FACTORS AFFECTING THE EPIFAUNAL COMMUNITY ASSOCIATED WITH *RIFTIA PACHYPTILA* AT DEEP-SEA HYDROTHERMAL VENTS ON THE EAST PACIFIC RISE

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by

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ABSTRACT

Low-temperature hydrothermal vents host dense communities of large invertebrates that obtain their nutrition exclusively or primarily through symbioses with internal chemoautotrophic bacteria. The habitat provided by these foundation species supports diverse assemblages of smaller heterotrophic invertebrates. This dissertation consists of five chapters that characterize the ecology of hydrothermal vent communities associated with the giant vestimentiferan tubeworm *Riftia pachyptila* (Polychaeta: Siboglinidae) at the East Pacific Rise. The first chapter reviews the literature on the physical environment, the biology of the dominant species, and the patterns and dynamics of hydrothermal vent communities. The second chapter presents the results of a clearance and transplant experiment, designed to test the role of biological interactions in the succession of low-temperature hydrothermal vents. The unexpected results provide an opportunity to characterize the patterns of recruitment and community assembly associated with an aggregation of *R. pachyptila* that developed in less than one year. The third chapter examines the spatial and temporal variability of the *R. pachyptila* community, sampled at two discrete sites and in two consecutive years. Although the temperature ranges did not vary between sites or years, the chemical composition of the diffuse hydrothermal fluids was significantly different at each site. The physiological condition of the *R. pachyptila* individuals appeared to reflect the environmental conditions, but the structure and the composition of the community was remarkably similar between sites and years. The fourth chapter tests the hypothesis that the physical structure of *R. pachyptila* aggregations supports high local species diversity in a high productivity habitat. The results of deploying artificial tubeworm aggregations along a
productivity gradient for one year demonstrate the importance of physical structure, productivity and biological attributes of foundation species in the regulation of the epifaunal community structure. A summary of this work is discussed in the fifth chapter, integrating the results of quantitative sampling and experimental manipulations to investigate the roles of environmental variability, productivity, habitat provision and modification, and biological interactions in the structure of the epifaunal community associated with *R. pachyptila*. 
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CHAPTER 1
Ecology of hydrothermal vent communities at the East Pacific Rise

Overview

The East Pacific Rise (EPR) was first encountered during the historic Challenger expedition in 1875 (Murray 1895, Macdonald 1989). However, not until hydrothermal vents were discovered at the Galapagos Rift in 1977, was a human-occupied vehicle used to collect the exotic deep-sea fauna that populates the EPR (Corliss et al. 1979). Life at hydrothermal vents is inextricably linked to the tectonic and volcanic processes that first attracted the attention of geologists to mid-ocean ridges in the 1950s. As oceanic plates spread apart, new lithosphere rises and forms a long volcanic cone or ridge. Cold ambient seawater is entrained into the deformed oceanic crust, where it reacts with the subsurface rocks, heated by the shallow magma chamber. The hydrothermal fluids are released through cracks in the newly created seafloor, with high concentrations of toxic chemicals and heavy metals. In the interface of mixing hydrothermal fluids with the deep-ocean bottom water, chemolithoautotrophic bacteria harvest the energy from the oxidation of the reduced chemicals to fix inorganic carbon into simple sugars. Chemosynthetic bacteria form the base of the food web for a diverse assemblage of endemic hydrothermal vent species that have adapted to the highly variable hydrothermal vent ecosystem.

Physical environment

The East Pacific Rise (EPR) was created by the spreading of the Pacific and the Farallon oceanic plates in the early Mesozoic Era (Juniper and Tunnicliffe 1997). In the
mid-Tertiary Period (~28 mya), the Farallon plate was subducted under the North American plate and formed two smaller plates, the Cocos and the Nazca (Macdonald 1989, Tunnicliffe et al. 1996). Currently, the EPR runs NNW to SSW between 115° W to 105° W and stretches 9000 km from 21° N to 30° S (Macdonald 1989, Haymon et al. 1993, Smith and Demopoulos 2003). The summit of the EPR stands at 2000 m above the surrounding seafloor (2000-3000 m below sea level) and is cut into first-order segments by transform faults (Macdonald 1989, Fornari et al. 1998). The spreading rate of each segment generally increases from north to south. The northern-most segment, between the Tamayo and the Rivera fracture zones, has an intermediate spreading rate of 60 mm yr⁻¹ (Larson 1971, Macdonald 1989). The rest of the EPR has a much faster spreading rate, with the highest spreading rate (162 mm yr⁻¹) at the southern most segment between the Garrett fracture zone and the Easter microplate (Macdonald 1989, Carbotte and Macdonald 1992).

Between the Clipperton and the Siqueiros fracture zones, the EPR is spreading at a rate of 110 mm yr⁻¹ (Macdonald 1989, Carbotte and Macdonald 1992). The axial summit of this ridge segment is a flattened dome, a characteristic of a fast-spreading center. Within the dome, the tectonic movement of the plates has created a centralized valley (graben) that is wider than it is tall. The walls of the graben are sloped ~60°, and the basin is 100 m deep (2400 m below sea level) and 3000 m wide (Fornari et al. 1998). Within the graben is a steeper valley (caldera) that was formed by the collapse of ponded lava or a hollow lava tube (Fornari et al. 2004). A patchwork of high-temperature vents and low-temperature hydrothermal flow is localized within this axial summit caldera that

On the East Pacific Rise near 9°50’ N, end member hydrothermal fluids form 150 m to 1000 m below the surface of the seafloor (Fornari et al. 2004, Von Damm and Lilley 2004). Under extreme pressure and exposed to high temperatures, the hydrothermal fluids can boil and separate into a brine and vapor phase (Von Damm et al. 1997). The ratio of vapor to brine can be used to track the evolution of the hydrothermal fluids (Von Damm et al. 1995, Von Damm et al. 1997, Von Damm and Lilley 2004). High-temperature fluids are released from weak or thin sections of the seafloor (Fornari et al. 2004), and upon contact with the cold ambient seawater, metals in the solution precipitate and form sulfide deposits that create chimney-like structures (Haymon 1989, Haymon et al. 1993). Low-temperature hydrothermal fluids that escape from cracks in the basalt rock are a result of the subsurface dilution of end member fluids. Diffuse hydrothermal flow may be coupled with nearby high-temperature vents through subsurface conduits. Additional water-rock reactions and microbial activity can significantly alter the composition of the diluted hydrothermal fluids (Von Damm and Lilley 2004, Le Bris et al. submitted).

The chemistry of the ambient seawater at 2500 m depth in the eastern Pacific Ocean is relatively constant with temperatures close to 2 °C and with relatively high concentrations of oxygen (~ 110 µM), no sulfide, and very low concentrations of CH₄ and H₂ (Von Damm et al. 1997, Smith and Demopoulos 2003, Von Damm and Lilley 2004). In contrast, the hydrothermal vent habitat on the East Pacific Rise is characterized by rapidly changing temperatures and highly variable concentrations of oxygen and
reduced chemicals. End member hydrothermal fluids can be as high as 403°C, with no oxygen and millimolar concentrations of H$_2$S, H$_2$ and CH$_4$ (Von Damm et al. 1997). However, there are no animals that live in direct exposure to end member hydrothermal fluids and very few that experience even short pulses of temperatures ~ 100°C on the surface of high-temperature vents (Fisher 1998, Chevaldonné et al. 2000). Most of the endemic hydrothermal vent fauna live where diluted hydrothermal effluent mixes with ambient seawater (Hessler et al. 1985, Grassle 1986, Tunnicliffe 1991). In these areas of diffuse hydrothermal flow, the maximum temperatures are near 30 °C and maximum concentrations of H$_2$S, CH$_4$, and H$_2$ are in the micromolar range (Le Bris et al. 2003b, Von Damm and Lilley 2004, Le Bris et al. submitted). In this spatially and temporally variable habitat, sulfide concentrations can range from 0 to 300 µM and temperatures can fluctuate 1 °C s$^{-1}$ (Johnson et al. 1986, Johnson et al. 1988a, Johnson et al. 1988b).

**Biological patterns**

Megafaunal distribution at the EPR follows a gradient in hydrothermal fluid flux (Hessler and Smithey 1983, Grassle 1985, Hessler et al. 1985, Fustec et al. 1987, Etter and Mullineaux 2001). On the surfaces of high-temperature chimneys, alvinellid polychaetes are exposed to temperatures near 45 °C in their parchment-like tubes (Desbruyères et al. 1998). In areas of diffuse hydrothermal flow, vestimentiferan tubeworms form dense aggregations where temperatures can be up to 30 °C (Childress and Fisher 1992, Shank et al. 1998). Mussels occupy a wide range of environmental conditions from ~15 °C with vestimentiferans to close to ambient temperatures (~2 °C) with or without clams (Fisher et al. 1988a, Childress and Fisher 1992). Although
temperatures around the posterior end or dorsal side of the clams may be close to 2 °C, they may stick their foot into cracks where temperatures are as high as 7 °C (Fisher et al. 1988b, Childress and Fisher 1992). On the periphery of hydrothermal vent sites, serpulid polychaetes and barnacles can colonize large areas on the basalt substrate, where temperatures are generally no higher than a few tenths of a degree above ambient (Hessler and Smithey 1983, Micheli et al. 2002, Mullineaux et al. 2003).

The habitat created or modified by large or space-dominant species, such as vestimentiferans, mussels, and clams, and to a lesser extent, alvinellids and serpulids, can be considered “foundation species” (sensu Bruno and Bertness 2001), because they support diverse assemblages of smaller invertebrates. Alvinellids produce mucus and tubes that facilitate the formation of marcasite crust, which is occupied by other species of polychaetes and a few gastropod species (Fustec et al. 1987, Jollivet 1993, Juniper and Martineu 1995, Maginn et al. 2002). There is also a brachyuran crab that is found more often on high-temperature chimneys with alvinellids than in low-temperature hydrothermal flow on the basalt (Fustec et al. 1987). On the surfaces of vestimentiferan tubes and mussel shells, the density and diversity of species is the highest of any vent habitat and is also higher than on the surrounding seafloor (Hessler et al. 1988, Tunnicliffe 1991, Shank et al. 1998). A different brachyuran crab, a few species of fish, and octopods are also common in these habitats (Hessler et al. 1988). There appears to be high species overlap between communities dominated by either vestimentiferans or mussels, but there may also be unique species associated with one or the other in areas where they are not co-occurring. The physical structure of clams and serpulids may increase habitat complexity, but most of the macrofauna associated with either of these
species occurs more often on the seafloor than directly on their tubes and shells (Hessler and Smithey 1983). A galatheid squat lobster is also often abundant with serpulids (Hessler and Smithey 1983, Hessler et al. 1988).

Hydrothermal vent species are generally larger than taxonomically related species in other environments of the deep-sea (Gage and Tyler 1991). Although there is some evidence of a small amount of nutritional input from surface-derived particulate and dissolved organic carbon, the base of the food web at hydrothermal vents is formed by chemolithoautotrophic bacteria that convert the energy from the oxidation of reduced chemicals in the hydrothermal fluids for primary production (Karl et al. 1980, Jannasch 1983, 1995, Karl 1995, McCollom and Shock 1997). The largest of the foundation species in hydrothermal vent communities, including alvinellids, tubeworms, mussels, and clams, have symbiotic relationships with chemosynthetic bacteria (Fisher 1990, Childress and Fisher 1992). Alvinellids have episymbiotic sulfur-oxidizing bacteria that may serve as a food source as well as a detoxifying mechanism for reducing sulfide in their microhabitat on the surfaces of high-temperature chimneys (Desbruyères et al. 1998, Campbell et al. 2003). Vestimentiferans do not have a mouth, gut, or anus and rely on endocellular sulfur-oxidizing bacteria for their nutrition (Fisher 1990, Childress and Fisher 1992). Mussels and clams both have fully functional guts, but depend primarily on sulfur-oxidizing bacteria in their gills for food. By supplementing their diet by filter-feeding, mussels may occupy a wider range of environmental conditions, exploit multiple nutritional sources, and can survive during periods of waning hydrothermal flow (Smith 1985, Fisher et al. 1988a, Fisher et al. 1988b, Page et al. 1991). Although all of the symbiotic bacteria in this hydrothermal vent system are sulfur-oxidizers (γ-
proteobacteria), free-living bacteria can utilize electron donors other than sulfide and electron acceptors other than oxygen (Karl 1995). Common bacteria on the surfaces of vestimentiferan tubes, in the diffuse hydrothermal flow habitat, include σ-proteobacteria (sulfate reducers), ε-proteobacteria (aerobic and anaerobic oxidizers of sulfide, thiosulfate, and elemental sulfur and possibly iron (III) reducers), members of the Cytophaga-Flavobacterium-Bacteriodes (CFB) group (chitin degraders) and Verrucomicrobia (fermenters) (Lopez-Garcia et al. 2002). Most of the epifaunal species seem to prey on free-living bacteria, protists, and other invertebrates (Hessler and Smithey 1983, Grassle 1986, Van Dover and Fry 1989, Tunnicliffe 1991, Fisher et al. 1994, Micheli et al. 2002). Larger predators, including fish, crabs, and octopods are generalists that feed on gastropods, polychaetes and small crustaceans and may scavenge on bacterial mats, tubeworms, and mussels (Fisher et al. 1994, Voight 2000, Micheli et al. 2002, Sancho et al. 2005).

**Community dynamics**

Volcanic and tectonic processes have profound effects on regional and local ecological processes at hydrothermal vents. Compared to the sedimented deep-sea, hydrothermal vents are characterized by high primary productivity, high biomass, high endemicity, and relatively low species diversity. Among the biogeographic provinces associated with hydrothermal vents at other mid-ocean ridges, the East Pacific Rise (EPR) has the highest species diversity (Tunnicliffe et al. 1998, Van Dover et al. 2002). In addition to a greater number of species overall, there is also higher redundancy within taxonomic and functional groups at the EPR than at other ridges. For example, there are
at least three congeneric species of alvinellid polychaetes that live on the surfaces of high-temperature vents, there are three genera of vestimentiferan tubeworms that coexist in areas of vigorous low-temperature hydrothermal flow, and there are two families of bivalves that overlap but also occupy slightly different microhabitats in areas of more diffuse hydrothermal flow. In addition, there are at least five polynoid polychaetes and 15 gastropods that coexist in mussel beds (Van Dover 2002, 2003). Not enough is known about the autecology of most of these species to hypothesize the mechanisms of species coexistence at this time. High regional diversity at the EPR may be related to the fast spreading rate, high regional age, moderate habitat heterogeneity, and moderate to high habitat area (Juniper and Tunnicliffe 1997). Regional and historic factors may also influence local patterns of species diversity, and likewise, local processes can influence patterns of regional diversity. Community dynamics ultimately relate to volcanic and tectonic influences on hydrothermal fluid flux.

Changes in the hydrodynamics or the chemical composition of hydrothermal fluids may create small-scale disturbances that would result in lower growth rates, reduced reproductive output, or death in some species. The visible decline of a previously thriving population of *R. pachyptila* was coincident with a decrease in sulfide and an increase in iron concentrations (Shank et al. 1998). Catastrophic disturbances such as earthquakes, rock collapses, and volcanic eruptions can alter, create, or destroy hydrothermal vent habitats. A volcanic eruption in 1991 provided an opportunity to document the development of biological communities at nascent hydrothermal vents (Haymon et al. 1993, Shank et al. 1998). The lava released from the axial summit caldera scorched, burned, and covered some animals in molten rock (Haymon et al. 1993). Over
time, as the temperature and concentrations of hydrothermal fluids decreased, the number of species increased on the basalt substrate (Shank et al. 1998). Large disturbances are expected to occur at the decadal scale (Haymon et al. 1993), while small-scale variability in the hydrothermal fluid flux occurs within seconds and centimeters (Johnson et al. 1986, Johnson et al. 1988a, Johnson et al. 1988b, Luther et al. 2001, Le Bris et al. 2003a, Le Bris et al. 2003b, Le Bris et al. submitted).

Within months of an eruption near 9° 50’N on the East Pacific Rise, bacterial mats covered the basalt rock at nascent hydrothermal vent sites (Haymon et al. 1993, Shank et al. 1998). Mobile scavengers such as crabs and gastropods seemed to respond to the increased production of autotrophic biomass and migrated to the bacterial mats (Shank et al. 1998). After 11 months, the coverage area of the bacterial mat decreased significantly and the vestimentiferan tubeworm *Tevnia jerichonana* settled on the basalt. Colonization by a larger vestimentiferan *Riftia pachyptila* followed 20 months later, and within two and a half 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*. The transition from tubeworm dominance to mussel dominance has also been documented at hydrothermal vents on other segments of the EPR and at the Galapagos Rift (Hessler et al. 1985, Hessler et al. 1988). The mechanism of succession in hydrothermal vent communities is still not fully understood but may be due 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).

The strength or relative importance of biological interactions may also vary along the gradient in hydrothermal fluid flux (Micheli et al. 2002, Mullineaux et al. 2003). In the periphery of hydrothermal vent habitats, sessile species seem to facilitate the settlement of other sessile species (Mullineaux et al. 2003). Within areas of diffuse hydrothermal flow, the physical structure provided by vestimentiferans and mussels appears to increase local species diversity (Hessler and Smithey 1983, Tunnicliffe 1991, Shank et al. 1998). These foundation species benefit from a symbiotic relationship with chemoautotrophic bacteria (Fisher 1990), and compete with each other for resources (Johnson et al. 1994). Among tubeworms, where temperatures and concentrations of hydrothermal fluids are generally higher, mobile species, especially grazing gastropods, tend to inhibit the colonization of other species (Mullineaux et al. 2003). Predation by fish reduces the number of gastropods, and may subsequently have an indirect positive effect on larval recruits and increase species richness (Micheli et al. 2002). Mullineaux et al. (2003) suggests that positive species interactions would be more prevalent where hydrothermal fluid flux is lower and that negative species interactions would play a larger role in community structure and succession in areas of higher hydrothermal fluid flux, where productivity may be higher as well. The relationship between megafaunal distribution, productivity, faunal density, and species diversity needs to be tested through controlled experimentation to determine the role of hydrothermal fluid flux in regulating bottom-up and top-down ecological processes in hydrothermal vent communities.
Summary

At low-temperature hydrothermal vents on the East Pacific Rise, the giant tubeworm Riftia pachyptila obtains the essential nutrients to support an internal symbiosis with sulfur-oxidizing bacteria from the mixing of diffuse hydrothermal fluids with ambient seawater. In the habitat provided by the physical structure of R. pachyptila aggregations, the density and diversity of smaller heterotrophic species is higher than on the surrounding seafloor. The aim of this dissertation is to investigate ecological patterns and processes in the epifaunal community associated with R. pachyptila. First, a one-year-old aggregation of R. pachyptila and the associated fauna were collected to characterize a hydrothermal vent community of a known age. Then, with a quantitative sampling device, a total of eight aggregations of R. pachyptila and all of the associated fauna were collected at two sites in two years to examine the influence of environmental variability on the structure of the epifaunal community. Last, artificial substrates were constructed to mimic natural aggregations of R. pachyptila and deployed along a productivity gradient for one year to determine the role of physical structure and productivity in maintaining species diversity at hydrothermal vents. Local factors that regulate the epifaunal community associated with R. pachyptila, such as environmental variability, productivity and biological interactions, may also contribute to the high regional diversity at hydrothermal vents on the East Pacific Rise.
Literature cited


Van Dover, C. L. 2002. Community structure of mussel beds at deep-sea hydrothermal


CHAPTER 2
Composition of a one-year old Riftia pachyptila community following a clearance experiment: insight to succession patterns at deep-sea hydrothermal vents

Abstract

In the basalt-hosted hydrothermal vent habitat around 9°50’ N on the East Pacific Rise, vestimentiferan tubeworms Tevnia jerichonana and Riftia pachyptila (Polychaeta: Siboglinidae) commonly settle before the mussel Bathymodiolus thermophilus (Bivalvia: Mytilidae). We removed six aggregations of R. pachyptila and deployed mussels on the cleared sources of diffuse flow to test the effect of the B. thermophilus on the subsequent colonization by the tubeworms. None of the transplanted mussels persisted on the cleared sources of diffuse flow, however aggregations of R. pachyptila grew in half of the clearances. We collected one of the aggregations of R. pachyptila along with the associated fauna for determination of relative abundance and biomass in this one-year old community. This aggregation consisted of 647 R. pachyptila that hosted individuals of 24 species, including small individuals of T. jerichonana and B. thermophilus. The abundance of the associated fauna was numerically dominated by gastropods and the biomass was dominated by the Alvinellid polychaete Paralvinella grasslei.

Introduction

Following an eruption, vestimentiferan tubeworms Tevnia jerichonana and Riftia pachyptila (Polychaeta: Siboglinidae) quickly colonize the basalt-hosted hydrothermal vents around 9°50’ N (East Pacific Rise) and soon grow to visually dominate these habitats (Lutz et al. 1994, Shank et al. 1998, Mullineaux et al. 2000). Colonization by the vent mussel, Bathymodiolus thermophilus, often follows shortly, and the mussels
eventually overgrow the tubeworms at most sites (Hessler et al. 1988, Johnson et al. 1994, Shank et al. 1998). Both tubeworms and mussels harbor sulfur-oxidizing chemoautotrophic endosymbionts, which provide the bulk of their nutrition (Fisher 1990, Childress and Fisher 1992). However, mussels have also maintained the ability to filter-feed (Page et al. 1991) which apparently allows them to occupy a wider range of environmental conditions and better tolerate declining hydrothermal vent activity than the tubeworms (Fisher et al. 1988). The mechanism of ecological succession in these hydrothermal vent habitats is not fully understood, but may be regulated by a combination of pre-settlement factors, such as the use of biogenic cues (Mullineaux et al. 2000) and the response to geochemical changes (Shank et al. 1998), and/or post-settlement factors, such as physical overgrowth (Hessler et al. 1988) and resource competition (Johnson et al. 1994).

**Results and discussion**

We conducted a manipulative experiment to test the hypothesis that the mussel *B. thermophilus* prevents further colonization of a vent by tubeworms. In May 1998, six aggregations of the giant tubeworm *R. pachyptila* were cleared from a site named “Riftia Field” (9°50.705’ N 104°17.593’ W). The original location and source of diffuse flow for each aggregation were carefully marked and recorded on video. The temperatures of the venting fluid were measured using the low temperature probe of the DSV *Alvin*, after the aggregations were cleared, and ranged from 20 – 22 °C above ambient at the six locations. Then approximately 600 mussels were collected from a nearby site (“East Wall”, 9°50.614’ N 104°17.509’ W) and ~200 were deployed over each of three cleared
sources of diffuse flow (treatments). Mussels were not deployed on the three other cleared areas (controls). One month later, a French expedition (HOPE98, L’Atalante/Nautilus) to the same hydrothermal vent field reported that there were no mussels visible at Riftia Field (pers. obs., S. Hourdez, Station Biologique Roscoff). In April 1999, we confirmed that all but one of the mussels had disappeared without a trace, and found that aggregations of *R. pachyptila* had grown in three of the previously cleared diffuse flow sources. No disarticulated mussel shells were seen anywhere within this vent site, and it was not obvious whether the mussels had migrated or had been eaten. The single live mussel was observed attached to a syntactic foam marker, 50 cm above the ocean floor.

In a mensurative experiment to examine the fate of the mussel deployment and the rate at which they left the area, another 200 mussels were deployed over one of the cleared (and still uncolonized) sources of diffuse flow and their movement was documented with a time-lapse camera. The temperature at this source (21 °C above ambient) had not changed significantly since the year before. After 17.5 h, the two-dimensional surface area covered by mussels increased by 32% as they began to move away from the deployment site. The fastest of the mussels moved at an average speed of 0.74 cm h$^{-1}$ during the observation period. Why the adult mussels migrated away from the source of diffuse flow is unclear. Environmental conditions (i.e. sulfide concentrations or temperature) may have prevented the adult mussels from staying within the site of deployment, although the same species lives in apparently similar microhabitats on the Galapagos Rift (Fisher et al. 1988) and in this vent field (Mullineaux et al. 2003).

In April 1999, aggregations visually dominated by *R. pachyptila* had grown over three of the six cleared sources of diffuse flow (two treatment patches and one control).
There was no evidence of recolonization at the other three, although diffuse flow was present still at every site. The temperatures ranged from 21-30 °C above ambient at the sources of the diffuse flow. Considering the almost complete absence of adult mussels in 1999 and their motility, the absence of a treatment effect on the recolonization of *R. pachyptila* was not surprising. There was no *T. jerichonana* visibly present in video records of any of the recolonized patches, which is unexpected because *T. jerichonana* is often an early colonist to the basalt substrate in this area and has been hypothesized to facilitate *R. pachyptila* colonization (Lutz et al. 1994, Shank et al. 1998, Mullineaux et al. 2000, Hunt et al. 2004). However, *R. pachyptila* settlement has been previously documented on a variety of natural and artificial substrates without the prior establishment of *T. jerichonana* (Shank et al. 1998, Thiebaut et al. 2002, Hunt et al. 2004). In this experiment, the cleared patches had previously been colonized by *R. pachyptila* and were in close proximity to mature *R. pachyptila* aggregations, which may have facilitated conspecific settlement at this site. The apparent absence of mussels and *T. jerichonana*, along with the seemingly random settlement of *R. pachyptila* to some of the cleared sources of diffuse flow, provides additional evidence of the unpredictability of larval settlement around diffuse sources of hydrothermal flow.

At one of the recolonized patches, the base of the *R. pachyptila* tubes were tightly interconnected and centered directly above the venting source, which was confirmed during the previous year to be a single small hole (~3 cm in diameter). This aggregation of *R. pachyptila* was collected intact by its base, with the manipulator arm of *Alvin*, and placed into a sealed acrylic box for transport to the surface. Although some of the associated fauna were lost during the collection, review of the video record confirmed the
pilot’s report that very few individuals fell from the *R. pachyptila* aggregation as it was very carefully placed into the collection box. Over 600 individuals of *R. pachyptila* were collected in this sample, along with 24 other species (Table 2-1). All macrofaunal species (> 500 mm) were identified, enumerated and weighed for determination of relative abundance and biomass in this one-year old *R. pachyptila* community (Table 2-1).
Table 2.1: Species abundance, relative abundance, biomass (ash-free dry weight, g), and relative biomass of symbiont-containing species and all other species. The wet weight of *Riftia pachyptila* was estimated using methods described in Figure 2. The wet weight (frozen in preweighed bags), dry weight (dried for 12 h at 60 °C) and ash-free dry weight (combusted for 8 h at 500 °C) of a subset of the individuals was measured on a Mettler-Toledo (AG245) balance after returning to the laboratory. After all of the other species were identified to the lowest possible taxon, subsamples were dried and weighed following the above procedure to calculate the biomass in ash-free dry weight. Two species of dirivultid copepods were also collected with this aggregation, however the abundance and biomass of these meiofaunal species were not included in this table, which describes the macrofaunal composition of the community (pers. com., S. Ivaneneko, Moscow State University).

<table>
<thead>
<tr>
<th></th>
<th>Abundance</th>
<th>Relative abundance (%)</th>
<th>Biomass (g)</th>
<th>Relative biomass (%)</th>
</tr>
</thead>
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<tr>
<td><strong>Symbiont-containing species</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polychaeta</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><em>Riftia pachyptila</em></td>
<td>647</td>
<td>95.71</td>
<td>3252.94</td>
<td>99.99</td>
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<tr>
<td><em>Tevnia jerichonona</em></td>
<td>23</td>
<td>3.40</td>
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<td><strong>Bivalvia</strong></td>
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<td></td>
<td></td>
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<tr>
<td><em>Bathymodiolus thermophilus</em></td>
<td>6</td>
<td>0.89</td>
<td>0.23</td>
<td>0.01</td>
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<tr>
<td><strong>All other species</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
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<td>10.74</td>
<td>65.46</td>
<td>59.11</td>
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<td><em>Paralvinella pandorae irlandei</em></td>
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<td>0.88</td>
<td>0.09</td>
<td>0.08</td>
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<td><em>Amphisamytha galapagensis</em></td>
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<td><em>Hesiospina vestimentifera</em></td>
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<td>0.01</td>
<td>0.27</td>
<td>0.24</td>
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<tr>
<td><em>Galapagomystides aristata</em></td>
<td>211</td>
<td>0.88</td>
<td>1.22</td>
<td>1.10</td>
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<td><em>Branchinotogluma grasslei</em></td>
<td>14</td>
<td>0.06</td>
<td>0.09</td>
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<tr>
<td><em>Branchinotogluma hessleri</em></td>
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<td><em>Branchinotogluma sandersi</em></td>
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<td>0.04</td>
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<td><em>Branchiplicatus cupreus</em></td>
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<td>0.16</td>
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<td><em>Levensteiniella kincaidi</em></td>
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<td>&lt; 0.01</td>
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<td>12</td>
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<td>0.04</td>
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<td><strong>Gastropoda</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><em>Cyathermia naticoides</em></td>
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<td>13.94</td>
<td>12.59</td>
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<tr>
<td><em>Gorgoleptis spiralis</em></td>
<td>8</td>
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<td>&lt; 0.01</td>
<td>&lt; 0.01</td>
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<td>7123</td>
<td>29.63</td>
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<td>5.52</td>
<td>3.37</td>
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<td>0.59</td>
<td>0.71</td>
<td>0.64</td>
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<td><em>Rhynchopelta concentrica</em></td>
<td>2172</td>
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<td>9.52</td>
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<td><strong>Crustacea</strong></td>
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<tr>
<td><em>Bythograea thermydron</em></td>
<td>30</td>
<td>0.12</td>
<td>6.25</td>
<td>5.64</td>
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<tr>
<td><em>Ventiella sulfuris</em></td>
<td>28</td>
<td>0.12</td>
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<td>0.02</td>
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<tr>
<td><strong>Total (symbiont-containing species)</strong></td>
<td>676</td>
<td>3253.31</td>
<td></td>
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</tr>
<tr>
<td><strong>Total (all other species)</strong></td>
<td>24,041</td>
<td>110.74</td>
<td></td>
<td></td>
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<tr>
<td><strong>Total</strong></td>
<td>24,717</td>
<td>3364.05</td>
<td></td>
<td></td>
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</tbody>
</table>
Growth rates of *R. pachyptila* have been estimated from the length of their tubes (Lutz et al. 1994, Shank et al. 1998). However *R. pachyptila* can grow chitinous septa in the middle of their tubes and may inhabit only a portion of their total tube length (Gaill et al. 1997, Ravaux et al. 2000). Therefore, tube growth may not reliably reflect animal growth. In this collection of *R. pachyptila*, there was a strong negative relationship between the total length of the tube and the percentage of the tube occupied by the worm (Fig. 2-1). Some of the largest *R. pachyptila* only occupied 20% of their tube, and tubes greater than 60 cm were never more than 60% occupied. The tube of *R. pachyptila* serves to protect the soft tissue of the animal and also to place the gas-exchange organ (the plume) in the mixing zone of diffuse hydrothermal effluent and the ambient deep-ocean water. Thus tube shape and length will be affected by the position of an individual within an aggregation and the characteristics of the vent fluid flow to that aggregation. Therefore we consider it unlikely that the relation shown in Figure 1 will hold for *R. pachyptila* in other microhabitats, because the lack of direct correlation between tube length and animal length is characteristic of this species (pers. obs., C.R. Fisher). A size frequency histogram, constructed from the mass (wet weight) of all of the *R. pachyptila* individuals in this aggregation, suggests that this species either exhibits extremely (and we suggest “unbelievably”) variable individual growth rates, or that recruitment occurred throughout the previous year and included very recent settlement of *R. pachyptila* (Fig. 2-2). Approximately 45% of the *R. pachyptila* in the aggregation were sexually mature (with a sex ratio of 1 male to 1.3 females) and 16% weighed less than 1 g (Fig. 2-2). In 1997, *R. pachyptila* populations at the same site (Riftia Field) were similarly skewed to the smallest individuals and the sex ratio was also around 1 to 1 (Thiebaut et al. 2002).
Negative species interactions may contribute to high juvenile mortality, but the use of biogenic cues by adult *R. pachyptila* may facilitate gregarious settlement and result in high population turnover (Thiebaut et al. 2002, Mullineaux et al. 2003).

**Figure 2-1:** The percent of the *Riftia pachyptila* tube occupied by the individual worm decreases as the tube length increases. The occupied tube length was measured from the anterior opening of the tube to the first septum inside the tube.
This collection of an intact *R. pachyptila* aggregation along with the associated fauna provided an opportunity to gain insight into the structure of a *R. pachyptila* community of a known age. After one year, this aggregation included 647 individuals of *R. pachyptila*, weighing 3.25 kg (ash-free dry weight) (Table 2-1) and contributing 96.7% of the total community biomass. The surface area of the *R. pachyptila* tubes provided 4.75 m2 of biogenic substrate available for colonization by other species. At least 24 macrofaunal species occupied the surfaces and interstitial spaces of the tubes, representing 13 families from phyla Annelida, Mollusca, and Arthropoda (Table 2-1).
to those on basalt blocks that were embedded in vestimentiferan aggregations (Mullineaux et al. 2003). However, the reassembly of the community was much faster after this clearance experiment than after an eruption and creation of new hydrothermal vents. By the time *R. pachyptila* had formed dense aggregations (3.5 years post-eruption), the number of species observed was similar to the species richness in this one-year old *R. pachyptila* aggregation (Shank et al. 1998).

The macrofaunal species of this community are primarily grazers and scavengers and do not rely on *R. pachyptila* as their primary source of nutrition (Fisher et al. 1994, Micheli et al. 2002). The gastropods were the most abundant of the associated fauna, accounting for 85.4% of the total 24,041 individuals. The most common species were the snail *Cyathermia naticoides* (40.6%) and the limpets *Lepetodrilus elevatus* (29.6%) and *Rhyncopelta concentrica* (9.0%) (Table 2-1). Gastropods also dominate the abundance of communities associated with the vestimentiferan *Ridgeia piscesae* in the basalt-hosted hydrothermal vents at the Juan de Fuca Ridge in the northeast Pacific Ocean (Tsurumi and Tunnicliffe 2001, 2003), and *Lepetodrilus* spp. is often the dominant gastropod in a variety of vent habitats at the Juan de Fuca Ridge and the northern and southern East Pacific Rise (Sarrazin et al. 1997, Sarrazin and Juniper 1999, Tsurumi and Tunnicliffe 2001, Govenar et al. 2002, Van Dover 2002, Tsurumi and Tunnicliffe 2003, Van Dover 2003). Although only accounting for 10.7% of the associated fauna abundance, the polychaete *Paralvinella grasslei* contributed the largest fraction (59.1%) of the associated fauna biomass (Table 2-1). In this *R. pachyptila* aggregation, the density of *P. grasslei* was considerably higher than on basalt blocks deployed for 13 months in a similar habitat at this vent field (Mullineaux et al. 2003; unpubl. data, L. Mullineaux, Woods Hole
Oceanographic Institution). *P. grasslei* lives in a thick mucous casing at the base of *R. pachyptila* tubes and may preferentially live in association with *R. pachyptila*.

Among the species found attached to *R. pachyptila* tubes were 23 small *T. jerichonana* (maximum tube length < 4 cm) and 6 small *B. thermophilus* (maximum shell length < 1.5 cm). The presence of the juvenile mussels is especially interesting in the context of the emigration of the adults transplanted to these sites. The adult mussels were deployed directly on the source of diffuse venting, which may have exceeded their tolerance range. The juvenile mussels may have settled in a more suitable habitat on the *R. pachyptila* tubes. Situated well above the venting source, the juvenile mussels would have been exposed to less concentrated hydrothermal flow, where the temperatures and the concentrations of reduced chemicals are lower and oxygen concentration is higher than in fluids emanating from the basalt. In various marine environments, habitat created by foundation species can alter hydrodynamics, water chemistry, food availability, larval settlement, and biological interactions, in the addition to the provision of space for colonization and refuge from competitors and predators (Bruno and Bertness 2001, for review). The data presented here suggest that *R. pachyptila* may modify the vent habitat to facilitate the colonization of other species. In this way, *R. pachyptila* seems to play an important role in the succession of species and the composition of the community in the diffuse-flow habitat of basalt-hosted hydrothermal vents at the East Pacific Rise.
Notes

Melanie Freeman, Derk Bergquist, Galen Johnson, and Chuck Fisher were coauthors on the publication of this chapter and assisted in the editing of the manuscript. Chuck Fisher designed the clearance-transplant experiment, oversaw the collection of the aggregation of *Riftia pachyptila* and associated fauna, and provided logistic and financial support for this study. Melanie Freeman identified, enumerated, and weighed the specimens, and with the help of Derk Bergquist, began the characterization of the community collection. Galen Johnson used time-lapse photographs to determine the percent coverage by mussels and the rate of mussel movement in the second transplant experiment.

Literature cited


Lutz, R. A., T. M. Shank, D. J. Fornari, R. M. Haymon, M. D. Lilley, K. L. Von Damm,


Shank, T. M., D. J. Fornari, K. L. Von Damm, M. D. Lilley, R. M. Haymon, and R. A.


CHAPTER 3

Epifaunal community structure associated with *Riftia pachyptila* aggregations in chemically different hydrothermal vent habitats

Abstract

The vestimentiferan tubeworm *Riftia pachyptila* (Polychaeta: Siboglinidae) can dominate early succession stages and high productivity habitats at low-temperature hydrothermal vents on the East Pacific Rise. Eight aggregations of *R. pachyptila* and the associated epifaunal community were collected at two discrete sites, in December 2001 and December 2002. Due to the high spatial and temporal variability of the biotic and abiotic factors related to hydrothermal vent activity, significant differences in the structure and the composition of the community were expected to occur at the scale of either one year or 500 m distance between very different sites. There was no significant difference in the temperature range of the diffuse flow between sites or years, even though the environmental conditions were very different at the two sites. At one site (Riftia Field), the diffuse hydrothermal flow had relatively low concentrations of sulfide, low pH and high concentrations of iron. At the other site (Tica), the diffuse hydrothermal fluids had higher sulfide concentrations, the pH was closer to neutral, and iron was undetectable. The physiological condition of *R. pachyptila* seemed to reflect the availability of sulfide at each site. However, the structure and the composition of the epifaunal community were remarkably similar between sites and years, with the exception of a few less abundant species. Aggregations of *R. pachyptila* support high local species diversity relative to the surrounding basaltic rock seafloor and high community similarity in different hydrothermal vent habitats.
Introduction

A basic premise in ecology is that similar habitats support similar communities (MacArthur & Wilson 1963, Caswell 1976, Connor & Simberloff 1979, 1997, Hubbell 1997, Samuels & Drake 1997). When differences are observed in the local community structure or composition at various scales, researchers investigate the mechanisms which explain non-equilibrium dynamics or alternate stable states (Terborgh et al. 1996, Reice 1997, Micheli et al. 1999, Sousa 2001, Chase 2003, Petraitis & Dudgeon 2004, Ricklefs 2004). Although it is not possible to quantify all of the abiotic factors that characterize different habitats, any factor that directly affects the flow of energy and matter are likely to affect the structure of the community. Community changes along environmental gradients have been documented in a variety of terrestrial, aquatic, and marine systems (Menge & Sutherland 1987, Auerbach & Shmida 1993, Wootton & Power 1993, Ohmann & Spies 1998, Leach & Giovnish 1999, Petchey et al. 2002). However, the alternative pattern is rarely explored, in which community similarity is maintained in different habitats. High similarity (single equilibria) may be maintained in local communities with similar habitats, small regional species pools, high connectance, low productivity and high disturbance (Chase 2003, Leibold et al. 2004). However, high regional dispersal of a small pool of endemic species could also maintain high local community similarity in very different habitats.

Hydrothermal vents are ephemeral, dynamic, and patchily distributed along mid-ocean ridges. Between the Clipperton and Siqueiros fracture zones, near 9°50’ N on the East Pacific Rise (EPR), a patchwork of numerous high-temperature vents and areas of
diffuse hydrothermal flow are distributed within the axial summit caldera (ASC, maximum width ~ 70 m) (Haymon et al. 1991, Haymon et al. 1993). Although diffuse flow has been shown to be coupled with nearby high-temperature vents, dilution and subsurface processes can alter the composition and flow dynamics of the hydrothermal fluids (Von Damm & Lilley 2004). Within an area of diffuse flow, temperatures can vary widely over a scale of centimeters and can range ~10 °C within seconds at the same point (Johnson et al. 1986, Johnson et al. 1988a, Johnson et al. 1988b). The colonization patterns of endemic vent species to a site can vary substantially with time, hydrothermal flux, and as a result of biological interactions (Van Dover et al. 1988, Shank et al. 1998, Mullineaux et al. 2000, Micheli et al. 2002, Mullineaux et al. 2003, Hunt et al. 2004). Within months of the April 1991 eruption near 9°50’ N on the EPR, a few macrofaunal species had colonized nascent vent sites; and within 2.5 years, the giant vestimentiferan tubeworm, Riftia pachyptila formed dense aggregations (Shank et al. 1998). Within 1 year of the experimental removal of a R. pachyptila aggregation from an established site, a large aggregation of R. pachyptila and the associated community reassembled in the cleared source of diffuse flow (Govenar et al. 2004). Due to the heterogeneity in the dynamics and composition of hydrothermal fluids in the diffuse-flow habitat and variability in larval recruitment and biological interactions, significant differences in the structure or the composition of hydrothermal vent communities seem likely at both large and small spatial and temporal scales.

Compared to other deep-sea habitats, hydrothermal vent communities are characterized by high biomass, high productivity, high endemicity, and low species diversity. Within the vent ecosystem, high productivity habitats are associated with the
vigorous mixing of hydrothermal fluids and ambient seawater and may be related to the frequency or intensity of disturbances in the dynamic mixing zone. At fast-spreading ridges like the EPR, large magmatic and tectonic disturbances can occur on decadal scales, which can create new habitat or destroy existing communities (Haymon et al. 1993, Shank et al. 1998). Small-scale disturbances also occur on shorter time scales as a result of alterations in the flow or composition of the hydrothermal fluids (Fustec et al. 1987, Jollivet 1993, Shank et al. 1998), which can affect resource availability and subsequently affect species richness, density and biomass through bottom-up processes. Large and small disturbances may contribute to both the high productivity and the relatively low regional species diversity at hydrothermal vents.

At low-temperature hydrothermal vents of the EPR and the Galapagos Rift, *Riftia pachyptila* can form dense aggregations of high biomass in diffuse flow, where temperatures can range from 2 to 30 °C and sulfide concentrations can be as high as 330 µM (Johnson et al. 1986, Johnson et al. 1988a, Johnson et al. 1988b, Childress & Fisher 1992, Shank et al. 1998, Micheli et al. 2002, Mullineaux et al. 2003). *R. pachyptila* is reliant on intracellular sulfur-oxidizing bacteria for its nutrition, and must obtain carbon dioxide and sulfide from the hydrothermal fluid and oxygen from the ambient seawater to sustain chemoautotrophy (Childress & Fisher 1992, for review). Individuals of this species can reach 3 m in tube length and 650 g wet weight (Grassle 1986, Fisher et al. 1988b). Single aggregations of *R. pachyptila* may include 2000 individuals m⁻² (Shank et al. 1998), can comprise 96% of the community biomass (Govenar et al. 2004), and support a higher diversity and density of endemic hydrothermal vent species than the surrounding basaltic rock substrate (Tunnicliffe 1991, Shank et al. 1998).
In this study, epifaunal communities associated with *Riftia pachyptila* were sampled at two discrete sites near 9°50’ N on the EPR in December 2001 and again in December 2002. The primary objective was to quantify the structure and the composition of this type of hydrothermal vent community. By sampling in sequential years (2001 and 2002) and at distinct sites of low-temperature hydrothermal vent activity, factors that could influence patterns in the distribution of species abundance and biomass that characterize the *R. pachyptila* community were also investigated.

**Methods**

**Site description**

Eight aggregations of *Riftia pachyptila* and the associated epifaunal community were collected with a quantitative sampling device, operated from the DSV *Alvin*, near 9°50’N on the East Pacific Rise (EPR). Two aggregations of *R. pachyptila* and the associated fauna were collected at each of two discrete sites, Riftia Field (9°50.705’ N, 104°17.493’ W, 2500 m) and Tica (9°50.447’ N, 104°17.493’ W, 2500 m), in December 2001 and again in December 2002. These distinct sites of diffuse hydrothermal vent activity are separated by 500 m in the axial summit caldera, along the spreading axis of the EPR.

*Riftia pachyptila* colonized Riftia Field at least five years before Tica (pers. comm. J.P. Hickey, DSV Alvin pilot and expedition leader, Woods Hole Oceanographic Institution). When Riftia Field was first visited in the mid-1990s, the site was named for the dense populations of *R. pachyptila*. In May 1999, there continued to be large *R. pachyptila* aggregations and active larval recruitment (Govenar et al. 2004). In 2001 and
2002, the total abundance of *R. pachyptila* was greatly reduced and the few remaining aggregations were small and sparsely distributed. Individuals of *R. pachyptila* were often in recumbent position with tubes that were encrusted with iron oxide precipitates (rust); and they appeared to be in poorer physiological condition, inferred from the pallid pink color of the gas-exchange organ (the plume), which is normally bright red. At Tica, the overall health of *R. pachyptila* appeared to be much better. The plumes were bright red, and the white tubes formed dense thickets, perpendicular to the substrate.

Temperatures were measured with *Alvin*’s low-temperature probe at the base, center, and top of seven of the eight aggregations of *Riftia pachyptila*, which were subsequently sampled for community analyses. In 2002, the total labile sulfide (\( \Sigma H_2S = H_2S, HS^- \) and HS\(^2-\)) and ferrous iron concentrations in the diffuse hydrothermal fluids around aggregations of *R. pachyptila* at Riftia Field and Tica were determined using the *in situ* flow analyzer, “ALCHIMIST” (Le Bris et al. 2000). The ALCHIMIST was installed on the *Alvin* basket, and the 4 m long inlet tube was attached to the *Alvin* low-temperature probe, along with high-resolution pH electrode and a fast-response temperature probe. While continuously sampling the fluid, repeated Flow Injection Analysis (FIA) measurements were performed at a rate of 1 measurement per min, during each scan. Calibrations were performed in situ during each dive. The pH was measured using a one-point calibration on ambient seawater baseline and corrected for temperature effect (Le Bris et al. 2001). From these measurements, the relation between temperature and sulfide, iron, or pH, was determined for diffuse-flow fluids at Riftia Field and Tica (Le Bris et al. submitted).
Community sampling

All community samples were collected with a hydraulically-actuated collection net, named the “Bushmaster Jr.” (described by Urcuyo et al. (2003) and Bergquist et al. (2003)). The Bushmaster Jr. is lined with a 63 µm Nitex mesh and can sample areas up to 60 cm in diameter (0.28 m²). For these samples, the submersible pilot positioned the Bushmaster Jr. over an entire aggregation of *Riftia pachyptila* and then cinched it tightly closed around the base of the *R. pachyptila* aggregation, to collect and retain all of the associated fauna. Immediately after sampling, the intact aggregation was removed from the substrate, and the closed Bushmaster Jr. was placed in a custom-built holder (also lined with 63 µm Nitex mesh), which was mounted to *Alvin*’s basket for transport to the surface.

Upon the recovery of the submersible to the ship, any *R. pachyptila* individuals outside of the closed Bushmaster Jr. were removed and not considered in the subsequent community analyses. The Bushmaster Jr. and the holder were then emptied and rinsed with cold filtered seawater into a large container. The container was quickly relocated to a chilled room for further processing. Individuals of *Riftia pachyptila* and the mussels *Bathymodiolus thermophilus* were rinsed and removed for size and mass measurements. The length and anterior diameter of every *R. pachyptila* tube was measured to calculate the surface area (estimated as a cylinder) of each individual, and summed to determine the surface area of the entire aggregation. The tissue wet weight (WW) of smaller individuals (< 40 g) of both species was measured on a motion-compensated shipboard balance (Childress & Mickel 1980), and the WW of larger individuals was estimated by volume displacement in a graduate cylinder. Ten to fifteen individuals of both species,
representing a range of sizes, were frozen in preweighed bags for later determination of the ash-free dry weight.

The remaining fauna were rinsed in cold filtered seawater and retained on 1 mm and 63 µm sieves, fixed in 10% formalin, and transferred to 70% ethanol after 24 hours for storage and shipment. In the laboratory, the macrofauna (> 1 mm) were identified to the species level and enumerated by counting or estimation techniques. After the identification and enumeration of the macrofauna, subsamples of representative taxa from Riftia Field and Tica were weighed wet, dried at 60 °C to obtain the dry weight, and combusted in a muffle furnace at 500 °C to obtain the final ash-free dry weight (AFDW). The wet weight of the remaining individuals was multiplied by a site- and taxon-specific conversion factor to estimate the AFDW of each species. The frozen individuals and some fixed individuals of Riftia pachyptila and Bathymodiolus thermophilus were also weighed wet, dried, and combusted to obtain the final AFDW. For the individuals measured at sea, the volumes of the individuals were first converted to wet weights. Then all of the remaining individuals were weighed wet, and the AFDW was empirically determined by a site-, species- and preservation (frozen or fixed)- specific conversion factor. Non-permanent meiofauna (small individuals of macrofaunal species, 63 mm-1mm) were sorted, identified, and weighed wet at the University of Vienna. Permanent meiofauna (species < 1mm) were separated and are not included in this study. Conversion factors calculated for the macrofauna were applied to the wet weight of the non-permanent meiofaunal species to determine the total epifaunal AFDW.
Statistical analyses

The assemblage of species in each sample was described using univariate measures of community structure and multivariate measures of community composition. The species richness ($S$) is the number of species in a sample. The abundance and ash-free dry weight (AFDW) of each species was standardized to the surface area of the *Riftia pachyptila* tubes in each sampled aggregation. The standardized data were then used to calculate Pielou’s evenness ($J'$), Shannon-Wiener diversity ($H'_{\log_e}$), density (number of individuals per m$^2$ tube surface area) and biomass (g AFDW m$^2$ tube surface area) (Clarke & Gorley 2001). PRIMER v5 was used to calculate $J'$, $H'_{\log_e}$, and Bray-Curtis ($B-C$) similarity matrices (Primer-E Ltd). To construct similarity matrices for multivariate analyses, the density (number of individuals per m$^2$ tube surface area) and biomass (g AFDW per m$^2$ tube surface area) of each species was $4^\text{th}$ root transformed to down-weight the importance of the dominant species without losing the influence of the rarer species (Clarke & Gorley 2001). EstimateS v7.5.0 was used to generate species-effort curves from the species abundance data (standardized to the tubes surface area) for cumulative number of individuals and cumulative tube surface area (100 randomizations without replacement) (Colwell 2005). The foundation species, *R. pachyptila*, was excluded from all measures of community structure and composition.

For univariate measures of community structure, Wilcoxon rank-sum tests were used to evaluate the differences between sites and/ or between years, and Spearman-rank correlations were used to determine the relationship between $S$, $J'$, $H'_{\log_e}$, density, and biomass and to the environmental variables (maximum temperature, total biomass of *R. pachyptila*, and tube surface area of *R. pachyptila* aggregations) (JMP v6). Non-
parametric tests were selected because of the small sample sizes. For multivariate analyses of community composition, density and biomass similarity matrices were evaluated for site and year differences using several subroutines offered in PRIMER v5 (Clarke & Gorley 2001). ANOSIM (analysis of similarities) was used to determine whether there were significant differences in the similarity matrices between years and/or between sites, and SIMPER (similarity percentages) was used to evaluate which species contributed most to the dissimilarity between years and/or between sites (Primer E Ltd). Lastly, clustering methods were used to illustrate the patterns observed in the results of the ANOSIM tests (Primer E Ltd). In one analysis, a sample of the Riftia pachyptila community collected at Riftia Field in 1999 was included. This collection was not made with the Bushmaster Jr., however review of the video record confirmed the pilot’s report that very few individuals fell from the R. pachyptila aggregation, as it was placed into the collection box (Govenar et al. 2004). For this analysis, the standardized abundance data was divided by the total number of individuals (relative standardized abundance) before the 4th root transformation. Cluster dendrograms were constructed using the weighted mean of Bray-Curtis similarity coefficients between pairs in the data matrix (group-average linkage).

Results
The range of temperatures at Tica and Riftia Field was not significantly different between 2001 and 2002. The temperature measurements around the sampled Riftia pachyptila aggregations ranged from ambient (~ 2 °C) to a maximum of 22.7 °C (Table 3-1). In 2002, the maximum measured temperatures were higher at Riftia Field, but the
maximum sulfide concentrations were at least three times higher at Tica (Fig. 3-1). Therefore, the ratio of sulfide to temperature was much higher at Tica than Riftia Field. Furthermore, the diffuse hydrothermal fluid at Riftia Field had relatively high concentrations of iron (iron to sulfide ratio ~ 0.7) and was quite acidic (minimum pH ~ 5). In the diffuse flow at Tica, iron concentrations were undetectable, and the lowest measured pH was only moderately acidic (minimum pH ~ 6) (Le Bris et al. submitted).

Table 3-1: Environmental and biological characteristics of eight aggregations of Riftia pachyptila. The first two capital letters of the sample signifies the site where it was collected (Riftia Field, Tica) and the number signifies the year when it was collected (2001, 2002). Temperatures were measured with the low temperature probe of the DSV Alvin, number of measurements in parentheses. Sample area was estimated from the scar left on the substrate after the collection, using lasers (10 cm apart) on Alvin’s starboard sponson camera. *No lasers were available for this sample, so the sample area was estimated from the width of the manipulator arm when it was at a right angle with the substrate. ^Although the surface area was 0.03 m² on top of the lava pillar where this aggregation was collected, the “footprint” of the aggregation on the seafloor was ~ 0.16 m².

<table>
<thead>
<tr>
<th></th>
<th>Maximum temperature (°C)</th>
<th>Number of individuals</th>
<th>Total biomass (g AFDW)</th>
<th>Sample area (m²)</th>
<th>Tube surface area (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>RF1a</td>
<td>22.7 (5)</td>
<td>132</td>
<td>192.39</td>
<td>0.13</td>
<td>0.96</td>
</tr>
<tr>
<td>RF1b</td>
<td>18.2 (15)</td>
<td>209</td>
<td>698.39</td>
<td>0.06^</td>
<td>1.83</td>
</tr>
<tr>
<td>RF2a</td>
<td>19.8 (42)</td>
<td>167</td>
<td>1555.02</td>
<td>0.08</td>
<td>2.66</td>
</tr>
<tr>
<td>RF2b</td>
<td>18.8 (23)</td>
<td>11</td>
<td>94.02</td>
<td>0.02</td>
<td>0.22</td>
</tr>
<tr>
<td>TC1a</td>
<td>18.1 (9)</td>
<td>197</td>
<td>1959.69</td>
<td>0.06</td>
<td>5.23</td>
</tr>
<tr>
<td>TC1b</td>
<td>N/A</td>
<td>393</td>
<td>2988.90</td>
<td>0.03^</td>
<td>6.55</td>
</tr>
<tr>
<td>TC2a</td>
<td>10 (24)</td>
<td>96</td>
<td>2278.15</td>
<td>0.07</td>
<td>3.80</td>
</tr>
<tr>
<td>TC2b</td>
<td>13.1 (33)</td>
<td>102</td>
<td>3248.63</td>
<td>0.04</td>
<td>5.79</td>
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</table>
Figure 3-1: Total labile sulfide concentrations versus temperature in the diffuse hydrothermal fluids around aggregations of *Riftia pachyptila* at Riftia Field and Tica in 2002. Black circles represent samples from Riftia Field ($y = 1.60 x - 2.5, r^2 = 0.91, n = 37$) and white circles represent samples from Tica ($y = 9.54 x - 20.2, r^2 = 0.93, n = 133$).

The number of *Riftia pachyptila* in the sampled aggregations ranged from 11 to 393 individuals, occupying between 0.02 and 0.13 m$^2$ of the basalt substrate (Table 3-1). The widest diameter of most of the *R. pachyptila* aggregations was at the base of the aggregation, where it was in direct contact with the basalt. For these aggregations, the area of the sampling scar left by the collection was very similar to the coverage area or the “footprint” of the aggregation on the seafloor. The abundance of *R. pachyptila* varied among the eight samples, but the total biomass of *R. pachyptila* was consistently higher at Tica (Table 3-1). The total biomass of *R. pachyptila* was positively and significantly correlated with the surface area of the tubes in the aggregation ($\rho = 0.95, P = 0.0003$). The surface area of the *R. pachyptila* tubes in each sample ranged from 0.22 to 6.55 m$^2$. 
(Table 3-1), increasing the area available for the colonization of epifaunal species by at least an order of magnitude over the footprint of the aggregation on the seafloor. Despite the higher biomass and tube surface area of R. pachyptila aggregations at Tica, the relative abundance and biomass were similar between sites. Individuals of R. pachyptila only comprised between 0.5 and 3.4% of the total abundance, even though they contributed between 90.1 and 98.3% of the total biomass. R. pachyptila was excluded for subsequent descriptions of the epifaunal community, and the surface area of the tubes in each aggregation was used to standardize the abundance and biomass of the other species.

On and among the tubes of these eight Riftia pachyptila aggregations were 46 other species and > 119 000 individuals. The species richness (S) ranged from 19 to 35 in a single aggregation and was positively correlated with the surface area of the R. pachyptila aggregations (ρ = 0.69, P = 0.06). The total epifaunal density ranged from 1723 to 8216 individuals m⁻² and the biomass ranged from 10.06 to 47.37 g AFDW m⁻² (Table 3-2). There were no significant correlations between any of the univariate measures of community structure and the maximum temperature measured around the R. pachyptila aggregations or the total R. pachyptila biomass.
Table 3-2: Univariate measures of the epifaunal community structure associated with *Riftia pachyptila*. Species richness (*S*), Pielou’s evenness (*J’*), Shannon-Wiener diversity (*H’*), density, and biomass of the epifaunal species. Wilcoxon rank-sum tests were used to evaluate the differences between sites (RF vs TC) and between years (2001 vs 2002); the first number is Z value and the number in parentheses is the *P* value.

<table>
<thead>
<tr>
<th></th>
<th><em>S</em></th>
<th><em>J’</em></th>
<th><em>H’</em></th>
<th>Density (individuals m⁻²)</th>
<th>Biomass (g AFDW m⁻²)</th>
</tr>
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<tr>
<td>RF1a</td>
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<td>0.59</td>
<td>1.94</td>
<td>4332</td>
<td>21.91</td>
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<td>RF1b</td>
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<td>0.56</td>
<td>1.71</td>
<td>3601</td>
<td>11.65</td>
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<tr>
<td>RF2a</td>
<td>28</td>
<td>0.64</td>
<td>2.14</td>
<td>2032</td>
<td>13.11</td>
</tr>
<tr>
<td>RF2b</td>
<td>19</td>
<td>0.49</td>
<td>1.44</td>
<td>5186</td>
<td>10.06</td>
</tr>
<tr>
<td>TC1a</td>
<td>24</td>
<td>0.39</td>
<td>1.23</td>
<td>8216</td>
<td>38.22</td>
</tr>
<tr>
<td>TC1b</td>
<td>31</td>
<td>0.44</td>
<td>1.50</td>
<td>1723</td>
<td>13.37</td>
</tr>
<tr>
<td>TC2a</td>
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<td>0.52</td>
<td>1.66</td>
<td>6618</td>
<td>47.37</td>
</tr>
<tr>
<td>TC2b</td>
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<td>0.50</td>
<td>1.76</td>
<td>3884</td>
<td>27.37</td>
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<tr>
<td>RF vs TC</td>
<td>1.01</td>
<td>-1.59</td>
<td>-1.01</td>
<td>0.43</td>
<td>1.87</td>
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<td></td>
<td>(0.31)</td>
<td>(0.11)</td>
<td>(0.31)</td>
<td>(0.66)</td>
<td>(0.06)</td>
</tr>
<tr>
<td>2001 vs 2002</td>
<td>0.14</td>
<td>0.43</td>
<td>0.43</td>
<td>0.14</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td>(0.88)</td>
<td>(0.66)</td>
<td>(0.66)</td>
<td>(0.88)</td>
<td>(0.88)</td>
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</tbody>
</table>

Nine species were common to all of the *Riftia pachyptila* aggregations: the gastropods *Lepetodrilus elevatus*, *L. pustulosus*, *Rhynchopelta concentrica*, and *Cyathermia naticoides*, the polychaetes *Paralvinella grasslei*, *Galapagomystides aristata*, *Amphisamytha galapagensis* and *Ophryotrocha akessoni*, and the amphipod *Ventiella sulfuris*. These common species accounted for 87.1 to 99.5% of the epifaunal density and 47.3 to 88.8% of the epifaunal biomass. In every sample, either *L. elevatus* or *C. naticoides* dominated the epifaunal density, but the species that dominated the biomass varied between samples (Table 3-3). *P. grasslei* comprised 36.6 to 73.5% of the biomass in the aggregations from Riftia Field, while *L. elevatus* contributed the greatest fraction of the biomass in TC1a (36.5%), the crab *Bythograea thermydron* in TC1b (39.5%), and the mussel *Bathymodiolus thermophilus* in both samples from Tica collections in 2002 (29.9 and 32.6%, respectively for TC2a and TC2b) (Table 3-3).
Table 3-3: Composition of the epifaunal community associated with *Riftia pachyptila*. Macrofaunal density (dens.) and biomass (biom.) calculated per m² surface area of the *Riftia pachyptila* tubes in each sample. The first two capital letters of the sample signifies the site where it was collected (Riftia Field, Tica) and the number signifies the year when it was collected (2001, 2002). Biomass (g) is ash-free dry weight. *Excluded from statistical analyses.*

<table>
<thead>
<tr>
<th></th>
<th>RF1a</th>
<th>RF1b</th>
<th>RF2a</th>
<th>RF2b</th>
<th>TC1a</th>
<th>TC1b</th>
<th>TC2a</th>
<th>TC2b</th>
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<tbody>
<tr>
<td></td>
<td>dens.</td>
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<td>dens.</td>
<td>biom.</td>
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<td><strong>Polychaeta</strong></td>
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<td>5.30</td>
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<td>273</td>
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<td><strong>Aplacophora</strong></td>
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<td>Helicoradomenia spp.</td>
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<td>Leptodrillus elevatus</td>
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<td>730</td>
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<td>676</td>
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<td>1575</td>
<td>1.72</td>
<td>210</td>
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<td>1.26</td>
<td>201</td>
<td>0.64</td>
<td>137</td>
<td>0.57</td>
<td>141</td>
<td>0.19</td>
</tr>
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50
|                           |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
|                            | 346 | 0.48 | 331 | 0.76 | 235 | 0.98 | 45 | 0.12 | 185 | 0.59 | 36 | 0.16 | 151 | 0.57 | 112 | 0.48 |
| *Lepetodrilus pastulosus*  |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| *Lepetodrilus ovalis*      | 0 | 0 | 0 | 0 | 26 | 0.04 | 59 | 0.23 | 1 | <0.01 | 8 | 0.02 | 4 | 0.02 | 59 | 0.05 |
| *Lepetodrilus cristatus*   | 1 | <0.01 | 10 | 0.02 | 2 | 0.01 | 14 | 0.03 | 0 | 0 | 10 | 0.02 | 1 | <0.01 | <1 | <0.01 |
| *Peltopsira delicata*      | 0 | 0 | 0 | 0 | 0 | 41 | 0.05 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Nodopelta rigneae*        | 2 | 0.01 | 0 | 0 | 0 | 0 | 18 | 0.03 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Gorgolepis spiralis*      | 3 | <0.01 | 0 | 0 | 2 | <0.01 | 9 | <0.01 | 0 | 0 | <1 | <0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pachydermia laevis*       | 1 | <0.01 | 0 | 0 | 2 | <0.01 | 5 | <0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | <0.01 | 1 | <0.01 | 7 | 0.03 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Eupeetopsis vitrea*       | 1 | 0.02 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | <0.01 | 1 | <0.01 | 7 | 0.03 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Melanodrymnia aurantiaca* | 0 | 0 | 0 | 0 | <1 | <0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | <1 | <0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Neomphalus fretterae*     | 5 | 0.45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Peltopsira operculata*    | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Gymnobela sp. A*          | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Gorgolepis emarginus*     | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bathymargarites symplector*| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Gastropod juveniles a*    | 8 | <0.01 | 14 | <0.01 | 168 | 0.07 | 2 | <0.01 | 6 | <0.01 | 70 | 0.03 | 35 | 0.01 | 136 | 0.07 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Bivalvia**               |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| *Bathymodiolus thermophilus*| 0 | 0 | 0 | 0 | <1 | <0.01 | 0 | 0 | 14 | 2.59 | 8 | 0.25 | 11 | 14.17 | 31 | 8.93 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Arthropoda**             |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| **Decapoda**               |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| *Ventiella sulfuris*       | 60 | 0.01 | 21 | <0.01 | 53 | <0.01 | 664 | 0.14 | 500 | 0.28 | 460 | 0.16 | 1330 | 0.41 | 312 | 0.09 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bythograea thermydron*    | 13 | 0.68 | 2 | 1.93 | 7 | 4.20 | 0 | 0 | 3 | 5.03 | 13 | 5.28 | 5 | 0.45 | 2 | 1.13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dahillia caldariensis*    | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0.01 | 2 | <0.01 | 6 | 0.01 | 2 | <0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Alvinocaris tusca*        | 0 | 0 | 1 | <0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | <1 | <0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Decapod juveniles a*      | 0 | 0 | 0 | 0 | 2 | <0.01 | 16 | <0.01 | 0 | 0 | 1 | <0.01 | 2 | <0.01 | 3 | <0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Echinodermata**          |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| **Ophiuroidea**            |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| *Ophiura sp.*              | 0 | 0 | 0 | 0 | 0 | 0 | <1 | <0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0
There were no statistically significant differences in either the univariate measures of community structure \((S, J', H_{\log e}, \text{density}, \text{biomass})\) (Table 3-2) or in the multivariate measures of community composition (density: \(R = 0.03, P = 0.29\); biomass: \(R = -0.03, P = 0.49\); ANOSIM) between 2001 and 2002. More than half (63%) of the total species were collected in both years, and most of the species found exclusively in 2001 or 2002 were represented by one individual or in one sample (Table 3-3). The vestimentiferan *Oasisia alvinae* is one exception, which was only collected in 2001 at both sites (Table 3-3).

Cluster analyses illustrated the significant differences in the composition of species density and biomass between sites (density: \(R = 0.46, P = 0.03\); biomass: \(R = 0.45, P = 0.03\); ANOSIM), despite the high Bray-Curtis similarity values in pairwise comparisons (Fig. 3-2). The four samples from Tica clustered together with very high similarity \((B-C = 74.1-89.1\%)\), and three of the Riftia Field samples clustered together with high similarity \((B-C = 75.0-81.9\%)\). The smallest aggregation (RF2b), with the fewest number of individuals, species richness \((S)\) and epifaunal biomass, had the least similar community composition \((B-C = 53.9-63.1\%)\) to the other samples. Overall, the epifaunal density and biomass were higher at Tica than at Riftia Field. \(S\) was also higher at Tica, but evenness \((J')\) and diversity \((H_{\log e})\) were higher at Riftia Field. The slightly higher species diversity at Riftia Field was also evident in species-effort curves based on cumulative number of individuals and cumulative tube surface area of *Riftia pachyptila* aggregations (Fig. 3-3). Differences in the univariate measures of community structure between sites were not statistically significant (Table 3-2).
Figure 3-2: Cluster analysis (group-average linkage method) of Bray-Curtis similarity values, constructed from standardized relative abundances of every species for all samples. The same pattern is generated with Bray-Curtis similarity values constructed with standardized relative biomass. For each sample, abundance and biomass data were standardized to the surface area of the Riftia pachyptila aggregation, divided by the total, and 4th root transformed, before calculating Bray-Curtis similarity matrices.
Seventeen species were found exclusively at either Tica or Riftia Field. Of these, 11 species were represented by one individual or were present in only one sample (Table 3-3). Two species at each site were considered to be unique to those sites. The polynoid polychaete *Branchiplicatus cupreus* and the gastropod *Nodopelta rigneae* were present in
the sampled *R. pachyptila* aggregations from Riftia Field and not from Tica. Together, these two unique species contributed < 0.4% of the density and < 1.6% of the biomass in the epifaunal community, when they were present. The polynoid polychaete *Branchipolynoe symmytilida* and the leptostracan *Dahlella caldariensis* were collected in every sampled aggregation of *R. pachyptila* from Tica, but never at Riftia Field. These two unique species accounted for < 0.78% of the density and < 0.92% of the biomass in the epifaunal community. One species, *Bathymodiolus thermophilus* was much more abundant at Tica and contributed the most to the dissimilarity (12.79%) in the composition of species biomass between sites. After *B. thermophilus* was removed from the ANOSIM analysis, the difference in the species composition between sites was no longer significant for biomass ($R = 0.281, P = 0.06$; ANOSIM). However, the difference in the species composition between Riftia Field and Tica was still significant for density, without *B. thermophilus* ($R = 0.365, P = 0.03$; ANOSIM). The species that contributed most to the dissimilarity between sites were *C. naticoides*, *V. sulfuris* and *B. symmytilida* (Table 3-4).

Table 3-4: Individual species that contributed ≥ 5% to Bray-Curtis dissimilarity between epifaunal community composition at Riftia Field and Tica. Dissimilarity calculated from standardized and transformed abundances of all species except the mussel *Bathymodilus thermophilus*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Average density (number of individuals m$^{-2}$)</th>
<th>Contribution to dissimilarity (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cyathermia naticoides</em></td>
<td>RF 473 TC 865</td>
<td>6.52</td>
</tr>
<tr>
<td><em>Ventiella sulfuris</em></td>
<td>RF 200 TC 651</td>
<td>5.67</td>
</tr>
<tr>
<td><em>Branchipolynoe symmytilida</em></td>
<td>RF 0 TC 12</td>
<td>5.00</td>
</tr>
</tbody>
</table>
Discussion

At hydrothermal vents, endemic species are well adapted to the range of environmental conditions along the gradient of mixing between hydrothermal fluids and ambient seawater (Childress & Fisher 1992). However, the frequency or intensity of the environmental changes may exceed physiological tolerances, impact larval recruitment, or modify resource availability. In response to the spatial and temporal variation in physico-chemical conditions, biological interactions may further affect the composition of hydrothermal vent communities (Fustec et al. 1987, Hessler et al. 1988, Sarrazin et al. 1997, Shank et al. 1998, Sarrazin et al. 1999, Mullineaux et al. 2000, Mullineaux et al. 2003). The effects of top-down processes, such as predation and inhibition of mobile species have been shown to be greater in areas of active diffuse flow where productivity and disturbance are presumably higher (Micheli et al. 2002, Mullineaux et al. 2003), and the effect of facilitation by sessile species may be greater in areas of lower hydrothermal flux (Mullineaux et al. 2003, but see also Mullineaux et al. 2000).

The diffuse hydrothermal fluids around aggregations of Riftia pachyptila had very different chemical characteristics at Tica and Riftia Field, two discrete sites of low-temperature hydrothermal activity. In 2002, temperature and sulfide were strongly and positively correlated within each site, but the temperature to sulfide relationships were very different between sites. Thus, at the same temperature, the sulfide concentration was higher at Tica than at Riftia Field. The differences in the chemistry likely reflect differences in the composition of the source fluid and subsequent subsurface chemical processes (Le Bris et al. submitted, Von Damm & Lilley 2004). Although no chemical measurements were made in 2001, the rusty color of the Riftia tubes, pallid plumes, and
declining populations all indicate that fluid chemistry at Riftia Field in 2001 was similar to that in 2002, and different from Tica in both years.

The chemistry of the diffuse hydrothermal fluids could have influenced the availability of sulfide to *Riftia pachyptila*. In 2002, the pH was closer to neutral and iron was undetectable in the hydrothermal fluids at Tica; whereas the pH was quite acidic and iron concentrations were relatively high at Riftia Field. Subsurface iron sulfide precipitation might partly explain the sulfide depletion and acidification of the hydrothermal fluids at Riftia Field. Under these conditions, the free sulfide would have been predominantly H₂S rather than HS⁻ (Le Bris et al. submitted), which is the preferred form for *R. pachyptila* sulfide uptake (Goffredi et al. 1997). As a result, very little sulfide may have been available to *R. pachyptila*. The general appearance of the individuals and aggregations of *R. pachyptila* was further evidence of limiting resources for these animals. At Riftia Field, individuals appeared to be in relatively poor physiological condition, inferred from the pallid pink color of the plumes and the sparse distribution of small and recumbent aggregations. Within 55 months of the 1991 eruption in the same area, the only documented death of a previously thriving *R. pachyptila* colony was coincident with low sulfide and high iron concentrations, in active diffuse flow (Shank et al. 1998). At Tica, the HS⁻ fraction of the total free sulfide was higher (Le Bris et al. submitted). Accordingly, individuals of *R. pachyptila* seemed to be in much better physiological condition, with bright red plumes and white tubes; and densely distributed aggregations resembled the “haystack” morphology, typical of this species (Hessler & Smithey 1983, Hessler et al. 1988, Shank et al. 1998).
The consequence of the environmental chemistry on the apparent decline of *Riftia pachyptila* at Riftia Field may not have had an immediate effect on the resource availability to the heterotrophic species that comprise > 99% of the epifaunal density and > 67% of the epifaunal biomass. The biomass and tube surface area of *R. pachyptila* aggregations were greater at Tica, but none of the univariate measures of community structure (*S, J’, H’*, density, biomass) were significantly different between sites (Table 3-2). Multiple studies have suggested that none of the epifaunal species derive the bulk of their nutrition from *R. pachyptila* (Van Dover & Fry 1989, Fisher et al. 1994, Micheli et al. 2002, Jenkins et al. 2002, Kicklighter et al. 2004). Rather, chemoautotrophic bacteria form the base of the hydrothermal vent food web (Hessler & Smithey 1983, Grassle 1986, Van Dover & Fry 1989, Tunnicliffe 1991, Fisher et al. 1994, Micheli et al. 2002). Although sulfide-oxidizing bacteria are the most abundant microbes on the surface of *R. pachyptila* tubes (Lopez-Garcia et al. 2002), free-living bacteria can utilize a variety of electron donors other than sulfide for chemosynthetic primary production (Jannasch 1983, Karl 1995, McCollom 1997, Kelley et al. 2002).

The single species that contributed most to the low dissimilarity in the community composition between Riftia Field and Tica was the mussel *Bathymodiolus thermophilus*. Mussels were present in every collection from Tica (6.95 and 31.79% of the epifaunal biomass in 2001 and 2002, respectively), but only a single small mussel (shell length < 250 mm) was collected with one aggregation of *Riftia pachyptila* from Riftia Field in 2001 (RF1b). At the East Pacific Rise (EPR) and the Galapagos Rift, mussels typically overgrow vestimentiferan tubeworms (predominantly *R. pachyptila*) within a few years after settlement (Fustec et al. 1987, Hessler et al. 1988, Shank et al. 1998, Mullineaux et...
al. 2003). The directional replacement of species, associated with the succession from vestimentiferan dominance to mussel dominance, was evident in the species composition at Tica in 2001-2002. In addition to high relative density of *B. thermophilus*, a few other species were found exclusively at Tica that are commonly associated with mussels on the EPR. The polynoid polychaete *Branchipolyne symmytilida* lives in the mantle cavity of *B. thermophilus*, and has never been reported where mussels were absent. The leptostracan *Dahlella caldariensis* has been previously collected in mixed samples of vestimentiferans and mussels (Hessler 1984) and is common in some mussel beds on the EPR (Van Dover 2002). Although one individual of the gastropod *Eulepetopsis vitrea* was collected at Riftia Field, there was a much higher density of *E. vitrea* at Tica. *E. vitrea* is also commonly found in mussel beds at the EPR, even where *R. pachyptila* is absent (Hessler & Smithey 1983, McLean 1990, Van Dover 2002, 2003). After mussels were removed from multivariate analyses, the three species accounted for $\geq 5\%$ of the low dissimilarity in the species composition between sites either had either higher densities or were found only at Tica.

The successful colonization of mussels at Riftia Field may have been inhibited by a combination of low sulfide, low pH or high iron at Riftia Field, at the time of this study. Like vestimentiferans, *Bathymodiolus thermophilus* relies primarily on sulfur-oxidizing symbionts for its nutrition (Fisher 1990, Nelson et al. 1995). Low sulfide concentrations could have limited individual and population growth of *B. thermophilus* (Smith 1985, Fisher et al. 1988a). Unlike vestimentiferans however, *B. thermophilus* can also supplement its diet by filter-feeding (Page et al. 1991). High iron concentrations may signify high levels of other metals and mineral particulates (Desbruyères et al. 2000). At
another hydrothermal vent field on the Mid-Atlantic Ridge, the presence of mussels (Bathymodiolus spp.) was inversely related to high metal concentrations (including iron) in end-member fluids and ambient particulate flux (Desbruyères et al. 2000). In manipulative experiment at Riftia Field in 1998-1999, aggregations of R. pachyptila were removed and mussels were deployed on half of the cleared sources of diffuse hydrothermal flow (Govenar et al. 2004). Within 1 month, no mussels were evident within the site. One year later, there was 1 large mussel attached to a syntactic foam marker 50 cm above the ocean floor, and there were 6 very small mussels in one of the R. pachyptila aggregations that was collected (Govenar et al. 2004). At that time, there were small intermittent patches of rust on the basalt, but the population of R. pachyptila seemed to be in much better physiological condition at Riftia Field in the late 1990s than in 2001-2002. Changes in the composition of the hydrothermal fluids over ~ 4 years may have caused the decline in R. pachyptila populations and may have prevented the establishment of mussels at Riftia Field.

Despite the presence of a few small mussels in 1999 and the apparent change in the chemistry from 1999, the composition of the epifaunal community associated with a one-year old aggregation of R. pachyptila sampled at Riftia Field in 1999 was more similar to the other samples from Riftia Field than any of the samples from Tica, in this study (Fig. 3-2). Two of the species found exclusively at Riftia Field in 2001 and 2002 (the polynoid polychaete Branchiplicatus cupreus and the gastropods Nodopelta spp.) were also present in the sample from 1999 (Govenar et al. 2004). In addition, the polychaete Paralvinella grasslei dominated the epifaunal biomass in all sampled aggregations at Riftia Field in 1999, 2001, and 2002. The presence of B. thermophilus,
B. cupreus, Nodopelta spp. and the dominance of P. grasslei in 1999 and later in 2001 and 2002, after the chemical composition of hydrothermal fluids appears to have changed, also reflects the importance of larval dispersal and biological interactions in the distribution of hydrothermal vent fauna.

The high similarity in the structure and the composition of the community associated with Riftia pachyptila is primarily due to nine common species that dominated the epifaunal density and biomass. Some of the common species in the R. pachyptila community are also present in high relative density in mussel beds in this hydrothermal vent field (Van Dover 2003). These species included the gastropod L. elevatus, the polychaetes Amphisamytha galapagensis and Ophryotrocha akessoni, and the amphipod Ventiella sulfuris. Some other species, including the gastropods Cyathermia naticoides, L. pustulosus, and Rhynchopelta concentrica and the polychaetes P. grasslei and G. aristata, have been found less frequently in mussel beds (Van Dover 2003). The few species that accounted for the small differences in the community composition between sites, contributed very little to the cumulative epifaunal density and biomass associated with R. pachyptila. The lack of significant differences in the Riftia pachyptila community between sites and years may be due to the small number of samples. However, high local community similarity has also been documented between sites at the Juan de Fuca Ridge (Tsurumi & Tunnicliffe 2001, Govenar et al. 2002, Tsurumi & Tunnicliffe 2003), the northern and southern East Pacific Rise (Van Dover 2002, 2003), and Mid-Atlantic Ridge (Van Dover & Trask 2000). High regional dispersal of a small pool of endemic species could maintain high local community similarity in the patchy and dynamic habitats of hydrothermal vents, where productivity and disturbance

**Conclusions**

At the East Pacific Rise in 2001-2002, species richness in *R. pachyptila* aggregations was positively correlated with the surface area of *R. pachyptila* and the total biomass of *R. pachyptila*. The total biomass of *R. pachyptila* was greater at Tica than at Riftia Field, but no statistically significant differences were detected in univariate measures of the epifaunal community structure between sites. The greater biomass of *R. pachyptila* aggregations and the associated epifaunal community may reflect the energy input from higher sulfide concentrations, without a direct effect on the species richness, evenness or diversity. At both sites, the surface area provided to the epifauna by the *R. pachyptila* aggregation was greater than the space occupied on the basalt substrate by at least an order of magnitude. In addition to the increase in available substrate, the three-dimensional structure of the *R. pachyptila* aggregation increases environmental heterogeneity, modifies hydrodynamic patterns, and may provide protection from predators, which could subsequently facilitate higher local species diversity relative to the surrounding seafloor (Bruno & Bertness 2001). The differences in the species composition may be attributable to local factors within the community, such as productivity, nutrient availability, disturbance, larval settlement, competition, predation, or other non-trophic and positive biological interactions.
Notes

Nadine Le Bris, Sabine Gollner, Joanne Glanville, Adrienne Aperghis, Stéphane Hourdez, and Chuck Fisher were coauthors on the preparation and assisted in the editing of this chapter, which was submitted for consideration as a publication in January 2005. Chuck Fisher initiated this study, designed the custom-built sampling device used for these collections and provided financial and logistical support. Nadine Le Bris designed the ALCHIMIST, which was used to measure the temperature, pH, sulfide, and iron around the aggregations of *Riftia pachyptila* that were collected in 2002. Sabine Gollner identified, enumerated, and weighed the non-permanent meiofauna. Joanne Glanville and Adrienne Aperghis assisted with the sorting of specimens. Stéphane Hourdez assisted with the species identifications and sorting of specimens at sea.

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characteristic habitats of the EPR 13° N and 9° N vent fields. AGU Fall Meeting, San Francisco, CA.


Evolution 17: 373-387.


mechanism varies along a gradient in hydrothermal fluid flux at deep-sea vents.


Monograph 144.

CHAPTER 4

Influence of habitat provision and productivity on the epifaunal community associated with aggregations of *Riftia pachyptila* at deep-sea hydrothermal vents

Abstract

Habitat created or modified by the physical architecture of foundation species plays an important role in structuring communities in a variety of terrestrial, aquatic, and marine habitats. At low-temperature hydrothermal vents on the East Pacific Rise, the giant tubeworm *Riftia pachyptila* forms large and dense aggregations in a spatially and temporally variable environment. The density and diversity of smaller invertebrates is higher in association with aggregations of *R. pachyptila* than on the surrounding basalt rock seafloor. Artificial substrates, designed to mimic *R. pachyptila* aggregations, were deployed along a gradient in productivity for one year to test the hypothesis that high local species diversity is maintained by the provision of physical structure in a high productivity habitat. Species assemblages were compared between artificial aggregations in low, intermediate, and high productivity zones and to natural aggregations of *R. pachyptila*. Endemic hydrothermal vent fauna colonized every artificial aggregation, but the epifaunal density and species richness was highest in areas of high chemosynthetic primary production. Compared to natural aggregations of *R. pachyptila*, the average species richness was similar and Shannon-Wiener’s species diversity was higher in artificial aggregations deployed in high and intermediate productivity zones. Thus, complex physical structure alone can support local species diversity in areas of chemosynthetic primary production. Differences in the species composition between natural and artificial aggregations may reflect differences in
hydrothermal fluid flux and biological interactions associated with ecological succession at low-temperature hydrothermal vents. These factors may further contribute to the maintenance of regional species diversity in hydrothermal vent communities on the East Pacific Rise.

Introduction

2004), serpulids (Kaiser et al. 1999, Schwindt et al. 2004), siboglinids (Sarrazin and Juniper 1999, Tsurumi and Tunnicliffe 2001, Govenar et al. 2002, Bergquist et al. 2003, Tsurumi and Tunnicliffe 2003, Govenar et al. 2004, Urcuyo et al. in press), crinoids (Fishelson 1974, Zmarzly 1985), and ascidians (Fielding et al. 1994). The physical structure of foundation species can facilitate species coexistence and increase species diversity by increasing the surface area available for colonization, altering hydrodynamic patterns, stabilizing the substrate, obstructing foraging by consumers, creating refuge from predators, retaining propagules, and concentrating nutrients and food sources (Bruno and Bertness 2001, and references therein). Biological interactions with foundation species can have additional positive effects at population, community and ecosystem levels, by modifying environmental conditions (temperature, pH, chemical composition) of the aquatic medium (Redfield 1958) and/ or providing cues for larval settlement (Pawlik 1992, Walters et al. 1996). While foundation species may be a source of food for consumers (Bustamante et al. 1995) or consume some potential colonists by filter-feeding larvae (Crooks 1998), these trophic interactions are not directly related to habitat provision or modification.

At basalt-hosted hydrothermal vents of the East Pacific Rise, the density and diversity of smaller invertebrates associated with the giant tubeworm *Riftia pachyptila* is higher than on the surrounding seafloor (Tunnicliffe 1991, Shank et al. 1998, Govenar et al. in press). *R. pachyptila* relies on an obligate internal symbiosis with sulfide-oxidizing chemoautotrophic bacteria for nutrition (Fisher 1990, Childress and Fisher 1992) and grows quickly to large sizes and forms dense aggregations in areas were diffuse hydrothermal fluids mix vigorously with ambient seawater (Fisher et al. 1988b, Lutz et
al. 1994, Shank et al. 1998). Despite the abundant source of biomass provided by *R. pachyptila*, none of the epifaunal heterotrophic species seem to derive the bulk of their nutrition directly from *R. pachyptila* (Van Dover and Fry 1989, Fisher et al. 1994). Rather, free-living bacteria form the base of the food web (Jannasch, Karl 1995, Kelley et al. 2002). While sulfide-oxidizing bacteria are the most abundant microbes on the surface of *R. pachyptila* tubes (Lopez-Garcia et al. 2002) and sulfide-oxidation is the most common chemoautotrophic pathway at hydrothermal vents (Karl 1995, McCollom and Shock 1997), sulfide inhibits aerobic cellular respiration. Thus, sulfide is toxic to most metazoans, even though endemic hydrothermal vent fauna are often well adapted to sulfide exposure (Childress and Fisher 1992). Due to the costs and benefits associated with sulfide exposure, a previous study predicted differences in epifaunal communities associated with *R. pachyptila* aggregations at high and low sulfide sites (Govenar et al. in press). *R. pachyptila* appeared to be in poor physiological condition at the low sulfide site, but the density and biomass of the epifaunal community in *R. pachyptila* aggregations was not significantly different from the high sulfide site. There were also no significant differences in the species richness, evenness or diversity, and the community composition was remarkably similar between sites. Moreover, the species richness was positively correlated with the tube surface area of the *R. pachyptila* aggregations, at both sites (Govenar et al. in press). Therefore, the relative importance of the habitat provided by *R. pachyptila* aggregations may have outweighed the effects of the environmental chemistry in regulating the structure and composition of the epifaunal community. As both free-living bacterial primary production and growth rates of *R. pachyptila* are dependent on chemoautotrophy, it cannot be determined whether the
increase in species richness was due to higher productivity at the scale of an individual aggregation, larger habitat area provided by the physical structure of the aggregation, or biological attributes of the habitat provided or modified by \textit{R. pachyptila}.

The aim of this study was to further examine the role of \textit{R. pachyptila} as a foundation species in hydrothermal vent communities and to test the hypothesis that local species diversity in the epifaunal community associated with \textit{R. pachyptila} is maintained by the provision of complex physical structure in high productivity habitats. The use of artificial substrates in this experiment allowed the opportunity to decouple the size of \textit{R. pachyptila} aggregations from the bottom-up processes associated with productivity and to provide the physical structure of \textit{R. pachyptila} aggregations along a productivity gradient, where \textit{R. pachyptila} would not naturally occur.

**Methods**

In this study, four artificial aggregations were deployed in each of three locations within a diffuse-flow site, “Tica” (9°50.447’N, 104°17.493’W, 2500 m depth), which is located on the segment of the East Pacific Rise between the Siqueiros and Clipperton transform faults. Tica is ~200 m north of the northern-most location of the “Biogeotransect”, established by R. Lutz and collaborators (Shank et al. 1998) and was colonized by \textit{Riftia pachyptila} in 1997 (Fornari et al. 2004). Based on patterns observed at similar hydrothermal vent areas on the East Pacific Rise and the Galapagos Rift, conditions at Tica characterized the early to middle succession stages of biological community development (Hessler et al. 1988, Shank et al. 1998). At the time of this study, from November 2002 to November 2003, there were dense aggregations of \textit{R.}
*Pachyptila*, distributed in patches throughout the site, and small to medium-sized mussels (*Bathymodiolus thermophilus*) among the tubeworms and on the basaltic substrate.

Artificial aggregations were constructed from clear, low-grade PVC (polyvinyl chloride) hose to resemble natural *R. pachyptila* aggregations. The relationship of tube length to anterior diameter, the relative size frequency, and the density (individuals m\(^{-2}\)) were determined from aggregations of *R. pachyptila* collected at the East Pacific Rise in 2001 and 2002, including four aggregations from Tica (Govenar et al. in press) and used to design the artificial aggregations. Each artificial aggregation consisted of 80 tubes in four size classes: 20 individuals (10 cm length, 1.25 cm diameter), 28 individuals (15 cm length, 1.25 cm diameter), 20 individuals (20 cm, 2.5 cm diameter), and 12 individuals (30 cm, 2.5 cm diameter). The total surface area of the tubes in each artificial aggregation was 1.28 m\(^2\).

The end of each tube was packed with a cellulose sponge to prevent animals from colonizing the interior surfaces of the tubes. Prior to packing, the sponges were thoroughly rinsed in filtered seawater. To form an aggregation, the tubes were held together by plastic cable ties and secured to a Vexar plastic mesh (49 mm\(^2\) opening) base. A 30 cm piece of steel chain, coated in plastic, was attached to the base in order to weigh down the aggregation, orient it perpendicularly to the substrate, and still allow for water to pass through the interstitial spaces between the tubes. After all of the aggregations were constructed, they were rinsed and incubated in filtered seawater for 48 hours, changing the seawater after the first 24 hours, and then deployed by the DSV *Alvin*.

Four artificial aggregations were deployed in each of three locations. Artificial aggregations embedded in a large aggregation of *R. pachyptila* were considered to be in a
high productivity zone. Artificial aggregations deployed ~ 50 cm away from *R. pachyptila* aggregations, on uncolonized basalt, were considered to be in an intermediate productivity zone. Artificial aggregations deployed ~ 20 m away from visible hydrothermal activity and any individuals of *R. pachyptila* were considered to be in a low productivity zone.

One aggregation from each of the treatments was recovered with *Alvin* in November 2002, 10 days after the deployment, in order to develop and test recovery methods. Very few individuals colonized the short-term deployments (data not shown). The remaining nine aggregations were recovered approximately one year later (346 ± 1 days). On three consecutive dives, using the DSV *Alvin*, each aggregation was lifted by the polypropylene rope handle and placed carefully into separate boxes, mounted on an “elevator”. After the all of the boxes were securely closed, the elevator weight was released, and it rose to the surface and was recovered to the deck of the R/V *Atlantis*. Each aggregation was removed from the box and placed into a container. Then, the water was drained from the box into the same container that held the corresponding aggregation.

In the laboratory, on board the ship, each artificial aggregation was disassembled in the water, and the tubes were examined for attached specimens and thoroughly rinsed with filtered seawater into the same container. Specimens were collected on 1 mm, 250 mm, and 63 mm sieves, fixed in formalin for 24 hours, and transferred to 70% ethanol for shipment and storage. In the laboratory at PSU, all of the macrofaunal species retained on 63 mm and larger size sieves were identified and enumerated.
The average abundance, species richness (S), Pielou’s evenness (J’), and Shannon-Wiener’s diversity ($H'_{\log e}$) were compared between treatments. To compare univariate measures of community structure in artificial and natural aggregations, the abundance of each species was first divided by the surface area before calculating species evenness (J’) and species diversity ($H'_{\log e}$). Bray-Curtis similarity matrices were constructed from 4th root transformed abundance data for two multivariate analyses, from the subroutines offered in PRIMER v5 (Clarke and Gorley 2001). Clustering techniques were used to determine the similarity in the species composition between artificial aggregations in high, intermediate, and low productivity zones, and non-metric multidimensional scaling (MDS) was used to compare the species composition in artificial and natural R. pachyptila aggregations. Analysis of variance (ANOVA) and Tukey’s post-hoc comparisons were used to evaluate the differences in univariate measures of species diversity (S, J’, and $H'_{\log e}$) between treatments.

As part of a previous study, a quantitative sampling device was used to collect four R. pachyptila aggregations along with all of the associated fauna from Tica, (Govenar et al. in press). The species abundance data from these collections were used to compare univariate measures of community structure and the composition of the species assemblages between natural and artificial aggregations.

**Results**

**Artificial aggregations**

Endemic hydrothermal vent fauna colonized all of the artificial aggregations along the productivity gradient. In total, 9519 individuals were collected in nine artificial
aggregations, representing 52 taxa; 41 were identified to the species-level, two were identified to the genus-level, and ten were identified to the family-level, five of which may be undescribed species. Nine species were found in every treatment; the polychaetes *Amphisamytha galapagensis*, *Ophryotrocha akessoni*, and *Prionospio sandersi*, the gastropods *Bathymargarites symplector*, *Clypeosectus delectus*, and the crustaceans *Bythograea thermydron*, *Ventiella sulfuris*, and two unidentified amphipod species (spp. 2 and 4). Of these species, only *O. akessoni* and *C. delectus* were present in every artificial aggregation, and *O. akessoni* dominated the abundance in all treatments (Table 4-1).
Table 4.1: Composition of species assemblages in artificial aggregations. Number of individuals m⁻² for all species and univariate measures of community structure in each artificial aggregation.

<table>
<thead>
<tr>
<th></th>
<th>Low</th>
<th>Intermediate</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L1</td>
<td>L2</td>
<td>L3</td>
</tr>
<tr>
<td><strong>Annelida</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Polychaeta</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amphisamithy galapagensis</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Archinome rosacea</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Branchinotoglumella grasslei</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Branchinotoglumella hessleri</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Branchinotoglumella sandersi</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Branchipolyne symmytilida</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Galapagomystides aristata</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Hesiospina vestimentifera</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Hesionid spp nov.</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Iphionolla risensis</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lepidnotopodium atalantae</td>
<td>1</td>
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<td>Lepidnotopodium rifense</td>
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<td>Lepidnotopodium williamsae</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Levensteiniella kincaidi</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Levensteiniella plicata</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Polynoid spp nov.</td>
<td>0</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Nereis sandersi</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nicomache ardwesoni</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ophryotrocha akessoni</td>
<td>38</td>
<td>11</td>
<td>27</td>
</tr>
<tr>
<td>Oasisia alvinae</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Prionospio sandersi</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Mollusca</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Aplacaphora</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Helicoradomenia spp.</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Bivalvia</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bathypecten vulcani</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Bathymodiolum thermophilus</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Gastropoda</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bathymargarites symplector</td>
<td>0</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Clypeoscopectus deflectus</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Cyathermia naticoides</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Euleptopseps vitrea</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lepetodrilus cristatus</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lepetodrilus elevatus</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lepetodrilus ovalis</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lepetodrilus pustulosus</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Melanodryma aurantiaca</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nodopelta rigneae</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Peltospira operculata</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rhynchopelta concentrica</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Provanna ios</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Phymorrhyncus major</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
The average species richness and the density of individuals were significantly lower in the low productivity zone than the other treatments (Table 4-2). In this treatment, the average species evenness was slightly higher but very similar to the intermediate and high productivity zones (Table 4-2). The intermediate and high productivity zones were not significantly different in any of the univariate measures of community structure, even though the average density was ~35% higher in the high productivity zone (Table 4-2).
Table 4-2: Univariate measures of community structure for artificial aggregations in low, intermediate and high productivity zones and natural aggregations of Riftia pachyptila. Average density, species richness (S), Pielou’s evenness ($J'$), Shannon-Wiener diversity ($H'_{\text{log}_e}$) of macrofaunal species; standard deviation in parentheses. *Significantly different from other treatments, $P < 0.05$.

<table>
<thead>
<tr>
<th></th>
<th>Density</th>
<th>S</th>
<th>$H'_{\text{log}_e}$</th>
<th>$J'$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low ($n = 3$)</td>
<td>43 (9)*</td>
<td>11 (2)*</td>
<td>1.54 (0.55)</td>
<td>0.65 (0.18)</td>
</tr>
<tr>
<td>Intermediate ($n = 3$)</td>
<td>961 (189)</td>
<td>30 (0)</td>
<td>2.14 (0.31)</td>
<td>0.63 (0.09)</td>
</tr>
<tr>
<td>High ($n = 3$)</td>
<td>1475 (1254)</td>
<td>27 (4)</td>
<td>2.07 (0.25)</td>
<td>0.63 (0.07)</td>
</tr>
<tr>
<td>Natural ($n = 4$)</td>
<td>5110 (2881)</td>
<td>29 (5)</td>
<td>1.54 (0.23)</td>
<td>0.46 (0.06)</td>
</tr>
</tbody>
</table>

The composition of the species assemblages in artificial aggregations clustered into two groups, which corresponded to the low and the intermediate and high productivity zones (Fig. 4-1). Artificial aggregations in the intermediate productivity zone (M1, M2, and M3) were had the most similar species composition. Two of the artificial aggregations (H1 and H2) in the high productivity zone were more similar the intermediate productivity zone than one of the aggregations (H3), which was not in the same location as where it was deployed one year earlier.

Figure 4-1: Cluster analysis of pair-wise Bray-Curtis similarity coefficients between all of the artificial aggregations along the productivity gradient (H1, H2, H3 = high productivity zone; M1, M2, M3 = intermediate productivity zone; L1, L2, L3 = low productivity zone).
In the low productivity zone, artificial aggregations were deployed at least 20 m away from any individuals of *R. pachyptila*. The species that were found exclusively in the low productivity zone were two undescribed polychaetes (a polynoid and a hesionid), one undescribed species of amphipod (sp. 5), the pectenid bivalve *Bathypecten vulcani*, and a small individual of the galatheid *Munidopsis subsquamosa* (carapace width < 1 cm). The species overlap between aggregations in the low productivity zone and the intermediate and high productivity zones was 26.1 and 23.4 %, respectively.

Within the intermediate productivity zone, the species richness was the same in the three artificial aggregations, deployed on uncolonized basalt rock, < 0.5 m away from aggregations of *R. pachyptila* (Table 4-1, Table 4-2). Attached to two of the aggregations (M2 and M3) were several individuals of the mussel *Bathymodiolus thermophilus* (Table 4-1). The other aggregation (M1) had no individuals of *B. thermophilus*, however the several of the plastic tubes were covered with what appeared to be filamentous bacteria. This aggregation had a much lower species density and slightly different species composition than the aggregations that were colonized by *B. thermophilus* (Table 4-1). There were five species found only in the intermediate productivity zone: the polynoid polychaete *Iphionella risensis*, the gastropods *Lepetodrilus cristatus*, *Nodopelta rigneae*, and *Melanodrymia aurantiaca*, and the amphipod *Euonyx mytilis*. Of these species, *I. risensis* and *M. aurantiaca* were found in every artificial aggregation in this treatment (Table 4-1). The species overlap between aggregations in the intermediate and high productivity zones was 70.2 %.

Within the high productivity zone, three artificial aggregations were deployed in a large aggregation of *R. pachyptila*. At the time of the recovery, one artificial aggregation
(H1) remained embedded in the center of the aggregation of *R. pachyptila*, one (H2) was recumbent and embedded along the edge the same aggregation, and one (H3) apparently fell out of the aggregation and was found on the uncolonized basalt substrate, ~ 1 m away from other aggregations *R. pachyptila*. The species richness was highest in the artificial aggregation embedded in the center of the *R. pachyptila* aggregation and lowest in the aggregation that was not in contact with *R. pachyptila* or directly exposed to hydrothermal flow (Table 4-2). The species found exclusively in the high productivity zone were the phyllodocid polychaete *Galapagomystides aristata*, the snail *Cyathermia naticoides*, and two crustaceans, an unidentified tanaid and the leptostracan *Dahlella caldereinsis* (Table 4-1). *G. aristata* and *C. naticoides* were present in all three artificial aggregations (H1, H2, and H3).

**Artificial and natural aggregations of Riftia pachyptila**

In natural aggregations of *R. pachyptila*, the density of individuals was much higher than in any of the artificial aggregations (Table 4-2). However, the species richness in the intermediate and high productivity zones fell within the range of the species richness of natural *R. pachyptila* aggregations. Over 75% (78.1%) of species collected in natural aggregations were also present in artificial aggregations. Species that were shared between natural and artificial aggregations fell into two groups. All of the species in the first group were most abundant in natural aggregations and generally increased in abundance along the productivity gradient in artificial aggregations, and all of the species in the second group were most abundant in artificial aggregations in either the intermediate or the high productivity zones (Fig. 4-2).
Figure 4-2: The density (number of individuals m$^{-2}$) of shared species between natural and artificial aggregations. The first panel is the species that were more abundant in natural aggregations (R), and the second panel is the species that were more abundant in artificial aggregations (L = low, M = intermediate, and H = high productivity zones).

An MDS (non-metric multi-dimensional scaling) plot grouped the species assemblages into three groups: low productivity zone, intermediate and high productivity...
zones, and natural aggregations of *R. pachyptila* (Fig. 4-3). Similar to the results of the cluster analysis, the aggregations in the low productivity zone (L1, L2, L3) were the least similar to the other groups, and the aggregations in the intermediate productivity zone (M1, M2, M3) were the most similar to each other (Fig. 4-3). However, the MDS plot provides further insight into the differences in the species composition between the natural and artificial aggregations (Fig. 4-3). The aggregation (H3) that was no longer embedded within an aggregation of *R. pachyptila* and was found ~ 1 m away from any individuals of *R. pachyptila* tended toward similarity with the artificial aggregations in the low productivity zone. The aggregation (H2) that was embedded near the edge of an *R. pachyptila* aggregation was most similar to the artificial aggregations in the intermediate productivity zone. The aggregation (H1) that was embedded in the middle of an *R. pachyptila* aggregation tended toward similarity with natural aggregations of *R. pachyptila*. 
Figure 4-3: Non-metric multidimensional scaling (MDS) plot of pairwise Bray-Curtis similarity coefficients between natural aggregations of Riftia pachyptila (TC1a, TC1b, TC2a, TC2b) and artificial aggregations in high (H1, H2, H3), intermediate (M1, M2, M3), and low (L1, L2, L3) productivity zones. Natural aggregations are named for the collection site (Tica = TC) and year (2001 = 1 and 2002 = 2).

Discussion

Complex physical structure alone seemed to have facilitated the colonization of some species to the artificial aggregations. The dorvilleid polychaete *Ophryotrocha akessoni* and the slit limpet gastropod *Clypeosectus delectus* were found in every artificial aggregation, and the trochid gastropod *Bathymargarites symplector* and the amphipod *Ventiella sulfuris* were found in eight of nine artificial aggregations. The presence of these endemic species on all of the artificial substrates in all productivity zones reflects the extent of hydrothermal vent larval dispersal and the lack of specificity in the larval settlement of these species.

Some species found in artificial aggregations in the low productivity zone may not be endemic to hydrothermal vents. Of the five species found exclusively in this
treatment, three may be new to science and none have ever been found in natural R. *pachyptila* aggregations. The uncommon and new species found in artificial aggregations in the low productivity zone likely reflect a relative lack of sampling effort in the periphery of active hydrothermal flow.

In addition to the complex structure provided by artificial aggregations, chemosynthetic primary production played an important role in the distribution of species. The presence of the mussel *Bathymodiolus thermophilus*, which harbors chemoautotrophic symbionts, in all of the artificial aggregations in the high productivity zone and either mussels or free-living filamentous bacteria on all of the artificial aggregations in the intermediate productivity zone indicate that artificial aggregations in both of these treatments were exposed to sufficient sulfide to support chemoautotrophy. Consequently, the epifaunal density was at least ten times higher and there were twice as many species in artificial aggregations in the intermediate and high productivity zones than in the low productivity zone.

Despite the larger surface area provided by natural *R. pachyptila* aggregations and the higher epifaunal density in natural aggregations, the species richness was similar between natural and artificial aggregations (Table 4-2). The numerical dominance of a few species may have contributed to the reduction of both the species diversity ($H'$) and limited the species richness in natural aggregations. Gastropods, often the limpet *Lepetodrilus elevatus*, dominate the abundance and biomass of the epifaunal community in natural *R. pachyptila* aggregations (Govenar et al. 2004, Govenar et al. in press). These limpets graze on microbial films and prey on invertebrate larval colonists. Grazing can thus reduce the survival of new recruits and could lower the species richness by
removing rare species. Species diversity ('') would then be reduced either by grazing and removing invertebrate colonists and by the numerical dominance of limpets in natural aggregations of *R. pachyptila*.

Predation by fish and other predators may reduce the abundance of limpets and lead to an increase in species diversity in hydrothermal vent communities (Micheli et al. 2002, Sancho et al. 2005). The effects of predation and inhibition have been shown to be greater along an increasing gradient in hydrothermal fluid flux, using caged and uncaged basalt blocks (Micheli et al. 2002, Mullineaux et al. 2003). However, *R. pachyptila* aggregations may increase habitat complexity and provide a refuge from predation. The physical structure of artificial aggregations would presumably inhibit predators as well as natural aggregations, but the relative abundance of limpets was much lower in artificial aggregations, and the effect of grazing may have been subsequently less important.

The patterns in the distribution of some species are best explained by either environmental differences at the microhabitat-scale, succession processes, or biological interactions between species. *R. pachyptila* and another vestimentiferan *Tevnia jerichonana* were absent from artificial aggregations, although both species have been shown to recruit to plastic (Tygon) tubing (Hunt et al. 2004). These two vestimentiferan species are often early colonists to new areas of active diffuse hydrothermal flow (Fustec et al. 1987, Shank et al. 1998). The polychaete *Paralvinella grasslei*, which contributes a large portion of the epifaunal biomass in natural aggregations (Govenar et al. 2004, Govenar et al. in press), was also absent in artificial aggregations. *P. grasslei* typically occurs on the surface of high-temperature vents and at the base of *R. pachyptila* tubes, where maximum temperatures can be ~ 30 °C (Fustec et al. 1987, Jollivet 1993, Juniper
and Martineu 1995, Shank et al. 1998, Govenar et al. in press). Although artificial aggregations were deployed within a natural aggregation of *R. pachyptila* and were exposed to environmental conditions typical of the habitat of *R. pachyptila*, the base of the artificial aggregation was several centimeters above the substrate and may have been exposed to lower temperatures and concentrations of hydrothermal fluids than the source of diffuse flow on the basalt rock. Some species were less abundant in artificial aggregations than natural aggregations of *R. pachyptila*, including the polychaete *Galapagomystides aristata*, the gastropods *Cyathermia naticoides*, *Lepetodrilus elevatus*, *L. pustulosus*, *Rhynchopelta concentrica* and the amphipod *Ventiella sulfuris*. These species increased in abundance along the productivity gradient in artificial aggregations and usually dominate the abundance and biomass of the epifaunal community associated with *R. pachyptila* aggregations (Govenar et al. 2004 and Govenar et al. in press). Two of these species, *G. aristata* and *C. naticoides* were collected exclusively in the three artificial aggregations in the high productivity zone. The absence and lower abundance of some species in artificial aggregations suggests that these species may be associated with higher hydrothermal fluid flux, early succession stages, or biological attributes of *R. pachyptila*.

Many species that were more abundant in artificial aggregations than natural aggregations of *R. pachyptila* also generally occur more frequently in mussel beds than with *R. pachyptila* (Van Dover 2003, Govenar et al. 2004, Govenar et al. in press). These species include the polychaete *Archinome rosacea*, the gastropods *Eulepetopsis vitrea*, *Lepetodrilus ovalis*, *Bathymargarites symplector*, the leptostracan *Dahlella caldariensis* and an undescribed ophiuroid in the genus *Ophiura* (Van Dover 2002, Govenar et al. in
press). In addition, the polynoid polychaete *Levensteiniella plicata* and the amphipod *Euonyx mytilis* were found exclusively in artificial aggregations that had been colonized by mussels, in the intermediate and high productivity zones. The transition from vestimentiferan dominance to mussel dominance has been documented at other sites on the East Pacific Rise and the Galapagos Rift (Hessler et al. 1985, Hessler et al. 1988, Shank et al. 1998). The mechanism of succession may be related to a combination of geochemical changes coupled with waning hydrothermal fluid flux and biological interactions between vestimentiferans and mussels (Hessler et al. 1985, Hessler et al. 1988, Shank et al. 1998, Mullineaux et al. 2000, Mullineaux et al. 2003, Hunt et al. 2004). The species composition associated with either *R. pachyptila* or mussels may reflect the directional replacement of species associated with the succession of hydrothermal vent communities.

Local species diversity in the epifaunal community associated with aggregations of *R. pachyptila* at low-temperature hydrothermal vents on the East Pacific Rise is maintained partly by the provision of complex physical structure of the foundation species in high productivity habitats. The total density, the distribution of species, and the community composition is strongly influenced by bottom-up processes, including productivity and nutrient availability, as well as top-down processes, such as predation and competition. The presence of some of the epifaunal species with either *R. pachyptila* or mussels, suggest that foundation species may not be interchangeable (Machicote et al. 2004). As a result, source-sink dynamics between communities associated with either foundation species and species turnover with the succession from *R. pachyptila*
dominance to mussel dominance may increase species diversity at the regional scale of hydrothermal vents on the East Pacific Rise (Leibold et al. 2004).

Notes

Chuck Fisher is a coauthor on the manuscript that will develop from this chapter. In addition to financial and logistic support for this study, he provided valuable insight in the experimental design and the interpretation of the results.

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CHAPTER 5

Ecological patterns and processes in hydrothermal vent metacommunities

At low-temperature hydrothermal vents on the East Pacific Rise, the giant vestimentiferan tubeworm *Riftia pachyptila* grows quickly and forms dense aggregations (Lutz et al. 1994, Shank et al. 1998). *R. pachyptila* relies on internal sulfur-oxidizing bacteria for nutrition, and must obtain carbon dioxide from the diffuse hydrothermal fluids and oxygen from ambient seawater to sustain chemoautotrophy (Childress and Fisher 1992, for review). Sulfur-oxidation is the principal chemical reaction used for primary production by symbiotic and free-living chemosynthetic bacteria, which form the base of the food web (Jannasch 1983, Fisher 1990, Karl 1995). As a result of the high individual and population growth rates of *R. pachyptila* and free-living chemoautotrophic bacteria, productivity in this diffuse-flow hydrothermal vent habitat could rival rates of primary production in kelp forests and coral reefs.

The physical structure of *R. pachyptila* aggregations could change hydrodynamic patterns, retain larvae and food sources, provide refuge from predation, and increase the area available for colonization by an order of magnitude compared to the area of the seafloor occupied by *R. pachyptila* (Tunnicliffe 1991, Shank et al. 1998, Micheli et al. 2002, Govenar et al. 2004, Govenar et al. in press). Metabolic activities of *R. pachyptila* could additionally alter the chemical environment (i.e. sulfide concentrations and pH) (Childress and Fisher 1992, Goffredi et al. 1997, Goffredi et al. 1999, Girguis et al. 2002, Le Bris et al. 2003, Le Bris et al. submitted), which may serve as cues for larval settlement (Shank et al. 1998, Mullineaux et al. 2000, Hunt et al. 2004). The habitat
created by *R. pachyptila* aggregations may facilitate species coexistence as well as
maintain local and regional species diversity in hydrothermal vent communities. The
density and diversity of smaller heterotrophic invertebrates is higher in association with
aggregations of *R. pachyptila* than the surrounding basalt rock substrate (Tunnicliffe
1991, Shank et al. 1998), and the species richness of the epifaunal community increases
with the surface area of *R. pachyptila* aggregations (Govenar et al. in press).

Before this study, the animals associated with *R. pachyptila* had only been
haphazardly collected and described. Community patterns had been characterized from
photographic documentation at annual intervals or longer (Hessler and Smithey 1983,
relative importance of predation and inhibition in structuring the community associated
with *R. pachyptila* had been explored with manipulative field experiments (Micheli et al.
2002, Mullineaux et al. 2003). However, the abundance, biomass, and species diversity
of the epifaunal community had never been described or quantified, and the relative
importance of biogenic structure and productivity to the community had never been
explored. This thesis focuses on patterns of community structure and the patterns that
regulate these patterns.

After the complete removal of six aggregations of *R. pachyptila*, approximately
200 mussels were deployed on three of the exposed sources of diffuse hydrothermal flow
(Govenar et al. 2004). One year later, all but one of the mussels had disappeared and
aggregations of *R. pachyptila* reestablished in half of the clearances. One of the
aggregations was collected to characterize the composition of the community associated
with a *R. pachyptila* aggregation of a known age. Although a few individuals of *R.*
were > 1 m in tube length, the largest individuals never occupied > 60% of their total tube. The population also was highly skewed to the smallest individuals, which suggests that recruitment occurred throughout the previous year and included very recent settlement of *R. pachyptila*. Among the epifaunal species collected in this aggregation of *R. pachyptila*, there were six small mussels. While adult mussels may have not been able to tolerate the temperature or concentration of the hydrothermal fluids in the cleared sources of diffuse flow, the habitat provided by the physical structure of the *R. pachyptila* aggregation may have ameliorated the environment or facilitated the colonization of mussels and 23 other species.

An additional eight aggregations of *R. pachyptila* were collected at two discrete sites in two consecutive years to investigate variations in the epifaunal community structure at small spatial and temporal scales (Govenar et al. in press). The temperature ranges at both sites were similar, however the diffuse hydrothermal fluids at one site had high iron, low sulfide and relatively acidic pH; and the other site had no detectable iron, high sulfide and close to neutral pH (Govenar et al. in press, Le Bris et al. submitted). At the low-sulfide/ high-iron site, rust covered patches of the basalt rock substrate and the shells and tubes of the resident invertebrates. In addition, the physiological condition of *R. pachyptila* seemed to be in decline from previous years. In contrast, the *R. pachyptila* was in seemingly excellent physiological condition at the high-sulfide site. Despite the differences in the environmental conditions, the structure and the composition of the epifaunal communities were remarkably similar. The abundance and the biomass of the epifaunal communities were dominated by nine common species, found in all of the sampled aggregations. The few unique species to each site occupied relatively little of
the epifaunal abundance or biomass. The physical structure provided by *R. pachyptila* aggregations may have outweighed the effects of environmental sulfide concentrations in regulating the structure and composition of the epifaunal communities.

Artificial substrates, designed to mimic *R. pachyptila* aggregations, were deployed along a gradient in productivity for one year (Chapter 4). Endemic hydrothermal vent fauna colonized all of the artificial aggregations, and the species richness in intermediate and high productivity zones were as high as natural aggregations of *R. pachyptila*. These results suggest that while the physical structure of aggregations of *R. pachyptila* can maintain local species diversity in the presence of chemosynthetic primary production, productivity and biological interactions also play important roles in the distribution of individual species and community composition.

At the East Pacific Rise and the Galapagos Rift, mussels typically overgrow *R. pachyptila* within a few years, as hydrothermal activity wanes and temperatures and sulfide concentrations decrease (Hessler et al. 1985, Hessler et al. 1988, Shank et al. 1998). Alternatively, changes in the chemical composition of the hydrothermal fluids may result in the decline of *R. pachyptila* populations and inhibit mussel colonization (Shank et al. 1998, Govenar et al. in press). The directional replacement of species following the succession from *R. pachyptila* dominance to mussel dominance was evident in the distribution of a few species in natural and artificial aggregations (Govenar et al. in press, Chapter 4). Larval dispersal and migration of mobile species may contribute to the high species overlap between epifaunal communities, while small differences in the community composition associated with either *R. pachyptila* or mussels may maintain regional diversity.
Local species diversity at low-temperature hydrothermal vents may be maintained by the physical structure of foundation species (Chapter 4). The epifaunal community also seems to be remarkably similar between aggregations of *R. pachyptila* at small temporal and spatial scales (Govenar et al. in press). High community similarity has been documented in diverse assemblages of invertebrates associated with vestimentiferan aggregations at the Juan de Fuca Ridge (Sarrazin et al. 1997, Sarrazin and Juniper 1999, Tsurumi and Tunnicliffe 2001, Govenar et al. 2002, Tsurumi and Tunnicliffe 2003) and mussel beds at the East Pacific Rise and the Mid-Atlantic Ridge (Van Dover and Trask 2000, Van Dover 2002, 2003). On mid-ocean ridges, similarity between local hydrothermal vent communities may be maintained by high dispersal of a small pool of endemic species (Chase 2003, Govenar et al. in press). A group of local communities with high connectance of constituent species maybe viewed as a metacommunity (Wilson 1992, Leibold 1998, Leibold et al. 2004). Environmental factors related to hydrothermal fluid flux drive local processes, including productivity and the provision of biogenic structure, which can explain patterns at the regional scale of a metacommunity (Shurin et al. 2000, Mouquet and Loreau 2002, 2003, Cottenie and De Meester 2004, Leibold et al. 2004). High regional species diversity at the East Pacific Rise has been attributed to large-scale ecological factors such as geologic age, fast spreading rate, high to intermediate disturbance frequency and intensity, and large areas of diffuse hydrothermal flow (Tunnicliffe 1988, Juniper and Tunnicliffe 1997, Van Dover 2002, Van Dover et al. 2002, Van Dover 2003). However, results from this body of work, suggest that habitat provision or environmental modification at local scales by different foundation species may also help to maintain regional species diversity. At the global scale, the East Pacific
Rise is the only mid-ocean ridge where both vestimentiferan aggregations and mussel beds are present, which may increase the regional species diversity relative to the Juan de Fuca Ridge, which does not have dense mussel beds, and the Mid-Atlantic Ridge, where vestimentiferans have never been reported.

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Three *Ridgeia piscesae* assemblages from a single Juan de Fuca Ridge sulphide edifice: structurally different and functionally similar

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Introduction

At the Endeavour Segment of the Juan de Fuca Ridge, Sarrazin et al. (1997, 1999) and Sarrazin & Juniper (1999) developed a dynamic succession model for sulphide edifice communities by characterizing the dominant fauna, biomass distribution, and environmental parameters of different neighbouring species assemblages on a single sulphide edifice. According to the model, *Paralvinella sulfincola* Desbruyères & Laubier, 1993, is the first metazoan to colonize sulphide edifices in areas of high temperature and active fluid flow (assemblage I). As temperatures cool and fluid flow slows, populations of *Paralvinella palmiformis* Desbruyères & Laubier, 1986, develop (assemblage II) and are eventually displaced by the recruitment of *Lepetodrilus fucensis* McLean, 1988 and *Depressigyra globulus* Warén & Bouchet, 1988, (assemblage III). Over time, *Ridgeia piscesae* Jones, 1985, start to emerge among the gastropods and come to dominate the assemblage as fluid flow slows and temperature drops (assemblage V-Low Flow). Alternatively, *R. piscesae* may appear with *P. palmiformis* in more active hydrothermal flow (assemblage V-High Flow).

In this study, we describe five quantitative collections of three epifaunal assemblage-types with the vestimentiferan *R. piscesae*, from a single sulphide edifice in the Main Endeavour Field, at the Endeavour Segment of the Juan de Fuca Ridge. A primary objective is to present the species composition, the size frequency distribution of the dominant fauna, and the total biomass within a defined sample area, for each collection, and compare this to the assemblage descriptions in Sarrazin & Juniper (1999). Using these quantifiable ecological parameters, we evaluate structural differences between the assemblage-types to develop a better understanding of the function of *R. piscesae* in these assemblages. We also compare these results to data from a previous study of a quantitative collection of a basalt aggregation in the Main Endeavour Field. This allows us to illustrate the functional similarity among the three assemblage-types that contain *R. piscesae* in the dynamic sulphide edifice environment to the *R. piscesae* basalt community in a different, more stable environment.

Material and methods

In September 1999, we employed the DSRV *Alvin* to collect five quantitative samples of three epifaunal assemblages from a single sulphide edifice, “Bastille” (47° 57’ N, 129°08’ W, 2200 m), in the Main Endeavour Field (Endeavour Segment, Juan de Fuca Ridge). Before each collection, we surveyed the temperature and water chemistry of each sampling site and classified the species assemblages (assemblages I-IV, V-LF, V-HF) using Sarrazin & Juniper’s (1999) scheme. We collected one sample each of assemblage III and assemblage IV (*Alvin* dive 3463); and three samples of assemblage V-HF, named V1, V2, and V3 respectively (*Alvin* dive 3460). Note that although the species list of assemblage III in Sarrazin & Juniper (1999) (which is based on a single grab) does not include *R. piscesae*, the original description (Sarrazin et al., 1997) indicates that small *R. piscesae* are occasionally present in this assemblage-type.

We sampled each assemblage with the “Chimneymaster”, a custom built, hydraulically actuated collection device that has an open diameter of 30 cm and is lined with a 63 µm Nitex net. We considered a collection to be quantitative (all visible biological material collected from a defined surface area) if the observers in the *Alvin*
indicated that all went well, and a careful review of the video record confirmed the presence of a clean sampling scar on the surface of the sulphide edifice, and no loss of material as the sample was contained in an isolated compartment of a polyvinyl chloride (PVC) collection box. This device does not make quantitative collections from all surfaces, but the five collections considered here all met the above criteria. After the recovery of the samples on board, we preserved all of the collections in either 10% formalin or 70% ethanol for morphological and genetic identification techniques, and later moved all of the samples to fresh 70% ethanol for shipping and storage.

For each of the five collections, we sorted and identified all of the macrofauna (>250 µm) to the species level. We constructed size frequency histograms for the dominant fauna of all five collections using morphometric measurements that are highly correlated with preserved wet weight (R² > 90% for all, data not shown). For *L. fucensis* we used a geometrically increasing sieve series (0.25, 0.5, 1, 2, and 4 mm) to divide the species population into size classes. For *P. palmiformis*, we measured the width of the seventh setiger (see McHugh, 1989) and for *R. piscesae*, we measured the total worm length. Several morphometric measurements of *R. piscesae* were good estimates of size, including tube anterior diameter, tube length, and worm vestimentum length. From each species population, at least one quarter of the individuals were processed to determine a preserved wet weight to ash-free dry weight conversion factor. Then we calculated the total ash-free dry weight of each species population by multiplying the conversion factor by the preserved wet weight of all of the remaining individuals and adding the ash-free dry weight of the subsample. To calculate the biomass (g m⁻²) of the two-dimensional sample area, we used the area of the open Chimneymaster collection device (0.07 m²) to estimate the surface area originally occupied by the community. To calculate the surface area contributed by the tubes of *R. piscesae*, we calculated the surface area of the frustrum of a cone with the total length (L) and the measured radii of the anterior (A) and posterior (P) ends of the tubes (SA = (p/2)(A+P)L) for the individuals processed for dry weight determination (about 25% of the population). We then extrapolated to the total number of individuals in the sample.

In order to consider these assemblages in the context of the full range of *R. piscesae* assemblage types, we compared the data from our collections to that from a basaltic aggregation of *R. piscesae* collected from a very different microhabitat (Eckner, 1999; Urcuyo, 2000). This species assemblage, collected from a diffuse-flow habitat at Easter Island (47°57' N, 129°06' W, 2200 m), in the Main Endeavour Field, was sampled with a similar, but larger, custom-built device operated by *Alvin*, named the “Bushmaster”. This collection was processed using the same methods as for the sulphide edifice communities (see Eckner, 1999; Urcuyo, 2000).

We characterized the species composition in each collection with three different indices: species richness (S) = the total number of species in a sample; evenness (E) = the variability in the distribution of individuals among species; and the Shannon-Weiner index of species diversity (H'), a measure of the combined influence of species richness and evenness in quantitative samples (Begon et al., 1999). To compare species richness and evenness between assemblages, we employed the Morisita-Horn similarity coefficient (CMH). This coefficient is designed to detect niche overlap between similar species of a community by calculating the proportion of common species between two samples. A value of 0 indicates no overlap, and a value of 1 indicates identical proportional species composition (Horn, 1966). From the resulting matrix of similarity coefficients of the five collections and the basalt aggregation, we constructed a dendrogram. In size frequency histograms of the dominant fauna in each collection, we illustrate a representation of the periodicity of reproduction and growth of the species population in the sample area. Next we constructed a table of the density and the biomass of all of the species in each collection. Then we used a rank abundance curve to examine niche partitioning among species of an assemblage. A geometric distribution would indicate that species within an assemblage are dividing resources evenly, while a logarithmic distribution would indicate that species within an assemblage divide niches disproportionately (May, 1975). Last we compared the species diversity to the *R. piscesae* tube surface area in all collections.

### Results and Discussion

The species composition and biomass of each assemblage-type that was included in the dynamic succession model of Sarrazin et al. (1997, 1999) and Sarrazin & Juniper, (1999) was based on single collections of assemblages I, II, III, IV, V-LF and V-HF. Here we use five collections of three visibly different assemblages, using a different sampling tool, to provide additional data on species composition and biomass of different assemblage types and test the generality of their model. In our collections, the number of macrofaunal species was higher and the density of each species was generally higher in each assemblage type than reported by Sarrazin & Juniper (1999). The single exception was the density of *L. fucensis* in assemblage III, which was 3.7 times lower than their sample. The total biomass of each assemblage-type was within the range reported for all vestimentiferan assemblages at the Juan de Fuca Ridge (Sarrazin & Juniper, 1999). The biomasses of all three collections of assemblage V-HF were similar to that reported by Sarrazin & Juniper (1999), but the biomasses of our quantitative collections of assemblages III and IV were substantially higher; approximately 4.5 times higher for type III and over 40 times higher for type IV. These differences may be due in part to differences in the efficacy of the collection methods, but also likely reflect natural variation between sites and collections. Clearly, additional work will be needed to resolve these discrepancies and more completely characterize all of the assemblage types.

Community structure may be described as the distribution and abundance of component species, the number of individuals, the size frequencies of individual species populations, or the distribution of biomass among
species within a community (Begon et al., 1999). The full range of species richness among the five collections (III, IV, V₁, V₂, V₃) is found in the three samples of assemblage V-HF that show the greatest range of species richness (8-13 species) (Table 1). Assemblages III and IV have species richness values that fall within this range (Table 1). The diversity indices (H’) vary between 0.90 and 1.31 for all of the collections, with all three samples of assemblage V-HF displaying the lowest values. Most of the individuals in the assemblage V-HF samples are distributed among only a few species, thus the low species evenness yields a low diversity. Conversely, assemblage III has the highest index of diversity because the individuals are more evenly distributed among species (Fig. 1). However, relative species abundances reveal important differences between assemblages that are not reflected in species richness, evenness or diversity. For example, assemblage IV has a similar species richness and diversity index to the collection V₁, but they have very different dominant species. *L. fucensis* and *D. globulus* (gastropods) dominate assemblage IV, whereas *R. piscesae* and *P. palmiformis* (polychaetes) dominate assemblage V-HF (Fig. 1).

**Table 1.** Three indices of species composition for each collection.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Species Richness (S)</th>
<th>Evenness (E)</th>
<th>Shannon-Weiner diversity index (H’)</th>
</tr>
</thead>
<tbody>
<tr>
<td>III</td>
<td>12</td>
<td>0.53</td>
<td>1.31</td>
</tr>
<tr>
<td>IV</td>
<td>9</td>
<td>0.59</td>
<td>1.29</td>
</tr>
<tr>
<td>V₁</td>
<td>8</td>
<td>0.49</td>
<td>1.01</td>
</tr>
<tr>
<td>V₂</td>
<td>12</td>
<td>0.46</td>
<td>1.16</td>
</tr>
<tr>
<td>V₃</td>
<td>13</td>
<td>0.35</td>
<td>0.90</td>
</tr>
</tbody>
</table>

**Figure 1.** Relative abundance of all of the species present in a collection; no individuals present (no square), 0.01- 10% (white squares), 10- 33% (gray squares), >33% (black squares). (For the genus names see Table 2).

Community function is defined as the biological interactions among species and between species and the environment, and can be described by the role of the community in ecosystem processes (succession, trophic organization, or niche partitioning between the component species) (Begon et al., 1999). In the size frequency histograms of assemblage IV, small individuals dominate the populations of *R. piscesae* and *P. palmiformis*, and large individuals dominate the population of *L. fucensis* (Fig. 3). These size distributions suggest that there has been a recent recruitment of small worms, and smaller limpets are not replacing larger individuals. If age is proportional to size, this pattern could demonstrate the transition from assemblage IV to V-HF, where a new recruitment of *R. piscesae* and *P. palmiformis* is replacing a declining population of *L. fucensis*. According to the model of Sarrazin & Juniper (1999), IV would be replaced by V-LF in the presence of decreased hydrothermal flow. We suggest that if flow increases (as a result of a tectonic event, for example) V-HF could follow IV, and gastropods would no longer be present in high densities due to mortality or migration. In our sample of assemblage III, most (>90%) of the *R. piscesae* tubes were empty. This suggests that an environmental change in fluid flow or chemistry may have caused a reversion from assemblage V-LF to assemblage III. Although Sarrazin & Juniper (1999) do not consider this type of reversion, it is generally consistent with the mechanism of their dynamic succession model. The species composition is measurably different between assemblage-types, the biological succession from IV to V-HF and reversion from V-LF to III, suggests that the different assemblages (III, IV and V-HF) of *R. piscesae* may represent different stages within a single dynamic community.
The distribution of biomass among trophic guilds in assemblages IV and V-HF is dominated first by the “primary producer” *R. piscesae* and second by the primary consumers *P. palmiformis* and *L. fucensis*. In collections IV, V1, V2, and V3, *R. piscesae* comprises 48 to 72% of the total biomass. Where *R. piscesae* is not dominant (assemblage III), the biomass distribution is dominated by *P. palmiformis*, a primary consumer (Table 2). In all assemblages, secondary consumers (predators) contribute very little to the total biomass (Table 2). Predators are reported to be relatively uncommon on sulphide edifices in general, possibly due to the environmental stresses of variable high temperature and high sulphide concentration (Vöight, 2000; MacDonald et al., this volume).

All the rank abundance curves of the sulphide edifice assemblages follow a geometric series distribution (Fig. 4). According to May (1975) this suggests that most species are competing equally for a shared resource. We also observe a significant negative relationship between species diversity and *R. piscesae* surface area (Fig. 5). This is consistent with the trends in Sarrazin & Juniper (1999) for *R. piscesae* surface area and the species richness in assemblages IV, V-LF, and V-HF. In contrast, a basalt community from the same site shows much higher abundance and species richness, and the rank

### Table 2. Biomass and density of all macrofaunal species in each collection.

<table>
<thead>
<tr>
<th>Species</th>
<th>Collection</th>
<th>III</th>
<th>IV</th>
<th>V1</th>
<th>V2</th>
<th>V3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Symbiont-containing species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ridgeia piscesae</em></td>
<td></td>
<td>23.3</td>
<td>983.2</td>
<td>757.2</td>
<td>1408.2</td>
<td>742.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(212)</td>
<td>(18250)</td>
<td>(14996)</td>
<td>(21263)</td>
<td>(9903)</td>
</tr>
<tr>
<td>Primary consumers</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Amphisamytha galapagensis</em></td>
<td></td>
<td>&lt;0.1</td>
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1 Biomass is presented as ash-free dry weight (g m⁻²) with density (number of individuals m⁻²) in parentheses. 2 There is inconclusive evidence that both of these gastropods may harbor chemosynthetic symbionts, but the nutritional relation between the host and the symbiont is unknown (McLean, 1988; Eckner, 1999).
abundance curves follow a logarithmic distribution (Fig. 4). This implies that a few dominant species occupy a greater amount of the niche. In the diffuse-flow microhabitat of basaltic aggregations, the often metre-long tubes of *R. piscesae* may increase habitat heterogeneity by spanning microhabitats that range from direct exposure to diffuse flow (around their base) to undetectable exposure to vent flow (around their anterior ends), and thus provide more niches for a greater variety of species (Urcuyo, 2000).

Although *R. piscesae* is present in both sulphide edifice and basalt communities, it may play a very different ecological role in each habitat.

**Conclusion**

We began our investigation of the productivity and the energy flow of Northeast Pacific hydrothermal vent ecosystem with a quantification of the biomass of the different assemblage-types present on Juan de Fuca Ridge sulphide edifices. By employing measurable ecological parameters, we were able to distinguish structural differences between assemblages III, IV, and V-High Flow.

Our results generally support Sarrazin et al.’s dynamic succession model (Sarrazin et al., 1997, Sarrazin & Juniper, 1999), although the community biomass and densities here are often much greater than previously reported. Overall, we demonstrate that visibly distinct species assemblages can be functionally similar and likely represent a single dynamic community. In future work, we will compare other collections of epifaunal assemblages from different sulphide edifices within the Main Endeavour and at High-Rise Field (sampled in August 1998) to further test the general applicability of the dynamic succession model (Sarrazin et al., 1997; Sarrazin & Juniper, 1999) and better constrain species distributions and biomass estimates for each assemblage type. This project marks a preliminary step in our long-term goal of quantitatively modeling productivity and energy flow in the hydrothermal vent ecosystem, of the Endeavour Segment of the Juan de Fuca Ridge.

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**References**


VITA

Breea Govenar

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Research experience

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Publications


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Department of Biology travel award, The Pennsylvania State University
RIDGE travel award, RIDGE program (NSF)
Braddock Fellowship, The Pennsylvania State University
France-Amérique Prize, Tulane University

Professional organizations
Ecological Society of America (2000- present)
The American Society of Naturalists (2001- present)
American Geophysical Union (2003- present)