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

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ABSTRACT: The vestimentiferan tubeworm *Riftia pachyptila* (Polychaeta: Sibloglinidae) often dominates early succession stages and high productivity habitats at low-temperature hydrothermal vents on the East Pacific Rise. We collected 8 aggregations of *R. pachyptila* and the associated epifaunal community at 2 discrete sites of diffuse hydrothermal activity, in December 2001 and December 2002. Because of 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 1 yr or 500 m distance between very different sites. There was no significant difference in the temperature ranges of the diffuse flow between sites or years, even though the environmental conditions were very different at the 2 sites. At 1 site (Riftia Field), the diffuse hydrothermal fluids 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* appeared 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 species. Aggregations of *R. pachyptila* support high local species diversity relative to the surrounding seafloor and high community similarity in different hydrothermal vent habitats.

KEY WORDS: Hydrothermal vent · East Pacific Rise · *Riftia pachyptila* · Community structure · Epifauna · Benthos

INTRODUCTION

A basic premise in ecology is that similar habitats support similar communities (Samuels & Drake 1997). Within a particular habitat, changes in community structure may be explained by non-equilibrium dynamics or alternate stable states (Sousa 2001, Petraitis & Dudgeon 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 is 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, Wootton & Power 1993, Ohmann & Spies 1998). 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). However, high regional dispersal of a small pool of endemic

species could also maintain high local community similarity in different habitats.

Compared to other deep-sea habitats, hydrothermal vents 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 East Pacific Rise (EPR), large magmatic and tectonic disturbances can occur on decadal scales, which can create new habitat and 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.

Hydrothermal vent habitats are ephemeral, dynamic, and patchily distributed along mid-ocean ridges. Between the Clipperton and Siqueiros fracture zones, near 9° 50′ N on the EPR, a patchwork of numerous high-temperature vents and areas of diffuse hydrothermal flow are distributed within the axial summit caldera (Haymon et al. 1993). Although the source of the diffuse flow may 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 scales of centimeters and seconds at the same point (Luther et al. 2001, Von Damm & Lilley 2004). Colonization patterns of endemic vent species to a site can vary substantially with time, hydrothermal flux, and as a result of biological interactions (Shank et al. 1998, Mullineaux et al. 2000, 2003, Micheli et al. 2002, Hunt et al. 2004). Within months of the April 1991 eruption near 9° 50′ N on the EPR, a few macrofaunal species colonized nascent vent sites; and within 2.5 yr, the vestimentiferan tubeworm *Riftia pachyptila* formed dense aggregations (Shank et al. 1998). Within 1 yr 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). Because of 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 would seem likely at both large and small spatial and temporal scales.

At low-temperature hydrothermal vents of the EPR, *Riftia pachyptila* can form dense aggregations of high biomass in areas of vigorous diffuse flow, where temperatures can range from 2 to ~30°C and sulfide concentrations can be as high as 725 µM (Shank et al. 1998, Luther et al. 2001, Mullineaux et al. 2003, Le Bris et al. in press). *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 (review by Childress & Fisher 1992). Individuals of this species can reach 3 m in tube length and 650 g wet weight (Grassle 1986, Fisher et al. 1988a). Single aggregations of *R. pachyptila* may comprise 2000 individuals m^{-2} (Shank et al. 1998), can comprise 96% of the community biomass (Govenar et al. 2004), and often 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, the epifaunal community associated with *Riftia pachyptila* was sampled at 2 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 diffuse 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.

MATERIALS AND METHODS

Site. We collected 8 aggregations of *Riftia pachyptila* and the associated epifaunal community with a quantitative sampling device, operated from the DSV 'Alvin', near 9° 50′ N on the East Pacific Rise (EPR); 2 aggregations of *R. pachyptila* and the associated fauna were collected at each of 2 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.

Individuals of *Riftia pachyptila* colonized Riftia Field at least 5 yr before Tica (J. P. Hickey, DSV 'Alvin' pilot and expedition leader, Woods Hole Oceanographic Institution, pers. comm.). 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 (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, mostly perpendicular to the substrate.

Temperatures were measured with the 'Alvin's' low-temperature probe at the base, center, and top of 7 of the 8 aggregations of *Riftia pachyptila*, which were subsequently sampled for community analyses. In 2002, the total labile sulfide ($\Sigma H_2S = H_2S$, HS^- and S^{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 min^{-1} during each scan. Calibrations were performed *in situ* during each dive. The pH was measured using a 1-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. in press).

Community sampling. All community samples were collected with a hydraulically-actuated collection net, named the 'Bushmaster Jr.'. The Bushmaster Jr. is lined with a 63 µm Nitex mesh and can sample areas up to 60 cm in diameter (0.28 m^2). 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 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 the 'Alvin' basket for transport to the surface.

Upon recovery of the submersible to the ship, any *Riftia pachyptila* individuals outside the closed Bushmaster Jr. were removed and not considered in 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 *R. pachyptila* and the mussel *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, and the WW of larger individuals was estimated by volume displacement in a graduated cylinder. For later determination of ash-free dry weight, 10 to 15 individuals of both species, representing a range of sizes, were frozen in preweighed bags.

The remaining fauna were rinsed in cold filtered seawater and retained on 1 mm, 250 and 63 µm sieves, fixed in 10% formalin, and transferred to 70% ethanol after 24 h for storage and shipment. In the laboratory, the macrofauna (>1 mm) were identified to species level and enumerated by counting or estimation techniques. After identification and enumeration of the macrofauna, subsamples of representative taxa from Riftia Field and Tica were wet-weighed, dried at 60°C to obtain dry weight, and combusted in a muffle furnace at 500°C to obtain 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 wet-weighed, 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 remaining individuals were wet-weighed, 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 µm to 1 mm) were also sorted, identified, and wet-weighed. Permanent meiofauna (species < 1 mm) 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. 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 m^{-2} tube surface area) and biomass (g AFDW m^{-2} tube surface area) (Clarke & Gorley 2001). PRIMER Version 5 was used to calculate J', $H'_{\log e}$, and Bray-Curtis (B-C) similarity matrices (Primer-E). To construct similarity matrices for multivariate analyses, the density (number of individuals m^{-2} tube surface area) and biomass (g AFDW m^{-2} tube surface area) of each species was 4th root transformed to down-weight the importance of the dominant species without losing the influence of the rarer species (Clarke & Gorley 2001). EstimateS Version 7.50 was used to generate species-effort curves from the species abundance data (standardized to the tube surface area) for cumulative number of individuals and cumulative tube surface area (100 randomizations without replacement) (Colwell 2005: EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. Persistent URL <purl.oclc.org/estimates>). 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 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 *Riftia pachyptila*, and tube surface area of *R. pachyptila* aggregations) (JMP Version 6). 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 Version 5 (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 between sites (Primer E). Lastly, clustering methods were used to illustrate the patterns observed in the results of the ANOSIM tests (Primer E). In 1 analysis, a sample of the *R. 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

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

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 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 8 samples, but the total biomass of *R. pachyptila* was consistently higher at Tica (Table 1). The total bio-

Table 1. *Riftia pachyptila*. Environmental and biological characteristics of 8 aggregations on East Pacific Rise. Sample designation indicates the site of collection (RF = Riftia Field, TC = Tica) and the year of collection (1 = 2001, 2 = 2002). Temperatures measured with low temperature probe of the DSV 'Alvin' (number of measurements in parentheses). Sample area estimated from scar left on substrate after the collection, using lasers (10 cm apart) on the DSV's starboard sponson camera. n: no. of individuals; na: not available

Sample	Max. T (°C)	n	Total biomass (g AFDW)	Sample area (m^2)	Tube surface area (m^2)
RF1a	22.7 (5)	132	192.39	0.13	0.96
1b	18.2 (15)	209	698.39	0.06[a]	1.83
2a	19.8 (42)	167	1555.02	0.08	2.66
2b	18.8 (23)	11	94.02	0.02	0.22
TC1a	18.1 (9)	197	1959.69	0.06	5.23
1b	na	393	2988.90	0.03[b]	6.55
2a	10 (24)	96	2278.15	0.07	3.80
2b	13.1 (33)	102	3248.63	0.04	5.79

[a]No lasers available, so sample area estimated from width of the manipulator arm at right angles with substrate

[b]Although surface area was 0.03 m^2 on top of the lava pillar where this aggregation was collected, the 'footprint' of the aggregation on the seafloor was ~0.16 m^2
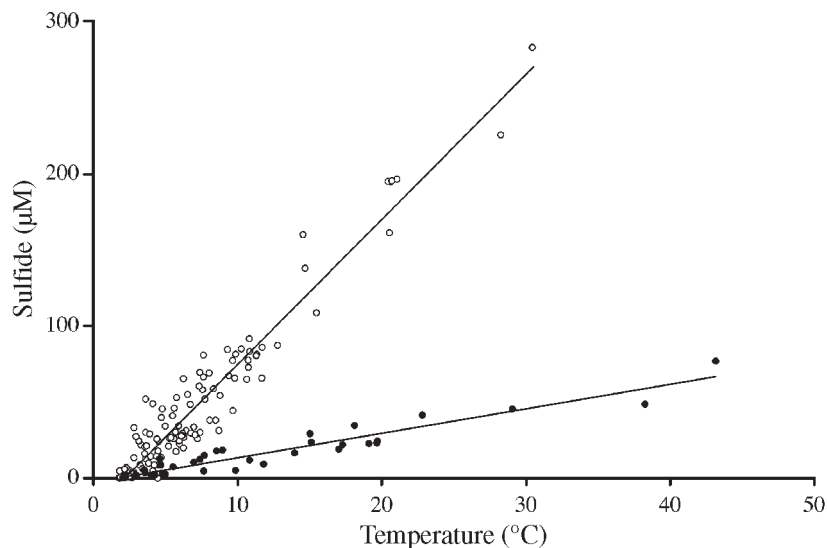
Fig. 1. Total labile sulfide concentrations versus temperature in diffuse hydrothermal fluids around aggregations of *Riftia pachyptila* at Riftia Field and Tica sites in 2002. (●) Samples from Riftia Field ($y = 1.60x - 2.5$, $r^2 = 0.91$, n = 37) and (○) samples from Tica ($y = 9.54x - 20.2$, $r^2 = 0.93$, n = 133)

Amphisamytha galapagensis, *Ophryotrocha akessoni*, and *Galapagomystides aristata*; the gastropods *Lepetodrilus elevatus*, *Cyathermia naticoides*, *Rhynchopelta concentrica*, and *L. pustulosus*; 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). *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 Sample TC1a (36.5%), the crab *Bythograea thermydron* in Sample TC1b (39.5%), and the mussel *Bathymodiolus thermophilus* in both samples from Tica collections in 2002 (29.9 and 32.6%, respectively for Samples TC2a and TC2b.

There were no statistically significant differences in either the univariate measures of community structure (*S*, *J'*, $H'_{\log e}$, density, biomass) (Table 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 1 individual or occurred in 1 sample (Table 3). The vestimentiferan *Oasisia alvinae* was an exception, being collected only in 2001 at both sites (Table 3).

mass of *R. pachyptila* was positively and significantly correlated with the surface area of the tubes in the aggregation (ρ = 0.95, p < 0.001). The surface area of the *R. pachyptila* tubes in each sample ranged from 0.22 to 6.55 m² (Table 1), increasing the area available for the colonization of epifaunal species by at least 1 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 of *R. pachyptila* 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 from 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 8 *Riftia pachyptila* aggregations were 46 other species and >119 000 individuals. The species richness (*S*) in a single aggregation ranged from 19 to 35 and was positively correlated with the tube surface area of the aggregation (ρ = 0.69, p = 0.06). Total epifaunal density ranged from 1723 to 8216 individuals m⁻² and biomass from 10.06 to 47.37 g AFDW m⁻² (Table 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.

Among all the *Riftia pachyptila* aggregations, 9 species were shared: the polychaetes *Paralvinella grasslei*,

Table 2. Univariate measures of epifaunal community structure associated with *Riftia pachyptila*: species richness (*S*), Pielou's evenness (*J'*), Shannon-Wiener diversity ($H'_{\log e}$), density, and biomass (ash-free dry wt, AFDW) of epifaunal species. Wilcoxon rank-sum tests used to evaluate differences between sites (RF vs. TC) and years (2001 vs. 2002), whereby first number is *Z*-value and number in parentheses is p-value

Sample	*S*	*J'*	$H'_{\log e}$	Density (ind. m⁻²)	Biomass (g AFDW m⁻²)
RF1a	26	0.59	1.94	4332	21.91
1b	1	0.56	1.71	3601	11.65
2a	28	0.64	2.14	2032	13.11
2b	19	0.49	1.44	5186	10.06
TC1a	24	0.39	1.23	8216	38.22
1b	31	0.44	1.50	1723	13.37
2a	25	0.52	1.66	6618	47.37
2b	35	0.50	1.76	3884	27.37
RF vs. TC	1.01	−1.59	−1.01	0.43	1.87
	(0.31)	(0.11)	(0.31)	(0.66)	(0.06)
2001 vs. 2002	0.14	0.43	0.43	0.14	0.14
	(0.88)	(0.66)	(0.66)	(0.88)	(0.88)

Table 3. Composition of epifaunal community associated with *Riftia pachyptila*. Macrofaunal density (D, ind. m^{-2} tube surface area) and biomass (B, g ash free dry wt m^{-2} tube surface area) of *R. pachyptila* tubes in each sample are given

Epifauna	RF1a D	RF1a B	RF1b D	RF1b B	RF2a D	RF2a B	RF2b D	RF2b B	TC1a D	TC1a B	TC1b D	TC1b B	TC2a D	TC2a B	TC2b D	TC2b B
Annelida																
Polychaeta																
Paralvinella grasslei	364	16.62	404	5.22	161	5.30	161	3.71	241	6.85	49	3.35	316	13.39	150	5.30
Amphisamytha galapagensis	348	0.07	172	0.03	246	0.03	273	0.04	43	0.01	59	0.02	78	0.02	139	0.04
Ophryotrocha akessoni	19	0	27	<0.01	164	0.01	418	0.07	3	<0.01	28	0.01	116	0.01	132	0.01
Galapagomystides aristata	265	0.86	70	0.26	46	0.14	141	0.43	45	0.24	36	0.24	138	0.70	22	0.10
Paralvinella pandorae	397	0.64	39	0.02	29	0.03	0	0	10	<0.01	30	0.07	6	<0.01	7	<0.01
Hesiospina vestimentifera	72	0.37	2	0.01	2	0.01	5	0.01	0	0	4	0.04	0	0	4	0.01
Branchipolynoe symmytilida	0	0	0	0	0	0	0	0	4	0.05	3	<0.01	14	0.51	28	0.18
Branchinotogluma grasslei	22	0.17	3	0.02	11	0.51	0	0	2	0.05	1	0.05	4	0.02	1	<0.01
Opisthotrochopodus alvinus	18	0.07	4	0.01	10	0.05	0	0	1	0.01	2	0.02	3	0.02	1	0.01
Nereis sandersi	4	0.02	0	0	2	0.07	5	0.19	1	0.02	2	0.05	1	0.09	12	0.36
Branchinotogluma hessleri	10	0.05	2	0.01	3	0.03	0	0	1	0.01	1	0.01	1	0.01	1	<0.01
Tevnia jerichonana	1	<0.01	0	0	<1	<0.01	9	1.53	<1	<0.01	4	0.81	1	0.28	0	0
Oasisia alvinae	6	0.05	0	0	0	0	0	0	1	<0.01	4	0.37	0	0	0	0
Lepidonotopodium williamsae	0	0	1	0.01	3	0.05	0	0	1	0.03	<1	<0.01	3	0.11	1	0.06
Levensteiniella kincaidi	0	0	0	0	0	0	9	0.01	0	0	0	0	0	0	0	0
Branchinotogluma sandersi	0	0	2	0.05	3	0.16	0	0	<1	<0.01	1	0.03	1	<0.01	1	0.02
Lepidonotopodium atalantae	3	<0.01	2	<0.01	1	<0.01	0	0	0	0	<1	<0.01	0	0	1	<0.01
Branchiplicatus cupreus	1	0.01	2	0.18	1	0.10	0	0	0	0	0	0	0	0	0	0
Archinome rosacea	0	0	0	0	1	<0.01	0	0	0	0	<1	<0.01	0	0	2	<0.01
Lepidonotopodium riftense	0	0	0	0	0	0	0	0	0	0	<1	<0.01	0	0	0	0
Prionospio sandersi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	<0.01
Iphionella risensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<1	<0.01
Polychaete juveniles[a]	0	0	0	0	10	<0.01	0	0	0	0	3	<0.01	4	<0.01	11	0.01
Mollusca																
Aplacophora																
Helicoradomenia spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	<0.01
Gastropoda																
Lepetodrilus elevatus	1907	0.75	730	0.75	676	0.77	3186	3.35	4924	13.95	929	2.25	2965	10.37	1947	5.50
Cyathermia naticoides	98	0.01	1575	1.72	210	0.05	5	0.02	1911	5.97	13	<0.01	930	2.24	608	2.37
Rhynchopelta concentrica	366	1.26	201	0.64	137	0.57	141	0.19	319	2.53	19	0.14	532	3.97	286	2.63
Lepetodrilus pustulosus	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 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
Peltospira delicata	0	0	0	0	0	0	41	0.05	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
Gorgoleptis spiralis	3	<0.01	0	0	2	<0.01	9	<0.01	0	0	<1	<0.01	0	0	0	0
Pachydermia laevis	1	<0.01	0	0	2	<0.01	5	<0.01	0	0	0	0	0	0	7	<0.01
Eulepetopsis vitrea	1	0.02	0	0	0	0	0	0	0	0	2	<0.01	1	<0.01	7	0.03
Melanodrymia aurantiaca	0	0	0	0	<1	<0.01	0	0	0	0	0	0	0	0	<1	<0.01
Neomphalus fretterae	5	0.45	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peltospira operculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	<0.01
Gymnobela sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.05
Gorgoleptis emarginus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	<0.01
Bathymargarites symplector	0	0	0	0	0	0	0	0	0	0	0	0	<1	<0.01	<1	<0.01
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
Bivalvia																
Bathymodiolus thermophilus	0	0	0	0	<1	<0.01	0	0	14	2.59	8	0.25	11	14.17	31	8.93
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
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
Dahlella caldariensis	0	0	0	0	0	0	0	0	5	0.01	2	<0.01	6	0.01	2	<0.01
Alvinocaris lusca	0	0	1	<0.01	0	0	0	0	0	0	<1	<0.01	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
Echinodermata																
Ophiuroidea																
Ophiura sp.	0	0	0	0	0	0	0	0	<1	<0.01	0	0	0	0	0	0

[a]Excluded from statistical analyses

Cluster analyses illustrated significant differences in the species composition 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. 2). The 4 samples from Tica clustered together with very high similarity (B-C = 73.3 to 86.9%), and 3 of the Riftia Field samples clustered together with high similarity (B-C = 75.3 to 81.8%). The smallest aggregation (Sample RF2b), with the fewest number of individuals, species richness (*S*) and epifaunal biomass, had the least similar community composition (B-C = 57.5 to 67.7%) to the other samples. Overall, 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 the cumulative number of individuals and cumulative tube surface area of *Riftia pachyptila* aggregations (Fig. 3). Differences in the univariate measures of community structure between sites were not statistically significant (Table 2).

Of 17 species found exclusively at either Riftia Field or Tica, 11 were represented by 1 individual or were present in only 1 sample (Table 3). At each site, 2 species were considered to be unique: The polynoid polychaete *Branchiplicatus cupreus* and the gastropod *Nodopelta rigneae* were present in the sampled *Riftia pachyptila* aggregations from Riftia Field and not from Tica. Together, these 2 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

Fig. 3. Species-effort curves based on (a) cumulative number of individuals and (b) cumulative tube surface area for epifaunal community associated with aggregations of *Riftia pachyptila* at Riftia Field (RF) and Tica (TC) sites
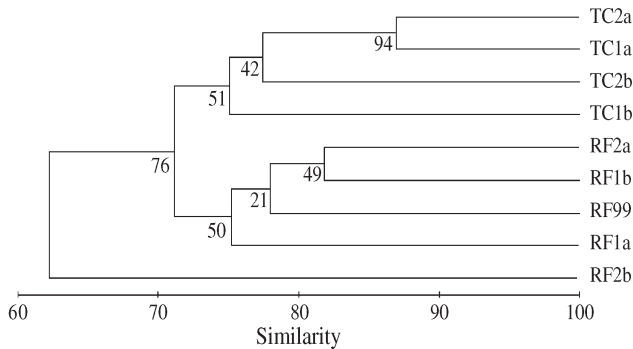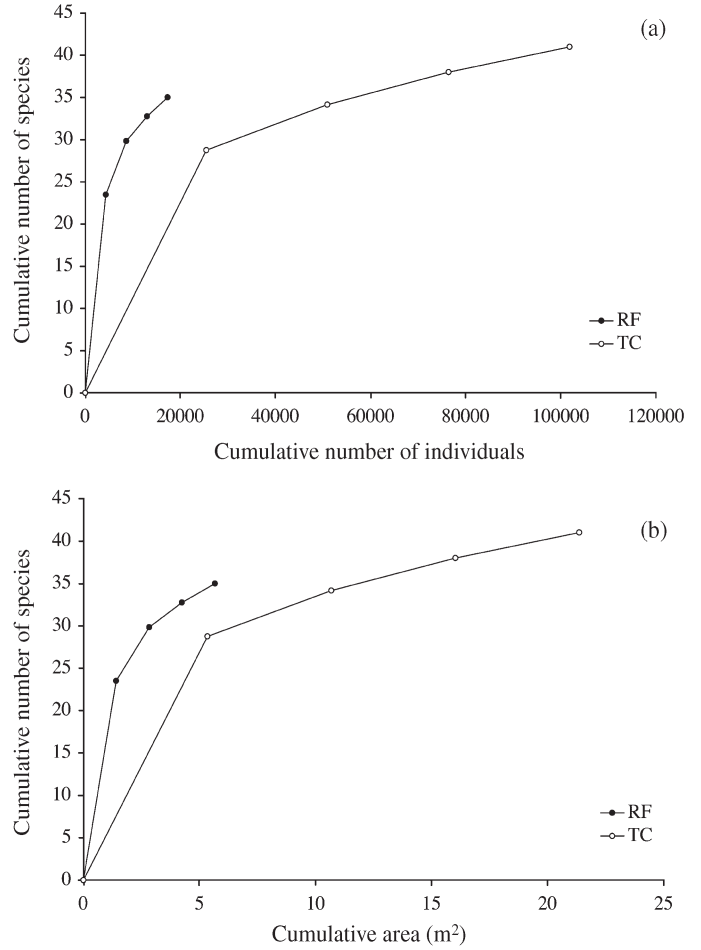

Fig. 2. Cluster analysis (group-average linkage method) of Bray-Curtis similarity values, constructed from standardized relative abundances of each species for all samples (sample designations as in Table 1). The same pattern is generated with Bray-Curtis similarity values constructed with standardized relative biomass. For each sample, abundance and biomass data were standardized to surface area of the *Riftia pachyptila* aggregation, divided by the total, and 4th root transformed, before calculating Bray-Curtis similarity matrices

the leptostracan *Dahlella caldariensis* were collected in every sampled aggregation of *R. pachyptila* from Tica, but never at Riftia Field. These 2 unique species accounted for <0.78% of the density and <0.92% of the biomass in the epifaunal community. At Tica, 1 species, *Bathymodiolus thermophilus* was much more abundant, and contributed 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 epifaunal density without *B. thermophilus* (R = 0.365, p = 0.03; ANOSIM). The species that contributed most to the dissimilarity between sites were *Cyathermia naticoides*, *Ventiella sulfuris* and *Branchipolynoe symmytilida* (Table 4).

Table 4. Species that contributed ≥5% to Bray-Curtis dissimilarity between epifaunal community composition at Riftia Field (RF) and Tica (TC). Dissimilarity calculated from standardized and transformed abundances of all species except mussel *Bathymodiolus thermophilus*

Species	Average density (no. ind. m^{-2})		Contribution to dissimilarity (%)
	RF	TC	
Cyathermia naticoides	473	865	6.52
Ventiella sulfuris	200	651	5.67
Branchipolynoe symmytilida	0	12	5.00

DISCUSSION AND CONCLUSION

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, Shank et al. 1998, Sarrazin et al. 1999, Mullineaux et al. 2000, 2003, Micheli et al. 2002). 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 Riftia Field and Tica, 2 discrete sites of low-temperature hydrothermal activity on the EPR. 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 probably reflect differences in the composition of the source fluids and subsequent subsurface chemical processes (Von Damm & Lilley 2004, Le Bris et al. in press). Although no chemical measurements were made in 2001, the general appearance of the site and the declining populations of *R. pachyptila* indicate that fluid chemistry at Riftia Field in 2001 was similar 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 H_2S rather than HS^- (Le Bris et al. in press), 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 mo 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. in press). Accordingly, individuals of *R. pachyptila* seemed to be in much better physiological condition, with bright red plumes and white tubes, and with densely distributed aggregations that resembled the 'haystack' morphology, typical for this species (Hessler et al. 1988, Shank et al. 1998).

Consequences 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'*$_{log\ e}$, density, biomass) were significantly different between sites. 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, Kicklighter et al. 2004). Rather, chemoautotrophic bacteria form the base of the hydrothermal vent food web (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).

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 µm) was collected with 1 aggregation of *Riftia pachyptila* from Riftia Field in 2001 (Sample RF1b). At the EPR and the Galápagos 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 to 2002. In addition to the 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 *Branchipolynoe symmytilida* lives in the mantle cavity of *Bathymodiolus thermophilus*, and has never been reported when mussels were absent. The leptostracan *Dahlella caldariensis* has been previously collected from mixed samples of vestimentiferans and mussels (Hessler 1984) and is common in some mussel beds on the EPR (Van Dover 2002). Although 1 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 when *R. pachyptila* is absent (McLean 1990, Van Dover 2002, 2003). After mussels were removed from multivariate analyses, the 3 species that accounted for ≥5% of the 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 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. 1988b). 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. 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 a manipulative experiment at Riftia Field in 1998–1999, 1 yr after aggregations of *Riftia pachyptila*

had been removed and mussels deployed on half of the cleared sources of diffuse hydrothermal flow, there was 1 large mussel attached to a syntactic foam marker 50 cm above the ocean floor and 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 yr 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 hydrothermal fluid chemistry from 1999, the composition of the epifaunal community associated with a 1 yr old aggregation of *Riftia pachyptila* sampled at Riftia Field in 1999 was more similar to the other samples from Riftia Field than to any of the samples from Tica in the present study (Fig. 2). Of the species found exclusively at Riftia Field in 2001 and 2002, 2 (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. 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 9 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 polychaetes *Amphisamytha galapagensis* and *Ophryotrocha akessoni*, the gastropod *Lepetodrilus elevatus*, and the amphipod *Ventiella sulfuris*. Some other species, including the polychaetes *Paralvinella grasslei* and *Galapagomystides aristata* and the gastropods *Cyathermia naticoides*, *Rhynchopelta concentrica* and *L. pustulosus* have been found less frequently in mussel beds (Van Dover 2003). The few species unique to each site contributed very little to the cumulative epifaunal density and biomass associated with *R. pachyptila* aggregations. The similarity in the *R. pachyptila* community structure between sites and years may be due in part to the small number of samples. However, high local community similarity has also been documented between sites at the Juan de

Fuca Ridge (Govenar et al. 2002, Tsurumi & Tunnicliffe 2003), the northern and southern EPR (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 gradients may be positively correlated (Kim & Mullineaux 1998, Mullineaux et al. 1998, Chase 2003).

At the EPR in 2001 and 2002, the species richness of the epifaunal community associated with *Riftia pachyptila* was positively correlated with the total biomass of *R. pachyptila* and the tube surface area of *R. pachyptila* aggregations. The total biomass of *R. pachyptila* was greater at Tica than at Riftia Field, where sulfide concentrations were higher, iron was undetectable, and the pH was close to neutral. However, no statistically significant differences were detected in univariate measures of the epifaunal community structure (S, J', $H'_{\log e}$, density, biomass) 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 1 order of magnitude. In addition to the increase in available substrate, the 3-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). Differences in the species composition may be attributable to other local factors within the community, such as productivity, nutrient availability, disturbance, larval settlement, competition, predation, or other non-trophic and positive biological interactions.

LITERATURE CITED

Bruno JF, Bertness MD (2001) Habitat modification and facilitation in benthic marine communities. In: Bertness MD, Gaines SD, Hay ME (eds) Marine community ecology. Sinauer Associates, Sunderland, MA, p 201–218

Chase JM (2003) Community assembly: when should history matter? Oecologia 136:489–498

Childress JJ, Fisher CR (1992) The biology of hydrothermal vent animals: physiology, biochemistry and autotrophic symbioses. Oceanogr Mar Biol Annu Rev 30:337–441

Clarke KR, Gorley RN (2001) PRIMER v5: user manual/tutorial, PRIMER-E, Plymouth

Desbruyères D, Almeida A, Biscoito M, Comtet T, Khripounoff A, Le Bris N, Sarradin PM, Segonzac M (2000) A review of the distribution of hyrothermal vent communities along the northern Mid-Atlantic Ridge: dispersal vs. environmental controls. Hydrobiologia 440:201–216

Fisher CR (1990) Chemoautotrophic and methanotrophic symbioses in marine invertebrates. Rev Aquat Sci 2: 399–436

Fisher CR, Childress JJ, Arp AJ, Brooks JM and 7 others (1988a) Physiology, morphology, and biochemical composition of *Riftia pachyptila* at Rose Garden in 1985. Deep-Sea Res A 35:1745–1758

Fisher CR, Childress JJ, Arp AJ, Brooks JM and 11 others (1988b) Microhabitat variation in the hydrothermal vent mussel *Bathymodiolus thermophilus*, at Rose Garden vent on the Galapagos Rift. Deep-Sea Res A 35:1769–1792

Fisher CR, Childress JJ, Macko SA, Brooks JM (1994) Nutritional interactions in Galapagos Rift hydrothermal vent communities: inferences from stable carbon and nitrogen isotope analyses. Mar Ecol Prog Ser 103:45–55

Fustec A, Desbruyères D, Juniper SK (1987) Deep-sea hydrothermal vent communities at 13° N on the East Pacific Rise: microdistribution and temporal variations. Biol Oceanogr 4:121–164

Goffredi SK, Childress JJ, Desaulniers NT, Lee RW, Lallier FH, Hammond D (1997) Sulfide acquisition by the vent worm *Riftia pachyptila* appears to be *via* uptake of HS⁻, rather than H_2S. J Exp Biol 200:2609–2616

Govenar BW, Bergquist DC, Urcuyo IA, Eckner JT, Fisher CR (2002) Three *Ridgeia piscesae* assemblages from a single Juan de Fuca Ridge sulphide edifice: structurally different and functionally similar. Cah Biol Mar 43:247–252

Govenar BW, Freeman M, Bergquist DC, Johnson GA, Fisher CR (2004) Composition of a one-year old *Riftia pachyptila* community following a clearance experiment: insight to succession patterns at deep-sea hydrothermal vents. Biol Bull 207:177–182

Grassle JF (1986) The ecology of deep-sea hydrothermal vent communities. Adv Mar Biol 23:301–362

Haymon RM, Fornari DJ, Von Damm KL, Lilley MD and 11 others (1993) Volcanic eruption of the mid-ocean ridge along the East Pacific Rise crest at 9° 45, 52′ N: Direct submersible observations of seafloor phenomena associated with an eruption event in April, 1991. Earth Planet Sci Lett 119:85–101

Hessler RR (1984) *Dahlella caldariensis*, new genus, new

species: a leptostracan (Crustacea, Malacostraca) from deep-sea hydrothermal vents. J Crustac Biol 4:655–664

Hessler RR, Smithey WM, Boudrias MA, Keller CH, Lutz RA, Childress JJ (1988) Temporal change in megafauna at the Rose Garden hydrothermal vent (Galapagos Rift; eastern tropical Pacific). Deep-Sea Res A 35:1681–1710

Hunt HL, Metaxas A, Jennings RM, Halanych KM, Mullineaux LS (2004) Testing biological control of colonization by vestimentiferan tubeworms at deep-sea hydrothermal vents (East Pacific Rise, 9° 50′ N). Deep-Sea Res I 51: 225–234

Jannasch HW (1983) Microbial processes at deep sea hydrothermal vents. In: Rona PA, Boström K, Laubier L, Smith KL (eds) Hydrothermal processes at seafloor spreading centers. Plenum Press, New York, p 677–709

Jollivet D (1993) Distribution et évolution de la faune associée aux sources hydrothermales profondes a 13° N sur la dorsale du Pacifique Oriental: le cas particulier des polychètes Alvinellidae. PhD thesis, Université de Bretagne Occidentale

Kicklighter CE, Fisher CR, Hay ME (2004) Chemical defense of hydrothermal vent and hydrocarbon seep organisms: a preliminary assessment using shallow-water consumers. Mar Ecol Prog Ser 275:11–19

Kim SL, Mullineaux LS (1998) Distribution and near-bottom transport of larvae and other plankton at hydrothermal vents. Deep-Sea Res II 45:423–440

Le Bris N, Sarradin PM, Birot D, Alayse-Danet AM (2000) A new chemical analyzer for *in situ* measurement of nitrate and total sulfide over hydrothermal vent biological communities. Mar Chem 72:1–15

Le Bris N, Sarradin PM, Pennec S (2001) A new deep-sea probe for *in situ* pH measurement in the environment of hydrothermal vent biological communities. Deep-Sea Res I 48:1941–1951

Le Bris N, Govenar B, Le Gall C, Fisher CR (in press) Processes controlling physico-chemical conditions in various diffuse flow environments at deep-sea vents. Mar Chem

Lopez-Garcia P, Gaill F, Moreira D (2002) Wide bacterial diversity associated with tubes of the vent worm *Riftia pachytptila*. Environ Microbiol 4:204–215

Luther GW III, Rozan TF, Talliefert M, Nuzzio DB, Di Meo CA, Shank TM, Lutz RA, Cary SC (2001) Chemical speciation drives hydrothermal vent ecology. Nature 410:813–816

McLean JH (1990) Neolepetopsidae, a new docoglossate limpet family from hydrothermal vents and its relevance to patellogastropod evolution. J Zool 222:485–528

Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am Nat 130:730–757

Micheli F, Peterson CH, Mullineaux LS, Fisher CR, Mills SW, Sancho G, Johnson GA, Lenihan HS (2002) Predation structures communities at deep-sea hydrothermal vents. Ecol Mongr 72:365–382

Mullineaux LS, Mills SW, Goldman E (1998) Recruitment variation during a pilot colonization study of hydrothermal vents (9° 50′ N, East Pacific Rise). Deep-Sea Res II 45: 441–464

Mullineaux LS, Fisher CR, Peterson CH, Schaeffer SW (2000) Tubeworm succession at hydrothermal vents: use of bio-

genic cues to reduce habitat selection error? Oecologia 123:275–284

Mullineaux LS, Peterson CH, Micheli F, Mills SW (2003) Successional mechanism varies along a gradient in hydrothermal fluid flux at deep-sea vents. Ecol Mongr 73:523–542

Nelson DC, Hagan KD, Edwards DB (1995) The gill symbiont of the hydrothermal vent mussel *Bathymodiolus thermophilus* is a phychrophilic, chemoautotrophic, sulfur bacterium. Mar Biol 121:487–495

Ohmann JL, Spies TA (1998) Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. Ecol Monogr 68:151–182

Page HM, Fiala-Médioni A, Fisher CR, Childress JJ (1991) Experimental evidence for filter-feeding by the hydrothermal vent mussel, *Bathymodiolus thermophilus*. Deep-Sea Res 38:1455–1461

Petraitis PS, Dudgeon SR (2004) Detection of alternative stable states in marine communities. J Exp Mar Biol Ecol 300:343–371

Samuels CL, Drake JA (1997) Divergent perspectives on community convergence. Trends Ecol Evol 12:427–432

Sarrazin J, Juniper SK, Massoth G, Legendre P (1999) Physical and chemical factors influencing species distributions on hydrothermal sulfide edifices of the Juan de Fuca Ridge, northeast Pacific. Mar Ecol Prog Ser 190: 89–112

Shank TM, Fornari DJ, Von Damm KL, Lilley MD, Haymon RM, Lutz RA (1998) Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents (9° 50′ N, East Pacific Rise). Deep-Sea Res II 45:465–515

Smith KL Jr (1985) Deep-sea hydrothermal vent mussels: nutritional state and distribution at the Galapagos Rift. Ecology 66:1067–1080

Sousa WP (2001) Natural disturbance and the dynamics of marine benthic communities. In: Bertness MD, Gaines SD, Hay ME (eds) Marine community ecology. Sinauer Associates, Sunderland, MA

Tsurumi M, Tunnicliffe V (2003) Tubeworm-associated communities at hydrothermal vents on the Juan de Fuca Ridge, northeast Pacific. Deep-Sea Res I 50:611–629

Tunnicliffe V (1991) The biology of hydrothermal vents: ecology and evolution. Oceanogr Mar Biol Annu Rev 29: 319–407

Van Dover CL (2002) Community structure of mussel beds at deep-sea hydrothermal vents. Mar Ecol Prog Ser 230: 137–158

Van Dover CL (2003) Variation in community structure within hydrothermal vent mussel beds of the East Pacific Rise. Mar Ecol Prog Ser 253:55–66

Van Dover CL, Fry B (1989) Stable isotopic compositions of hydrothermal vent organisms. Mar Biol 102:257–263

Van Dover CL, Trask JL (2000) Diversity at deep-sea hydrothermal vent and intertidal mussel beds. Mar Ecol Prog Ser 195:169–178

Von Damm KL, Lilley MD (2004) Diffuse flow hydrothermal fluids from 9° 50′ N East Pacific Rise: origin, evolution and biogeochemical controls. Am Geophys Union Monogr 144

Wootton JT, Power ME (1993) Productivity, consumers, and the structure of a river food chain. Proc Natl Acad Sci (USA) 90:1384–1387