver dams (Wright et al. 2002). In contrast, keystone species can have either positive or negative effects on other species, but are expressly defined by the large impact that they have on the associated community, relative to their abundance (Paine 1974; Mills et al. 1993; Power et al. 1996; Hacker and Gaines 1997). The most common examples are keystone predators (e.g. Paine 1969) that exert top-down control on biological community structure by removing a competitively dominant species and thus allow for greater species coexistence. Accordingly, the term “keystone” may be better used as a modifier of a particular biological interaction that emphasizes the relative importance or the strength of the interaction, whereas ecosystem engineers are characterized by the action rather than their impact of the interactions. The distinction between foundation species and either ecosystem engineers or keystone species is that habitat provision or modification by the presence of foundation species is a positive biological interaction that has a large impact on the structure of the associated community. Thus, it could be said that foundation species are keystone physical ecosystem engineers. Foundation species tend to be sessile, large, spatially dominant, or have complex physical structures, and their interaction with other species is defined by their presence, rather than their actions. Although foundation species may compete for resources with other species, serve as a source of food for some consumers, or consume potential colonists (Crooks 1998; Bustamante et al. 1995), these trophic interactions are not directly related to the role of habitat provision or modification.

At deep-sea hydrothermal vents and hydrocarbon seeps, the density and diversity of macrofaunal invertebrates are greater in association with foundation species than the adjacent seafloor. At vents and seeps, the most widely studied foundation species are siboglinid tubeworms and bathymodiolin mussels. Other tube-dwelling polychaetes, including frenulate tubeworms and alvinellid tube-dwelling worms, and bivalves such as vesicomyid clams, are also important foundation species in some vent and seep habitats. Many, if not most, foundation species at vents and seeps (e.g. tubeworms, mussels, and clams) have bacterial symbionts that use chemical rather than solar energy to fix inorganic carbon and are the primary source of nutrition to the animal. Consequently, tubeworms, mussels, and clams live in microhabitats where they are exposed to the mixing of reduced chemicals in either vent or seep fluids and relatively well-oxygenated seawater. Reduced chemicals, particularly hydrogen sulfide, can be lethal to animals by reducing the availability of oxygen or by inhibiting cellular respiration. Thus, some species may benefit from the positive biological interactions with foundation species but are also exposed to physiologically stressful conditions, where the source of energy to the ecosystem can also be lethal to the resident species.

This chapter examines the ecological role of habitat provision and modification by foundation species in deep-sea hydrothermal vent and hydrocarbon seep communities and how foundation species contribute to the maintenance of species diversity at local and regional scales in chemosynthesis-based ecosystems. At the local scale, the presence of foundation species coincides with access to high local productivity habitats; the physical structure of foundation species provides additional area available for colonization, increases environmental heterogeneity, or serves as a refuge from predation; and the physiological function of the foundation species can modify the physical or chemical environment by altering fluid flow or composition. At the regional scale, aggregations of foundation species form biogenic "islands" that connect biological communities through migration or dispersal. Changes to immigration and extinction rates are caused by the size and distance of islands (McArthur and Wilson 1967; Hanski 1998), the rate of production of colonists within an island, and the rate by which the resources to the foundation species are generated or depleted (Wright et al. 2004). Therefore, ecological factors that affect the distribution and abundance of foundation species can have either direct or indirect effects on associated species and impact the community structure at local and regional scales.

The first section of this chapter presents an overview of the habitats of vent and seep communities in the context of the underlying geology and fluid chemistry. The second section introduces how evolutionary and large-scale ecological processes affect global patterns of biogeography and regional species diversity at vents and seeps. The next section outlines local-scale patterns in the distribution of foundation species and the associated epifaunal communities. The fourth section discusses a range of the primary abiotic factors and biological interactions that have been shown to regulate the structure of vent and seep communities. The last section specifically focuses on the ecological role of foundation species, through a discussion of the mechanisms of (1) providing access to high productivity habitat,

(2) increasing habitat complexity, and (3) modifying the physical or chemical environment. This chapter does not provide an exhaustive characterization of the ecology or evolution of either vent or seep communities, which can be found in comprehensive reviews elsewhere (e.g. Tunnicliffe 1991 for vents, and Sibuet and Olu 1998; Levin 2005 for seeps). In fact, the examples in this chapter tend to be heavily weighted to the community types that have been studied with the greatest uniformity across habitats and study sites. To illustrate how vent and seep communities are shaped by foundation species, the most useful examples are siboglinid tubeworms and bathymodiolin mussels at hydrothermal vents in the eastern Pacific Ocean and the Atlantic Ocean and hydrocarbon seeps on the North American continental margins. Tubeworms and mussels have been found in other localities, and other organisms may act as foundation species (e.g. clams and serpulid tube-dwelling polychaetes), but they are not discussed here, because the associated communities have not been adequately sampled to examine the relationship between the foundation species and the associated community or to compare to other vent and seep communities. Lastly, some species (e.g. bacterial mats and highly mobile species, such as rimicarid shrimp) may be characteristic of a particular habitat and have unique associated species assemblages, but are not considered foundation species in the strict sense, if they do not provide or modify habitats through the physical architecture of their presence.

13.2 Overview of Vent and Seep Communities

Hydrothermal vents and hydrocarbon seeps are characterized by high concentrations of reduced chemicals that are used as an energy source to drive local primary production through chemolithoautotrophy. The most common reduced chemicals utilized to support chemosynthetic ecosystems at vents and seeps are sulfide and methane (Fisher 1990; McCollom and Shock 1997; Dubilier et al. 2008). Oxygen or other oxidants available in the seawater react with the reduced chemicals in the vent and seep fluids and provide the chemical energy needed to fix inorganic carbon into simple sugars. Despite the benefits of sulfide-oxidation for primary production, sulfide exposure has physiological costs to aerobic organisms. As a result, most organisms at vents and seeps are patchily distributed along the seafloor with respect to the concentration or rate of the fluid flow.

At mid-ocean ridges, back-arc basins, and other volcanically and tectonically active areas of the seafloor, hydrothermal vents are formed by seafloor spreading, where seawater is entrained into cracks in the deformed oceanic crust and transformed under high heat and pressure into hydrothermal fluids. End-member hydrothermal fluids are characterized by high temperatures and high concentrations of dissolved metals and other reduced chemicals. The highest recorded temperatures reach above 400°C, and concentrations of metals and reduced chemicals can be as high as several hundred millimolar (Von Damm and Lilley 2004). Mineralization, resulting from the mixing hydrothermal fluids with seawater, forms high-temperature vents or “chimneys” that are often characterized by the visible “black smoke” of dissolved metals precipitating from the rising hydrothermal fluids, at the opening of a chimney. The average maximum size of an individual chimney or chimney complex varies among oceanic spreading centers, from heights of ~20 m at the East Pacific Rise to 45 m at the Juan de Fuca Ridge (Haymon et al. 1991; Robigou et al. 1993). Vent fluids are also diluted with seawater and further modified in cracks and conduits below the surface of the seafloor to form diffuse-flow or low-temperature vents, where maximum temperatures are usually less than 50°C (Von Damm and Lilley 2004). Diffuse-flow hydrothermal vents are found at the base of chimneys or develop in patches along the seafloor and can extend up to several hundred square-meters. Hydrothermal vent habitats are considered to be ephemeral and patchy, because of the interconnected relationship between volcanism, tectonism, and hydrothermal circulation. Eruptions or dike injections can destroy and create hydrothermal vent habitats on decadal scales, as observed at the East Pacific Rise (Haymon et al. 1993; Fornari et al. 1998; Tolstoy et al. 2006). However, there are also hydrothermal vents, such as the TAG hydrothermal mound, that appear to have been continuously active for tens of thousands of years, if not longer (Rona et al. 1984; You and Bickle 1998).

Cold seeps are found in pockmarks, mud volcanoes, and other seafloor features on active and passive continental margins, where hydrocarbons leak from reservoirs buried under the sediment as dissolved methane, petroleum, and gas hydrates. As petroleum is degraded and gas hydrates are disturbed or exposed to seawater, additional methane is produced (Ergorov et al. 1999; Aitken et al. 2004). The cause of hydrocarbon release at seeps varies among localities, as a result of sediment compaction, slumping, or the movement of buried salt layers (Sibuet and Olu 1998). Anaerobic methane oxidation coupled with sulfate reduction produces sulfide, and in the presence carbon dioxide, carbonate crusts and deposits develop (Boetius et al. 2000). Concentrations of methane and sulfide can reach several millimolar at the sediment-seawater interface, but may be only a few micromolar to non-detectable concentrations among tubeworms and mussels (Julian et al. 1999; Smith et al. 2000; Bergquist et al. 2003a). While some seeps in the Gulf of Mexico and the Blake Ridge extend over several hundred square-meters and seem to persist for centuries (Cordes et al. 2003; Van Dover et al. 2003), other seeps on the northern California slope are smaller and more transient (Levin et al. 2000).

Compared to other deep-sea habitats, invertebrate communities at hydrothermal vents and hydrocarbon seeps are characterized by high biomass and low species diversity (Tunnicliffe 1991; Carney 1994). These ecological characteristics are ultimately related to the source of primary production in vent and seep ecosystems. The base of the food web is formed by chemolithoautotrophic bacteria, which utilize the chemical energy from the oxidation of reduced chemicals, present in vent and seep fluids, to fix inorganic carbon. The most common electron-donors are reduced sulfur species (H_2S, HS^-, S^{-2}), but other reduced chemicals, such as hydrogen and dissolved metals, can also be used to support chemolithoautotrophy- or “chemosynthesis” (Jannasch and Wirsen 1979; Karl 1995).

Another form of chemosynthetic primary production is methanotrophy, in which methane is used as both the carbon and the energy source. Some animals at vents and seeps have symbiotic relationships with chemoautotrophic, methanotrophic, or both types of bacteria, which can provide the bulk of the animal's nutrition or serve to detoxify the microhabitat of the animal (Fisher 1990, for review). Animals with chemoautotrophic or methanotrophic symbionts tend to grow to large individual sizes and/or high densities (reviewed in Tunnicliffe 1991; Sibuet and Olu 1998), and can contribute 75–90% of the biomass in vent and seep communities (Hessler and Smithey 1983; Govenar et al. 2005; Bergquist et al. 2003b). A greater number of endemic vent and seep animals do not have symbionts, but exhibit behavioral, physiological, and biochemical adaptations to tolerate different degrees of mixing between relatively homogeneous seawater and variable concentrations of potentially toxic, reduced chemicals in vent and seep fluids (Grieshaber and Volkel 1998).

The steep environmental gradients caused by the mixing of vent and seep fluids with background seawater may limit species diversity in chemosynthetic ecosystems (Tunnicliffe 1992; Carney 1994). Simply, the high concentrations of reduced chemicals could inhibit colonization by deep-sea fauna from neighboring habitats. The most abundant taxa are bivalve and gastropod molluscs, tube-dwelling and scale-covered (polynoid) polychaetes, and crustaceans; all of which posses protective coverings to shield their soft tissues from exposure to sulfide and heavy metals (Tunnicliffe 1992). Intrusions from deep-sea predators also appear to be reduced at vents and seeps, either because of evolutionary adaptations to exploit the soft-bodied animals that are more common in the deep-sea, or because of the chemical gradients associated with vent and seep fluids that deter opportunistic foraging (Carney 1994; Sahling et al. 2002). In the absence or reduction of predators, competition could further lead to the numerical dominance of one or a few species and a decrease in the species diversity.

13.3 Biogeographic Patterns and Regional Species Diversity

Evolutionary and ecological processes influence global patterns in biogeography and regional species diversity at hydrothermal vents and hydrocarbon seeps. Historical effects, such as plate tectonics, physical oceanographic processes, or other vicariance events open and close dispersal pathways, which lead to shifts in the species composition of different localities (Tunnicliffe et al. 1996; Van Dover et al. 2002). Ecological factors can also act on patterns caused by historical effects and either increase or decrease species diversity though immigration and extinction processes (McArthur and Wilson 1967; Ricklefs 1987). While often viewed separately, the evolutionary history of vents and seeps are intrinsically linked, as taxonomic and phylogenetic relationships among some species reveal many transitions between vent and seep habitats over geologic time (Tunnicliffe et al. 1998; Van Dover et al. 2002).

Among deep-sea hydrothermal vents, there are at least four biogeographic provinces, (1) the East Pacific Rise and Galapagos Rift, (2) mid-ocean ridges of the northeast Pacific Ocean, (3) the Mid-Atlantic Ridge, and (4) the spreading centers of the Southwest Pacific Ocean (Tunnicliffe et al. 1998; Van Dover et al. 2002; Bachraty et al. 2009). The distribution of the dominant foundation species and the regional species diversity varies among the four provinces. Different species of siboglinid tubeworms are found at the East Pacific Rise (and Galapagos Rift), the mid-ocean ridges of the northeast Pacific, and some vent sites in the southwest Pacific Ocean; but siboglinid tubeworms have not been reported from the Mid-Atlantic Ridge. Bathymodiolin mussels, on the other hand, form dense beds at the East Pacific Rise (and Galapagos Rift), throughout the southwest Pacific Ocean, and along the Mid-Atlantic Ridge. A few, small bathymodiolin mussels have been found at the Juan de Fuca Ridge (McKinness et al. 2005), but mussel beds have not been located. To date, the greatest regional species diversity is associated with the East Pacific Rise (Tunnicliffe et al. 1998; Van Dover et al. 2002). Large-scale ecological factors associated with seafloor spreading may contribute to this pattern, including the older geologic age, fast spreading rate, high to intermediate disturbance frequency and intensity, and large areas of diffuse hydrothermal flow at the East Pacific Rise (Tunnicliffe 1988; Tunnicliffe et al. 1996; Juniper and Tunnicliffe 1997; Van Dover et al. 2002; Van Dover 2003).

Rather than geographic differences, depth seems to play an important role in large-scale distribution patterns among seep communities (McMullin et al. 2003; Sahling et al. 2002; Cordes et al. 2007). In a comparison among deep methane seeps (3,200–4,500 m) along the Aleutian Margin and the Florida Escarpment, infaunal communities have lower densities but similar community structure to shallower seeps along the northern California margin (Levin and Mendoza 2007). However, in epifaunal communities associated with siboglinid tubeworm aggregations, densities are not significantly different between shallow and deep sites, but the species diversity decreases with depth (Cordes et al. 2007). Furthermore, the composition of seep communities in the deep Gulf of Mexico (>1,000 m) are more similar to deeper seep communities at the Blake Ridge and the Barbados accretionary prism than to communities that at closer, but shallower seeps on the upper continental slope of the Gulf of Mexico (Cordes et al. 2007).

In different habitats associated with bathymodiolin mussel beds, species diversity is greater in seep than vent communities (Fig. 13.1; Turnipseed et al. 2003, 2004; Levin 2005). Hydrocarbon seeps are embedded with the continental margin, either on the continental shelf or slope, where the species diversity background deep-sea fauna is much higher and increases with depth (Grassle and Maciolek 1992; Rex et al. 1993; Levin et al. 2001). In contrast, hydrothermal vents are more isolated on mid-ocean ridges and have greater endemicity (Tunnicliffe 1991, 1992). Although seep communities may have greater species diversity, seeps also have lower species endemicity, which may reflect the proximity of seep habitats to source populations (Carney 1994).

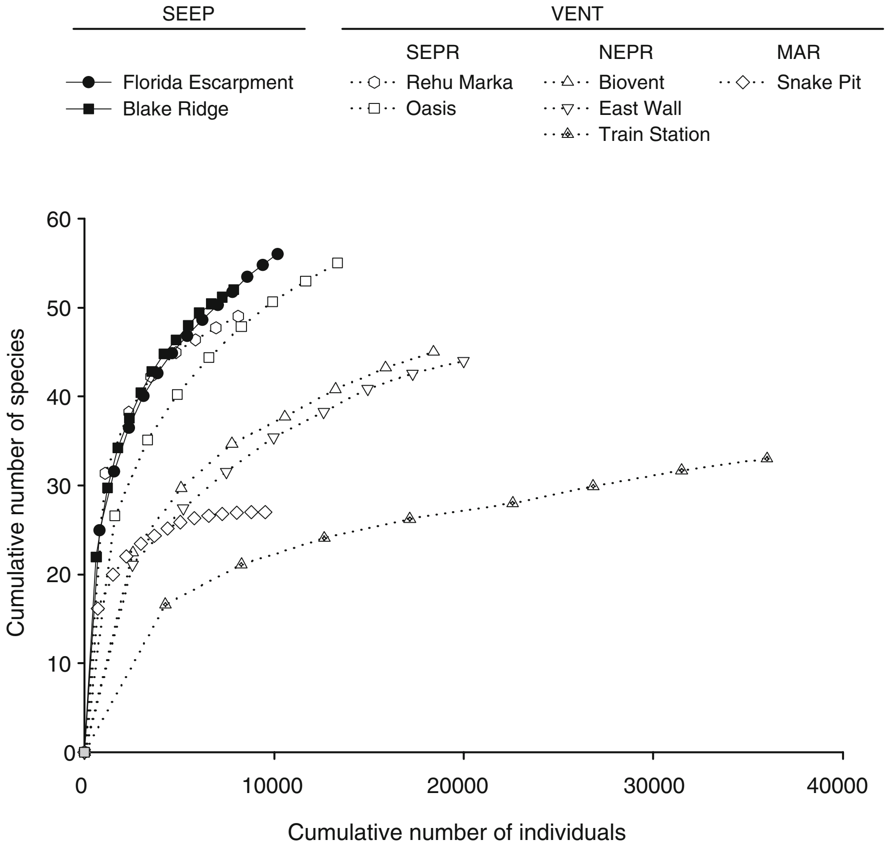

Fig. 13.1 Comparisons of species diversity between analogous vent and seep habitats (From Turnipseed et al. 2003)

13.4 Local-Scale Patterns in Vent and Seep Communities

Large-scale ecological factors play an important role in the distribution of organisms, but patterns at local scales provide critical insights for identifying processes that drive community dynamics and regulate community structure. A vent or a seep site generally refers to the semi-continuous area of visible fluid flow, bacterial mats, or benthic macrofauna. Several sites often comprise a locality (e.g. Hydrate Ridge, Cascadia Margin; East Pacific Rise, 9°50′N). Another important scale for observing local ecological processes is at the level of the foundation species (e.g. tubeworm aggregation, mussel bed). Abiotic factors and biological interactions that affect the distribution of foundation species may operate at scales that are different from other species within the epifaunal community. From another perspective, factors that determine the distribution of foundation species would thus have indirect effects on the epifaunal community structure. Therefore, it is important to first characterize the patterns before analyzing the processes that regulate community structure at vents and seeps (Underwood et al. 2000).

13.4.1 Spatial Patterns

The distribution of symbiont-containing foundation species at the East Pacific Rise follows a gradient in hydrothermal fluid flux. On the surfaces of high-temperature vents, the dominant megafauna are alvinellid polychaetes, which harbor episymbiotic chemoautotrophic bacteria, form colonies of parchment-like tubes (Desbruyères et al. 1998). In areas of vigorous diffuse-flow, siboglinid tubeworms with endocellular chemoautotrophic symbionts form dense aggregations where maximum temperatures are ~30–50°C (Hessler et al. 1988; Govenar et al. 2005; Le Bris et al. 2006a). Bathymodiolin mussels harbor chemoautotrophic symbionts and maintain the ability to filter-feed, which allows them to form extensive beds and occupy a wide range of environmental conditions, from ~15°C with tubeworms to close to ambient temperatures (~2°C) with or without vesicomyid clams (Fisher et al. 1988a; Childress and Fisher 1992). Clams also have functional feeding structures but rely more on chemoautotrophic symbionts for their nutrition, and although temperatures around the exposed (posterior) end of the clams may be close to 2°C, they may stick their foot (at the anterior end) into cracks and form small clusters, where temperatures can be as high as 7°C (Fisher 1988b; Childress and Fisher 1992).

While individual species at the East Pacific Rise also occupy different microhabitats along gradients of fluid flux, the structure of epifaunal communities associated with foundation species appears to vary at different scales. The numerically dominant species are similar in epifaunal communities associated with tubeworms and with mussels, but some species, including gastropods *Rhyncopelta concentrica* and *Cyathermia naticoides*, have greater relative abundances with tubeworms, and other gastropods *Bathymargarites symplector* and *Eulepetopsis vitrea* are relatively more abundant in mussel beds (Van Dover 2002, 2003; Dreyer et al. 2005; Govenar et al. 2005). Similarly, gastropod assemblages associated with alvinellids and siboglinid tubeworms are numerically dominated by one species, *Lepetodrilus elevatus*, but peltospirid gastropod species are relatively more abundant with alvinellids than with tubeworms (Matabos et al. 2008). In contrast, comparisons of epifaunal communities with the same foundation species in different habitats do not appear to vary significantly over local scales. The density and biomass in epifaunal communities associated with aggregations of the siboglinid tubeworm *Rifitia pachyptila* in high- and low-sulfide sites were not significantly different, and the community composition was remarkably similar between sites (Govenar et al. 2005). Epifaunal communities associated with *R. pachyptila* aggregations were also similar before and after a shift in the habitat chemistry from high sulfide concentrations and no apparent iron to low sulfide and high iron concentrations (Govenar et al. 2004, 2005). Epifaunal communities also had high similarity among mussel beds, geographically separated by ~30° of latitude (Van Dover 2002, 2003; Dreyer et al. 2005).

At the Juan de Fuca Ridge, there are two extreme morphotypes of the single species of sibolginid tubeworm, *Ridgeia piscesae*, which occur in different habitats (Carney et al. 2002), but the structure and composition of the epifaunal communities also differs between these two habitat types. A “short-fat” morphotype occurs on the surfaces of high-temperature chimneys, and a "long-skinny" morphotype occurs on the basalt, where temperatures and concentrations of hydrothermal fluids are considerably lower (Govenar et al. 2002; Urcuyo et al. 2003, 2007). Both types of *R. piscesae* harbor chemoautotrophic symbionts but appear to exhibit different physiological adaptations to acquire sulfide in the habitats where they occur (Anderson et al. 2006; Carney et al. 2007). The species diversity is considerably lower with the short-fat morphotype of *R. piscease*, where the high temperatures and concentrations of reduced chemicals or chronic disturbance may limit colonization or opportunist species (Sarrazin et al. 1999; Govenar et al. 2002). Communities associated with the long-skinny *R. picessae* have greater species diversity (Govenar et al. 2004; Bergquist et al. 2007), and the species composition among basalt-dwelling *R. piscesae* aggregations does not vary significantly with location, substrate type, or vent fluid temperature or chemistry (Tsurumi and Tunniclffe 2001, 2003).

Along the Mid-Atlantic Ridge, the dominant megafauna are bathymodiolin mussels and rimicarid shrimp, which occur in different microhabitats. Mussels have both chemoautotrophic and methanotrophic symbionts in varying proportions, depending on the vent fluid chemistry (Duperron et al. 2006), and the shrimp *Rimicaris exoculata* has episymbiotic bacteria in its gill chamber that use either sulfide-oxidation or iron-oxidation as an energy source for chemoautotrophy (Schmidt et al. 2008). Accordingly, mussels occur in habitats with lower temperature and hydrothermal fluid concentration than rimicarid shrimp, which form dense swarms around the openings of the high-temperature vents (Desbruyères et al. 2000; Cuvelier et al. 2009). Neither mussels nor shrimp are present at every site along the Mid-Atlantic Ridge, which may be explained by the lack of suitable habitat for one species or the other, or large-scale ecological factors, such as distance or difference in depth (Desbruyères et al. 2000). Water depth can affect phase separation and water-rock reactions, resulting in different fluid chemistry among hydrothermal vents (Von Damm and Lilley 2004). A comparison among the epifaunal communities associated with mussel beds at three sites, "Lucky Strike" (1,700 m, northern MAR), "Snake Pit" (3,480 m, 'southern' MAR), and "Logatchev" (3,050 m, 'southern' MAR) revealed high dissimilarity (<40%) across geographic and bathymetric differences, and relatively low dissimilarity across environmental differences and closely located sites (Gebruk et al. 2000; Van Dover and Doerries 2005).

The distribution of megfauna along environmental gradients is also common at hydrocarbon seeps. The patchiness in seep habitats is due to the deposition of organic material, which is reduced and migrates at different rates, given the permeability in the sediment (Sibuet and Olu 1998). Anaerobic methane oxidation and sulfate reduction can cause further heterogeneity by forming carbonates and areas of high sulfide concentrations (Levin et al. 2001). Like their vent relatives, siboglinid tubeworms and clams at seeps have sulfur-oxidizing chemoautotrophic symbionts and both occur in sulfidic sediments (Fisher 1990; Cordes et al. 2009 for review). Clams are able to burrow in the sediment, but tubeworms require a point of attachment for colonization and settle on exposed carbonate crusts (Bergquist et al. 2002; Olu-le Roy et al. 2004). Seep mussels have chemoautotrophic, methanotrophic or both types of bacterial symbionts (Fisher 1990; Cordes et al. 2009) and are found in areas with higher concentrations of methane (MacDonald et al. 1989; Bergquist et al. 2005, Olu-le Roy et al. 2007). Corals, such as the reef-forming *Lophelia pertusa* have been found in the vicinity of hydrocarbon seeps, but do not appear to derive their nutrition from chemosynthetic primary production (Becker et al. 2009) and host unique epifaunal communities that include background deep-sea fauna, seep endemic fauna, and coral specific associates (Cordes et al. 2008).

13.4.2 Temporal Patterns

Large-scale disturbances associated with seafloor volcanism and tectonism can create or destroy habitats at hydrothermal vents. Following a seafloor eruption at the East Pacific Rise (9°50′N), nascent areas of diffuse hydrothermal flow were colonized by the siboglinid species *Tevnia jerichonana* within 11 months (Shank et al. 1998). Colonization by a larger siboglinid *Riftia pachyptila* followed 20 months later, and within 2.5 years after the eruption had formed dense aggregations that spatially dominated the diffuse flow habitat. Six months later, small mussels (*Bathymodilus thermophilus*) appeared in cracks on the basalt, over the course of the following year, the density of mussels on the basalt increased and mussels were found among *R. pachyptila*. Another seafloor eruption occurred in the same area in 2005–2006, and similar patterns have been observed (Shank et al. 2006). The mechanisms of community succession is not fully understood, but the transition from *T. jerichonana* to *R. pachyptila* to *B. thermophilus* is likely to a combination of pre-settlement factors, such as geochemical changes (Shank et al. 1998) or biogenic cues (Mullineaux et al. 2000; Mullineaux et al. 2003), and post-settlement factors, including physical overgrowth (Hessler et al. 1988) and resource competition (Johnson et al. 1994). Eruptions have also been observed and documented on the Juan de Fuca Ridge, leading to rapid colonization and community assembly within 2 years (Tunnicliffe et al. 1997). However, predictable changes in the community structure have not been observed on annual scales and directional succession has not been described for vent communities on the JdFR (Sarrazin et al. 1997).

Small-scale disturbances on shorter timescales also influence community structure at hydrothermal vents. A mosaic of different faunal assemblages occurs on the surfaces of geologically young, high-temperature vents on the Juan de Fuca Ridge (Sarrazin et al. 1997). These structures are characterized by multiple channels of hydrothermal fluids that vary by fluid intensity and chemical composition. Exposed surfaces, caused by the opening of a fluid channel or a rock collapse, are colonized by the temperature-tolerant alvinellid polychaete *Paralvinella sulfincola* that secretes a mucus tube, which forms a marcasite crust and plugs conduits of fluid flow through the permeable substrate (Juniper et al. 1992). As fluid flow decreases, the next assemblage that develops is dominated by another alvinellid polychaete *P. palmiformis*. Over time, densities of the gastropods *Lepetodrilus fucensis* and *Depressigyra globulus* increase in density, and eventually the tubeworm *Ridgeia* *piscease* settles and forms dense aggregations (Sarrazin et al. 1997, 1999). The species diversity is greatest in the assemblages associated with the foundation species *R. piscesae* (Sarrazin et al. 1999), and species diversity is positively correlated with the tube surface area of *R. piscesae* aggregations (Govenar et al. 2002). Depending on the degree of reactivation of fluid channels or other small-scale disturbances, the faunal assemblage will revert to earlier stages, as demonstrated by the dynamic succession model for high-temperature vent communities at the JdFR (Sarrazin et al. 1997, 1999).

Environmental changes and ecological succession occur over much longer timescales at hydrocarbon seeps. The best example of the changes in fluid chemistry and community composition overtime is from seep habitats on the Upper Louisiana Slope of the Gulf of Mexico (reviewed in Cordes et al. 2009). Areas of active methane seepage are colonized by the mussel *Bathymodiolus childressi*, and the tubeworms *Lamellibrachia luymesi* and *Seepiophila jonesi* later settle on exposed carbonates, formed by anaerobic oxidation of methane (Bergquist et al. 2003a). Individuals of *B. childressi* may reach ages of 100–150 years old, but intact beds of mussel shells may persist for much longer (Nix et al. 1995). In a 10- to 30-year window during this period, there are high concentrations of methane and sulfide in seep fluids, and high settlement rates of *L. luymesi* and *S. jonsei* juveniles (Bergquist et al. 2002) coupled with low juvenile mortality result in fast population growth rates (Cordes et al. 2003). As aggregations of *L. luymesi* develop, the epifaunal community is dominated by high abundances of a small number of primary consumers that can profit from the physical structure of the foundation species, in areas of chemosynthetic primary production (Cordes et al. 2005). After 30–50 years, sulfide concentrations among the *L. luymesi* aggregations begin to decline, as a result of increasing carbonated precipitation and consumption by growing aggregations of *L. luymesi*. Once the sulfide concentrations are no longer detectable at the sediment-seawater interface, the epfiaunal community in the oldest (>200 years) includes more non-endemics and is dominated in terms biomass by higher-order consumers (Fig. 13.2; Bergquist et al. 2003; Cordes et al. 2005).

13.5 From Patterns to Processes: Local Ecological Processes

Variation in community structure over space and time is driven by a combination of abiotic factors and biological interactions. Although the reliance on chemical energy in chemosynthetic ecosystems underlines the importance of abiotic factors, such as reduced chemical concentrations, biological interactions also play an important role in the regulation of vent and seep communities. One of the important lessons learned from shallow-water marine habitats is that the relative strength or importance of negative or positive species interactions can vary over gradients in abiotic factors (Menge and Sutherland 1976; Bertness et al. 1999). A distinction of chemosynthetic ecosystems is that the relationship between productivity and physiological stress may be positively correlated along environmental gradients (Micheli et al. 2002).

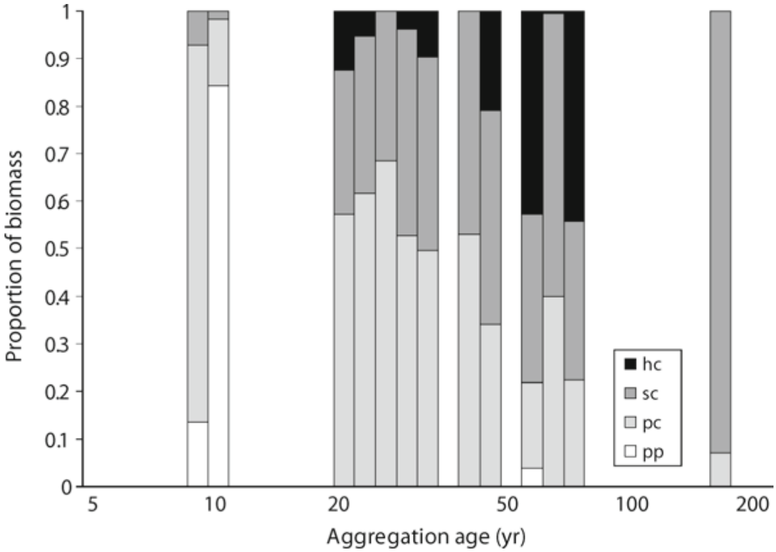

Fig. 13.2 Change over time in proportion of biomass contributed by primary producers (pp), primary consumers (pc), secondary consumers (sc), and higher consumers (hc) in seep communities associated with aggregations of *Lamellibrachia luymesi* (From Cordes et al. 2005)

13.5.1 Abiotic Factors

In chemosynthetic ecosystems, the primary abiotic factors are associated with variable mixing between seawater and either vent or seep fluids. In general, seawater in the deep sea is cold and relatively well oxygenated. In contrast, vent and seep fluids can have high concentrations of reduced chemicals, including sulfide, hydrocarbons, and dissolved metals. All reduced chemicals have essentially the same dual effect on vent and seep communities: as electron donors, reduced chemicals can both support chemosynthetic primary production and reduce local oxygen concentrations. Methane is important for chemosynthesis but is non-toxic. Sulfide and metals, on the other hand, can have further detrimental effects on animal physiology. High metal concentrations and temperatures are characteristic of most vent habitats, but seep fluids are typically not associated with elevated temperatures (Sibuet and Olu 1998). At vents, temperatures and chemical concentrations can vary over orders of magnitude within seconds and centimeters (Johnson et al. 1988; Scheirer et al. 2006). Patterns in temperature variation can also vary over larger spatial and temporal scales, as a result of volcanic and tectonic processes (Scheirer et al. 2006). Although seep fluid concentrations are considered to be more temporally stable, steep environmental gradients that can be found across the width of a single mussel bed demonstrate the high spatial variability in chemical concentrations in seep habitats (Smith et al. 2000; Van Dover et al. 2003).

The correlation between temperature and sulfide concentrations over time (Johnson et al. 1988) led to the question of whether temperature is a good proxy for chemical concentrations (e.g. Le Bris et al. 2006b). The relationship between sulfide concentrations and temperature can be linear within a site, but the sulfide to temperature ratio can vary substantially among sites (Le Bris et al. 2006a; Nees et al. 2008). The variation may be caused by water-rock reactions and biological processes that alters the composition of hydrothermal fluids, beyond a simple dilution of the source end-member (Le Bris et al. 2003, 2006a; Von Damm and Lilley 2004). For example, in high-temperature vent fluids, the formation of FeS reduces the overall concentration of free sulfide H_2S/HS^- (Luther et al. 2001), and in the absence of significant concentrations of iron, low pH shifts the equilibrium of sulfide species to a greater proportion of H_2S (Le Bris et al. 2005). Thus, point measurements of one or a few physicochemical parameters may not fully describe the physicochemical characteristics or environmental heterogeneity in vent or seep habitats.

Arguably, the most important abiotic factor in the distribution of vent and seep communities is hydrogen sulfide, which is a source of energy for chemosynthetic primary production and inhibits aerobic cellular respiration (Vismann 1991; Grieshaber and Volkel 1998). Many vent and seep animals exhibit physiological adaptations to cope with sulfide exposure, including trapping sulfide before diffusion across cell membranes, molecular detoxification or resistance to sulfide, or harboring sulfur-oxidizing symbionts (Vismann 1991; Childress and Fisher 1992). Sulfide can also serve as a chemical cue for colonization (Renninger et al. 1995). Consequently, the zonation pattern in visually dominant organisms at vents and seeps often correlates to gradients in sulfide exposure. At hydrothermal vents on the East Pacific Rise, the siboglind tubeworms *Riftia pachyptila* and *Tevnia jerichonana* occur in diffuse-flow habitats with vigorous mixing between hydrothermal fluids and the ambient seawater, where sulfide concentrations can be as high as several hundred micromolar. In contrast, the clam *Calpyptogena magnifica* lives in cracks where there is no detectable sulfide at their siphon, but low concentrations of sulfide near their foot (Arp et al. 1984; Fisher 1988b). On the Juan de Fuca Ridge, two genetically indistinguishable morphotypes of the tubeworm *Ridgeia piscesae* live in different habitats of high- and low-sulfide exposure (Carney et al. 2002). A "short-fat" morphotype with shorter diffusion distance across the gill epidermis and higher hemoglobin gene expression lives on the surfaces of high-temperature chimneys, where sulfide concentrations around the plume (anterior gas-exchange organ) can be over an order of magnitude higher than at the plume-level of a "long-skinny" morphotype of the same species, which occurs in cracks in the seafloor basalt (Andersen et al. 2006; Carney et al. 2007; Urcuyo et al. 2007). At seeps, the relative abundance of five vesicomyid clams varied with sulfide concentrations in Monterey Bay (Barry et al. 1997), and the distribution of microbial mats, vesicomyid clams, and solemyid clams followed a trend of decreasing sulfide concentrations within a seep at the Hydrate Ridge on the Cascadia Margin (Sahling et al. 2002). The distribution and abundance of individual vent and seep species is also strongly related to sulfide exposure, and the diversity and composition of macrofaunal communities varies with the visually dominant species along environmental sulfide gradients (e.g. Robinson et al. 2004; Matabos et al. 2008; Levin et al. 2009). However, sulfide concentrations do not necessarily explain the variation in macrofaunal communities associated with the same foundation species in different sulfidic conditions, which suggests that other factors contribute to the regulation of biological community structure at vents and seeps (Tsurumi and Tunnicliffe 2001; Govenar et al. 2005; Bergquist et al. 2003b).

Dissolved metals also have direct effects on species in hydrothermal vent communities. Heavy metals can cause oxidative stress and damage in aerobic organisms, but the specific impacts on vent fauna have been difficult to assess (e.g. Colaço et al. 2006; Company et al. 2008). Rather than simply exposure to high metal concentrations, the ratio of dissolved to particulate metal concentrations can serve as an important abiotic factor in determining the distribution of some vent species (Sarradin et al. 2007). Among hydrothermal vent fields on the Mid-Atlantic Ridge, the relative abundance of visually dominant species appears to be correlated with the metal concentrations in the fluids (Desbruyères et al. 2000). The mussels *Bathymodiolus azoricus* and *B. puteoserpentis* dominate vent habitats with lower mineral particle fluxes and metal concentrations (Desbruyères et al. 2000). High metal content in hydrothermal fluids may foul the filtering mechanism of mussels (Desbruyères et al. 2000). Nevertheless, low metal accumulation in the shells (Cravo et al. 2007) and high metal storage in the gills (Cosson et al. 2008) also suggests that mussels are able to tolerate elevated metal concentrations (Kadar et al. 2005a; Company et al. 2006, 2008). On the other hand, the highly mobile shrimp *Rimicaris exoculata* dominates habitats with higher metal contents (Desbruyères et al. 2000). Somewhat contrary to expectation, tissues of *R. exoculata* had lower metal concentrations than the same tissues in another shrimp, *Mirocaris fortunata* that occurs on the surfaces of high-temperature vents, but not exposed to the most vigorous hydrothermal fluid flow (Kadar et al. 2006). The lower metal accumulation in *R. exoculata* may reflect a physiological adaptation to the high metal content in hydrothermal fluids (Kadar et al. 2006). Metals, particularly iron, may also have an important indirect effect on biological communities by binding to sulfide and potentially ameliorating the habitat (Luther et al. 2001). The role of metals as an abiotic factor that influences biological community structure is still unclear and requires further study.

Although elevated temperatures are often coincident with high concentrations of reduced chemicals, temperature itself may play an important role in niche partitioning and species coexistence of closely related hydrothermal vent species. Gastropods at the Juan de Fuca Ridge and the East Pacific Rise appear to occupy distinct microhabitats, based on temperature (Bates et al. 2005; Mills et al. 2007). Similarly, physiological tolerances to temperature determine the habitat ranges of alvinellid polychaetes (Girguis and Lee 2006; Cottin et al. 2008). However, species do not necessarily respond in the same way to temperature fluctuations (Boutet et al. 2009), making it difficult to predict species distribution patterns based solely on temperature measurements. Like sulfide and metal concentrations, temperature can determine the distribution and abundance of single species or groups of closely related species, but the effect of these abiotic factors on the diversity and composition of hydrothermal vent communities may be confounded with other factors or only be observable at larger spatial and temporal scales.

13.5.2 Biological Interactions

In addition to steep environmental gradients and high heterogeneity associated with vent and seep habitats, biological interactions also play an important role in shaping vent and seep communities. A challenge in studying biological interactions in the remote deep-sea habitats of vents and seeps is identifying the limited resources that underlie negative or positive interactions and the consequences on the individual or population growth rates of the species. In the absence of frequent sampling or a sustained presence on the seafloor, manipulative field experiments have been invaluable for examining patterns and developing models of how biological interactions can shape vent and seep communities (Van Dover and Lutz 2004).

Competition for shared resources has been demonstrated among species in low- and high-temperature hydrothermal vent habitats. In the diffuse-flow communities at the Galapagos Rift and the East Pacific Rise, aggregations of the tubeworm *Riftia pachyptila* are commonly overgrown by beds of the mussel *Bathymodiolus thermophilus* (Hessler and Smithey 1983; Hessler et al. 1988). Both *R. pachyptila* and *B. thermophilus* harbor sulfur-oxidizing chemoautotrophic symbionts and must acquire sulfide from hydrothermal fluids (Fisher 1990, for review). Thus, the thick mat created by mussel beds may redirect the flow of hydrothermal fluids emanating from the seafloor, away from the gas-exchange organ or “plume” at the anterior end of the tubeworms. A clearance experiment demonstrated that removing mussels increased the concentrations of sulfide at the plumes of the tubeworms (Johnson et al. 1994). The formation of the bed would then have a negative effect on tubeworms, as well as a positive effect for conspecific mussels within the bed that may have greater access to the laterally dispersed vent fluids.

On the surfaces of high-temperature chimneys, the roles of resource partitioning and competition were examined through stable carbon and nitrogen isotope analyses (Levesque et al. 2003). Two species, *Paralvinella sulfincola* and *P. palmiformis* that occur together in high densities were found to have significantly different diets. However, a shared diet was found for *P. palmiformis* and *P. pandorae*. When the two species occurred together, individuals of *P. pandorae* were smaller than when *P. palmiformis* was absent, which suggests that *P. pandorae* is negatively affected by intra- or interspecific competition (Levesque et al. 2003). A similar approach has been used to examine the mechanisms of species coexistence in hydrothermal vent gastropods. Results of molecular identification of gut contents and stable isotope analysis reveal that three congeneric species may compete for a shared resource, which have a distinctly different diet than another species of a different genus (Govenar and Shank, in preparation). Additional work is needed to both reveal patterns of differences in relative abundance and to identify shared resources, including nutrients and food sources, to uncover other examples of competition that influence the structure of vent and seep communities.

While the intrusion of predators from the background deep-sea are relatively rare, vent endemic predators, such as zoarcid fish, can exert top-down control on vent and seep communities. In a manipulative field experiment on the East Pacific Rise, the effect of predation was strongest in the most vigorously mixing diffuse-flow habitat, where siboglinid tubeworms were the dominant foundation species (Micheli et al. 2002). The removal of predators from caged colonization blocks among siboglind tubeworm aggregations led to an increase in the abundance of gastropod limpets and amphipods. In agreement with the results of the caged block experiment, the gut contents of the zoarcid fish *Thermarces cerebus* contained mostly gastropod limpets and amphipods (Sancho et al. 2005). Increased limpet abundances, in the absence of predation, could contribute to decreased rates of colonization by siboglinid tubeworms and other sessile species (Micheli et al. 2002). Other predators and scavengers that prey on invertebrates at hydrothermal vents include octopods, bythograeid crabs, amphinomid and polynoid polychaetes and turrid snails, but their role in regulating community structure is less clearly defined (Micheli et al. 2002; Voight 2005; Voight and Sigwart 2007). Stable isotope analyses have identified background deep-sea and endemic predators in seep communities (MacAvoy et al. 2002, 2008), but role of predation in shaping seep communities has not been studied directly. Some vagrant deep-sea predators at hydrocarbon seeps, such as the hagfish *Eptatretus* sp., the giant isopod *Bathynomus giganteus* and the spider crab *Rochina crasse* make intrusions into seep habitats but feed mostly on background deep-sea fauna (MacAvoy et al. 2008), while others, including individuals the rat tail fish *Nezumia* sp. and the eels *Synaphobranchus* sp., *Ophicthus cruentifer* and *Dysomma rugos* derive their nutrition from food sources dependent on chemosynthetic primary production (MacAvoy et al. 2002) and may reduce faunal densities in seep communities, but the identity of the prey is not clear.

Positive species interactions are also prevalent in vents and seep communities. The most well-studied examples are invertebrates that harbor internal or external bacterial symbionts. In addition to the symbiont-containing foundation species, other vent and seep species have unique associations with bacteria that can serve as a source of nutrition or as a buffer from reduced chemicals (reviewed in Fisher 1990; Ott et al. 2005; Stewart et al. 2005). Another symbiont that occurs with bathymodiolin mussels at vents and seeps is a commensal polynoid polychaete that resides in the mantle of some individuals, where it presumably benefits from the protection of the mussel shell and the increase in food availability from the psuedofeces of the mussel (Fisher 1994; Chevaldonné et al. 1998). There does not appear to be any relationship between the size of the mussel and the size or the abundance of the commensal polychaetes, and rarely is there any evidence of a negative impact to the mussel (Fisher 1994).

Facilitation has also been shown to play an important role in larval settlement and community assembly at hydrothermal vents on the East Pacific Rise and the Mid-Atlantic Ridge. The tubeworm *Tevnia jerichonana* is the first sessile metazoan to colonize new diffuse-flow vents, created by seafloor eruptions, and is later replaced by the tubeworm *Riftia pachyptila* as the biomass dominant species (Shank et al. 1998). On colonization blocks deployed in different diffuse-flow habitats, *R. pachyptila* only colonized blocks where *T. jerichonana* had settled, which suggests that *T. jerichonana* may provide a biochemical cue that facilitates the colonization of *R. pachyptila* (Mullineaux et al. 2000). In a subsequent experiment, there was no relationship between the settlement of either *T. jerichonana* or *R. pachyptila* with the tubes of either species as colonization substrates, which led to the revised hypothesis that *T. jerichionana* may serve as a biogenic cue in the early stages of community development after an eruption (Hunt et al. 2004). A different experiment found that sessile colonists, such as serpulid polychaetes and foraminifers also facilitate the colonization of sessile colonists in the periphery of hydrothermal vents (Mullineaux et al. 2002). At the Juan de Fuca Ridge, the colonization of four out of five gastropod species appeared to be facilitated by gregarious settlement (Kelly and Metaxas 2007). The role of facilitation on colonization and community organization is likely to be an important factor in isolated habitats of hydrothermal vents on mid-ocean ridges and the patchy distribution of hydrocarbon seeps, embedded in the sedimented deep-sea.

13.6 Habitat Provision and Modification by Foundation Species

13.6.1 Access to Highly Productive Habitats

At vents and seeps, most foundation species have chemosynthetic symbionts and require access to both reduced chemicals and oxygen for carbon-fixation. Although foundation species may contribute the greatest proportion of the biomass in vent and seep communities (Hessler et al. 1988; Bergquist et al. 2003b; Govenar et al. 2005), very few endemic species base their nutrition on the consumption of the tubeworms and mussels (Fisher 1994; Colaço et al. 2002; Bergquist et al. 2007; Levin 2005). Instead, the presence of foundation species may coincide with availability of high productivity habitats, where heterotrophic macrofauna feed on particulate and dissolved organic matter, free-living bacteria, protists, and other small invertebrates.

As both free-living bacterial primary production and growth rates of symbiont-containing foundation species are dependent on chemoautotrophy, it cannot be determined whether increased species diversity with foundation species is due to higher local productivity or larger habitat area provided by the biogenic structure. To tease apart the variables of chemosynthetic primary production and the size of the area provided by foundation species, artificial tubeworm aggregations were constructed from flexible hose in a similar size frequency and density as natural tubeworm aggregations and were deployed along a gradient in hydrothermal fluid flux, representing three ranges of chemosynthetic primary production (Govenar and Fisher 2007; Plate 30). After 1 year, artificial aggregations in the low productivity treatment, ~20 m away from any visible source of hydrothermal fluid flow, had the lowest species density and species diversity. Aggregations in high productivity treatment, embedded in a natural

Table. 13.1 Univariate measures of community structure for artificial aggregations in low-, intermediate- and high-productivity zones and natural aggregations of *Riftia pachyptila*, collected at the same site (Tica) in 2001 and 2002

	Density (individuals m^{-2})	*S*	*J′*	*H′*
Low (n = 3)	14 (8)	10 (4)	0.94 (0.02)	2.09 (0.31)
Intermediate (n = 3)	617 (195)	28 (1)	0.71 (0.05)	2.38 (0.17)
High (n = 3)	942 (654)	25 (6)	0.65 (0.19)	2.09 (0.66)
Natural (n = 4)	4,301 (1,612)	26 (6)	0.51 (0.08)	1.65 (0.31)

Average density, species richness (S), Pielou's evenness (J′), Shannon–Wiener diversity (H′) of macrofaunal species; standard deviation in parentheses (From Govenar and Fisher 2007)

aggregation of tubeworms, had the greatest density. However, aggregations in the high productivity treatment had the same or lower species diversity than aggregations in the intermediate productivity treatment, <0.5 m away from natural tubeworm aggregations, on the bare basalt substrate. Furthermore, species diversity was similar between artificial aggregations, in high and intermediate productivity treatments, to natural aggregations collected at the same site in the previous year (Table 13.1; Govenar and Fisher 2007). The results of this experiment demonstrate the importance of the physical structure provided by foundation species in the regulation of the epifaunal community structure in areas of chemosynthetic primary production.

13.6.2 Physical Structure and Habitat Complexity

Added to the positive effects of increased access to high productivity habitats, epifaunal communities associated with foundation species at vents and seeps benefit from increased area and habitat complexity provided by the physical architecture of the foundation species. In the deep-sea, hard substrate and upright structures are limited resources that are often necessary for colonization and filter-feeding. In addition, the interstitial spaces among intertwined tubes of siboglinid tubeworm aggregations and among bivalve shells in mussel beds can create greater environmental variability and refuge from predation that can increase survivorship, promote species coexistence, and lead to increased species diversity, relative to the unmodified seafloor (Bruno and Bertness 2001).

The relative importance of the habitat provided by the foundation species may also outweigh the effects of the environmental chemistry in regulating the structure of the epifaunal community at vents and seeps. On the East Pacific Rise, epifaunal communities associated with mussels were similar despite the differences in the apparent age of the foundation species and geographic distance among sites (Van Dover 2002, 2003; Dreyer et al. 2005), with exception of epifaunal communities sampled from beds where most (~75%) of the mussels were dead (Van Dover 2002). Furthermore, the structure of the epifaunal communities associated with aggregations of *Riftia pachyptila* aggregations were remarkably similar between low- and high-sulfide sites, and species richness was positively correlated with the tube surface area of the *R. pachyptila* aggregations at both sites (Govenar et al. 2005). On the Juan de Fuca Ridge, epifaunal communities associated with aggregations of *Ridgeia piscease* did not vary significantly with the location, year of collection, temperature of vent fluids, or substratum type, but species richness was correlated with the structural complexity of the *R. piscesae* aggregations (Tsurumi and Tunniclffe 2003). The species diversity was greater in experimental treatments with complex structure than treatments that were a mimic of the seafloor (Kelly and Metaxas 2007). In the Gulf of Mexico, the species richness of epifaunal communities associated with aggregations of the tubeworms *Lamellibrachia luymesi* and *Seepiophila jonesi* tended to increase with the areal coverage and tube surface area of the tubeworm aggregations, and the epifaunal density increased with habitat complexity (tube surface area/areal coverage) (Bergquist et al. 2003).

13.6.3 Modification

In addition to providing access to high productivity habitats, adding area for colonization and increasing environmental heterogeneity, foundation species can also modify physical and chemical characteristics of vent and seep habitats. Foundation species with chemosynthetic symbionts must acquire sulfide and methane and subsequently alter the chemical composition of the surrounding fluids. In seep habitats associated with pockmarks in the North Atlantic and mud volcanoes in the Gulf of Cadiz, small frenulates can alter the distribution and composition of seep fluids (Dando et al. 2008; Sommer et al. 2009), by decreasing the rate of sulfide and methane release. The impact of the habitats created or modified by frenulates on other macrofaunal invertebrates is not well understood and warrants further investigation.

As individuals and aggregations of the siboglind tubeworm *Lamellibrachia luymesi* grow, interstitial sulfide concentrations are expected to similarly decrease. In fact, theoretical models suggest that sulfide reservoirs in seep habitats would not be sufficient to sustain the growth estimates for *L. luymesi* (Bergquist et al. 2000; Cordes et al. 2003, 2005). However, sulfate release from the posterior extension of *L. luymesi* tubes in the sediment (Dattagupta et al. 2006, 2008), stimulates sulfide production by sulfate-reducing bacteria and can allow tubeworm aggregations to persist for centuries (Bergquist et al. 2000, Cordes et al. 2003). As tubeworm aggregations age, less sulfide is present above the sediment-seawater interface and the composition of the epifaunal community changes (Bergquist et al. 2003a; Cordes et al. 2005).

13.6.4 Effect of Foundation Species on Regional Species Diversity

Differences in the epifaunal communities associated with biogenic islands, created by foundation species, may also contribute to higher regional species diversity at vents and seeps (Govenar and Fisher 2007; Cordes et al. 2008). Among artificial tubeworm aggregations deployed in a diffuse-flow vent habitat at the East Pacific Rise, there were significant differences in the species assemblages that provided insights into the relationship between foundation species and the associated epifaunal communities (Govenar and Fisher 2007). Although tubeworms have been shown to colonize plastic tubing (Hunt et al. 2004), no tubeworms were found on the surfaces of the artificial aggregations. In addition, numerically dominant species found in natural tubeworm aggregations were either absent or had lower relative abundance artificial aggregations. In contrast, mussels settled on artificial aggregations in the high and intermediate productivity treatments, and numerically dominant species in mussel beds at a nearby site had greater relative abundance in artificial than natural tubeworm aggregations. The similarity in the composition of the faunal assemblages fell between the epifaunal communities associated with either natural aggregations of tubeworms or mussels (Fig. 13.3). These patterns highlight the importance of the identity or functional traits of the foundation species (e.g. McGill et al. 2006). The tendency for some species to occur either with tubeworms or with mussels suggests that foundation species may not be interchangeable within vent communities (Machicote et al. 2004; Berkenbusch and Rowden 2007).

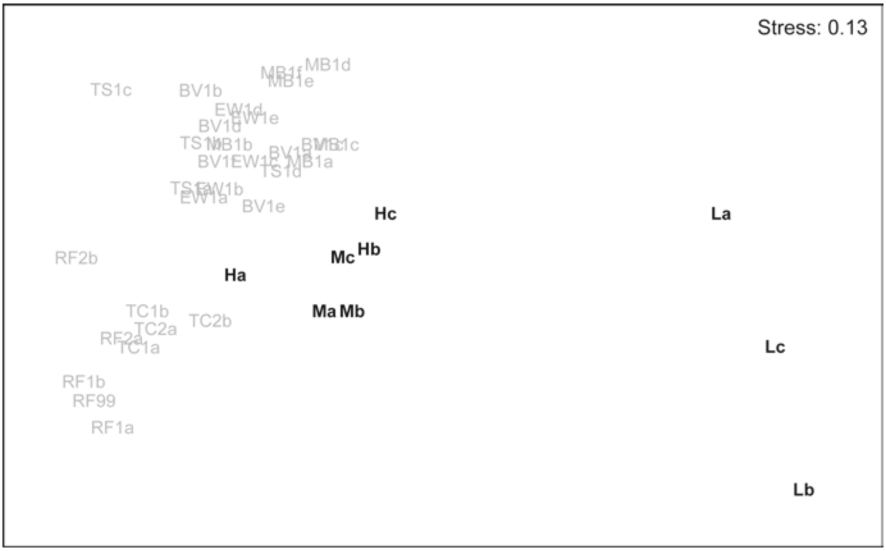

Fig. 13.3 Non-metric dimensional scaling plot of the Bray–Curtis similarity values (based on presence-absence data) between artificial aggregations in low (L), intermediate (M), and high (H) productivity zones, and natural aggregations of *Riftia pachyptila* from Riftia Field (RF) and Tica (TC) and mussel beds from Biovent (BV), Mussel Bed (MB), East Wall (EW), and Train Station (TS), on the East Pacific Rise (9°50′N). The number corresponds to the year 2001 (1) or 2002 (2), and the lowercase letter represents a unique replicate (Data from Dreyer et al. 2005; Govenar et al. 2004, 2005; Govenar and Fisher 2007)

Source–sink dynamics between communities associated with foundation species and species turnover associated with the succession from tubeworms dominance to mussel dominance may increase species diversity at the regional scale of the East Pacific Rise (EPR), relative to other mid-ocean ridges. High regional species diversity at the EPR has been attributed to large-scale ecological factors such as older geologic age, fast spreading rate, high to intermediate disturbance frequency and intensity, and large areas of diffuse hydrothermal flow (Tunnicliffe 1988; Tunnicliffe et al. 1996; Juniper and Tunnicliffe 1997; Van Dover et al. 2002; Van Dover 2003). Thus, habitat provision or modification at local scales by different foundation species may also contribute to the high regional species diversity at the EPR. At the global scale, the EPR and associated ridges is the only mid-ocean ridge system where both tubeworm aggregations and mussel beds are present. This may result in higher regional species diversity relative to the Juan de Fuca Ridge, which does not have dense mussel beds, and the Mid-Atlantic Ridge, where tubeworms have never been reported (Van Dover et al. 2002).

13.7 Conclusion

On the backdrop of historical events that lead to global biogeographic patterns, local ecological processes affect the composition of hydrothermal vent and hydrocarbon seep communities at local and regional scales. Plate tectonics and other vicariance events open and close pathways to dispersal and contribute to evolutionary processes that determine the composition of species in different localities. Geologic processes, including volcanism, tectonism, organic deposition, and sedimentation, regulate the flow and composition of vent and seep fluids that determine the distribution of species at large spatial and temporal scales. Abiotic factors and biological interactions further refine the structure of vent and seep communities and the maintenance of local and regional species diversity.

Habitat provision and modification by foundation species can facilitate species coexistence and increase species diversity relative to the surrounding seafloor. At vents and seeps, most foundation species have sulfur-oxidizing or methanotrophic bacterial symbionts and require access to both reduced chemicals and oxygen. Thus, epifaunal communities associated with foundation species are exposed to potentially harsh environmental conditions. However, the positive effects of habitat provision may outweigh the relative importance of the environmental chemistry. The presence of foundation species can increase rates of colonization or survivorship and local species diversity in epifaunal communities through the various ecological mechanisms, including (1) providing access to high productivity habitats, (2) adding area available for colonization, increasing environmental variability, and providing refuge from predation, and (3) ameliorating habitat conditions. Furthermore, habitats created or modified by foundation species form biogenic islands that can increase migration and dispersal and increase regional species diversity.

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