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: Siboglinidae) 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, Petroitiis & 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 endemcity, 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 flow, 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 chemosynthesis (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 \textit{R. pachyptila} aggregations and active larval recruitment (Govenar et al. 2004). In 2001 and 2002, the total abundance of \textit{R. pachyptila} was greatly reduced and the few remaining aggregations were small and sparsely distributed. Individuals of \textit{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 \textit{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 \textit{Riftia pachyptila}, which were subsequently sampled for community analyses. In 2002, the total labile sulfide (\(\text{H}_2\text{S} = \text{H}_2\text{S}, \text{HS}^- \text{and S}^2^-\)) and ferrous iron concentrations in the diffuse hydrothermal fluids around aggregations of \textit{R. pachyptila} at Riftia Field and Tica were determined using the \textit{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 \textit{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 \(\mu\)m 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 \textit{Riftia pachyptila} and then cinched it tightly closed around the base of the \textit{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 \(\mu\)m Nitex mesh), which was mounted to the ‘Alvin’ basket for transport to the surface.

Upon recovery of the submersible to the ship, any \textit{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 \textit{R. pachyptila} and the mussel \textit{Bathymodiolus thermophilus} were rinsed and removed for size and mass measurements. The length and anterior diameter of every \textit{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 \(\mu\)m 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-weighted, dried at 60\(^{\circ}\)C to obtain dry weight, and combusted in a muffle furnace at 500\(^{\circ}\)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 \textit{Riftia pachyptila} and \textit{Bathymodiolus thermophilus} were also wet-weighted, 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-weighted, 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 \(\mu\)m to 1mm) were also sorted, identified, and wet-weighted. 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 \textit{Riftia pachyptila} tubes in each sampled aggregation. The standardized data were then used to calculate Pielou’s evenness (\(J^e\)), Shannon-Wiener diversity (\(H_{\text{log}_3}\)), 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 <purrl.portal.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 m² 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).

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

<table>
<thead>
<tr>
<th>Sample</th>
<th>Max. T (°C)</th>
<th>n</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>1b</td>
<td>18.2 (15)</td>
<td>209</td>
<td>698.39</td>
<td>0.06</td>
<td>1.83</td>
</tr>
<tr>
<td>2a</td>
<td>19.8 (42)</td>
<td>167</td>
<td>1555.02</td>
<td>0.08</td>
<td>2.66</td>
</tr>
<tr>
<td>2b</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>1b</td>
<td>na</td>
<td>393</td>
<td>2988.90</td>
<td>0.03b</td>
<td>6.55</td>
</tr>
<tr>
<td>2a</td>
<td>10 (24)</td>
<td>96</td>
<td>2278.15</td>
<td>0.07</td>
<td>3.80</td>
</tr>
<tr>
<td>2b</td>
<td>13.1 (33)</td>
<td>102</td>
<td>3248.63</td>
<td>0.04</td>
<td>5.79</td>
</tr>
</tbody>
</table>

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

*Although 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.
mass of *R. pachyptila* was positively and significantly correlated with the surface area of the tubes in the aggregation (*p* = 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 (*p* = 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*, *Amphisamphyta galapagensis*, *Ophytrotrocha akessoni*, and *Galapagomystides aristata*; the gastropods *Leptodrilus elevatus*, *Cytheria naticoides*, *Rhynchopella 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 thermophila* 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*⁻logₑ, 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).

**Table 2. Univariate measures of epifaunal community structure associated with *Riftia pachyptila*: species richness (*S*), Pielou’s evenness (*J*), Shannon-Wiener diversity (*H*⁻logₑ), 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.**

<table>
<thead>
<tr>
<th>Sample</th>
<th><em>S</em></th>
<th><em>J</em></th>
<th><em>H</em>⁻logₑ</th>
<th>Density (ind. m⁻²)</th>
<th>Biomass (g AFDW m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>RF1a</td>
<td>26</td>
<td>0.59</td>
<td>1.94</td>
<td>4332</td>
<td>21.91</td>
</tr>
<tr>
<td>1b</td>
<td>1</td>
<td>0.56</td>
<td>1.71</td>
<td>3601</td>
<td>11.65</td>
</tr>
<tr>
<td>2a</td>
<td>28</td>
<td>0.64</td>
<td>2.14</td>
<td>2032</td>
<td>13.11</td>
</tr>
<tr>
<td>2b</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>1b</td>
<td>31</td>
<td>0.44</td>
<td>1.50</td>
<td>1723</td>
<td>13.37</td>
</tr>
<tr>
<td>2a</td>
<td>25</td>
<td>0.52</td>
<td>1.66</td>
<td>6618</td>
<td>47.37</td>
</tr>
<tr>
<td>2b</td>
<td>35</td>
<td>0.50</td>
<td>1.76</td>
<td>3884</td>
<td>27.37</td>
</tr>
<tr>
<td>RF vs. TC</td>
<td>1.01</td>
<td>–1.59</td>
<td>–1.01</td>
<td>0.43 (0.31)</td>
<td>1.87 (0.88)</td>
</tr>
<tr>
<td>2001 vs. 2002</td>
<td>0.14</td>
<td>0.43</td>
<td>0.43</td>
<td>0.14 (0.66)</td>
<td>0.14 (0.88)</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Epifauna</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>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>D</td>
<td>B</td>
<td>D</td>
<td>B</td>
<td>D</td>
<td>B</td>
<td>D</td>
<td>B</td>
</tr>
<tr>
<td>Annelida</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Paralvinella grasslei</em></td>
<td>364</td>
<td>16.62</td>
<td>404</td>
<td>5.22</td>
<td>161</td>
<td>3.71</td>
<td>161</td>
<td>3.71</td>
</tr>
<tr>
<td><em>Amphisamphyta galapagensis</em></td>
<td>348</td>
<td>0.07</td>
<td>172</td>
<td>0.03</td>
<td>246</td>
<td>0.03</td>
<td>273</td>
<td>0.04</td>
</tr>
<tr>
<td><em>Ophryotrocha akessoni</em></td>
<td>19</td>
<td>0</td>
<td>27</td>
<td>&lt;0.01</td>
<td>164</td>
<td>0.01</td>
<td>418</td>
<td>0.07</td>
</tr>
<tr>
<td><em>Galapagomystides aristata</em></td>
<td>265</td>
<td>0.86</td>
<td>70</td>
<td>0.26</td>
<td>46</td>
<td>0.14</td>
<td>141</td>
<td>0.43</td>
</tr>
<tr>
<td><em>Paralvinella pandoreae</em></td>
<td>397</td>
<td>0.64</td>
<td>39</td>
<td>0.02</td>
<td>29</td>
<td>0.03</td>
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<td><em>Hestiospina vestimentifera</em></td>
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<td>2</td>
<td>0.01</td>
<td>5</td>
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<tr>
<td><em>Branchipolynoe symmytilida</em></td>
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<td>0</td>
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<td>0</td>
<td>4</td>
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<tr>
<td><em>Opisthotrochopodus alvinus</em></td>
<td>18</td>
<td>0.07</td>
<td>4</td>
<td>0.01</td>
<td>10</td>
<td>0.05</td>
<td>6</td>
<td>0.03</td>
</tr>
<tr>
<td><em>Nereis sandersi</em></td>
<td>4</td>
<td>0.02</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0.07</td>
<td>5</td>
<td>0.19</td>
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<td><em>Branchinotogluma hessleri</em></td>
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<td>0.05</td>
<td>2</td>
<td>0.01</td>
<td>3</td>
<td>0.03</td>
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<td>0</td>
<td>&lt;0.01</td>
<td>9</td>
<td>1.53</td>
<td>1</td>
<td>0.03</td>
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<tr>
<td><em>Oasisia alvinae</em></td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
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<td>0</td>
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<tr>
<td><em>Leventineilla kincaidi</em></td>
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<td>0</td>
<td>9</td>
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<tr>
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<td>0.05</td>
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<td>2</td>
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<td>1</td>
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<tr>
<td><em>Lepidonotopodium riftenae</em></td>
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<td>0</td>
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<td>&lt;0.01</td>
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<tr>
<td><em>Prionospio sandersi</em></td>
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<tr>
<td><em>Iphionella risensis</em></td>
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<td>0</td>
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<td>0</td>
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<td>&lt;0.01</td>
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<td><em>Polychaeta juveniles</em></td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>&lt;0.01</td>
<td>0</td>
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</tr>
</tbody>
</table>

Mollusca

| Aplacophora                |       |       |       |       |       |       |       |       |
| Helicoradomenia spp.       | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     |

Gastropoda

| Lepetodrilus elevatus       | 1907  | 0.75  | 730   | 0.75  | 676   | 0.77  | 3186  | 3.35  |
| *Cytheramorpha naticoides*  | 98    | 0.01  | 1575  | 1.72  | 210   | 0.05  | 5     | 0.02  |
| *Rhynchopelta concentrica* | 366   | 1.26  | 201   | 0.64  | 137   | 0.57  | 141   | 0.19  |
| *Lepetodrilus pustulosus*  | 346   | 0.48  | 331   | 0.76  | 235   | 0.98  | 45    | 0.12  |
| *Lepetodrilus ovalis*      | 0     | 0     | 0     | 0     | 26    | 0.04  | 59    | 0.23  |
| *Lepetodrilus cristatus*   | 1     | <0.01 | 10    | 0.02  | 2     | 0.01  | 14    | 0.03  |
| *Peltospira delicata*       | 0     | 0     | 0     | 0     | 41    | 0.05  | 0     | 0     |
| *Nodopelta rigneae*        | 2     | 0.01  | 0     | 0     | 18    | 0.03  | 0     | 0     |
| *Gorgoleptis spiralis*     | 3     | <0.01 | 0     | 2     | <0.01 | 9     | <0.01 | 0     |
| *Pachydermia laevis*       | 1     | <0.01 | 0     | 2     | <0.01 | 5     | <0.01 | 0     |
| *Eulepetopsis vitrea*      | 1     | 0.02  | 0     | 0     | 0     | 0     | 2     | <0.01 |
| *Melandrymnia aurantiaca*  | 0     | 0     | 0     | <1   | <0.01 | 0     | 0     | 0     |
| *Neosphalus fretterae*     | 5     | 0.45  | 0     | 0     | 0     | 0     | 0     | 0     |
| *Peltosira plicata*        | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     |
| *Gymnobela sp. A*          | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     |
| *Gorgoleptis emarginus*    | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     |
| *Bathymargarites symplector* | 0    | 0     | 0     | 0     | 0     | 0     | <1    | <0.01 |
| *Gastropod juveniles*      | 8     | <0.01 | 14    | <0.01 | 168   | 0.07  | 2     | <0.01 |

Bivalvia

| Bathymodiolus thermodilus* | 0     | 0     | 0     | <1   | <0.01 | 0     | 0     | 14    |

Arthropoda

| Decapoda                  |       |       |       |       |       |       |       |       |
| Ventiella sulfuris       | 60    | 0.01  | 21    | <0.01 | 53    | <0.01 | 664   | 0.14  |
| *Bythograea thermydron*  | 13    | 0.68  | 2     | 1.93  | 420   | 0.20  | 0     | 3     |
| *Dahliea caldariensis*   | 0     | 0     | 0     | 0     | 0     | 0     | 5     | 0.01  |
| *Alvinocaris lusca*      | 0     | 0     | 1     | <0.01 | 0     | 0     | 0     | <1   |
| *Decapod juveniles*      | 0     | 0     | 0     | 2     | <0.01 | 16    | <0.01 | 0     |

Echinodermata

| Ophiuroidea               |       |       |       |       |       |       |       |       |
| Ophiura sp.               | 0     | 0     | 0     | 0     | 0     | 0     | <1   | <0.01 |

*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 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Average density (no. ind. m⁻²)</th>
<th>Contribution to dissimilarity (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cyathermia naticoides</td>
<td>473</td>
<td>RF 865</td>
</tr>
<tr>
<td>Ventiella sulfuris</td>
<td>200</td>
<td>TC 651</td>
</tr>
<tr>
<td>Branchipolyne symmytilida</td>
<td>0</td>
<td>12</td>
</tr>
</tbody>
</table>

**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 HS⁻ 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*, 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 collec-
tion from Tica (6.95 and 31.79% of the epifaunal bio-
mass 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 tube-
worms (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
*Dahliella 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 sul-
fide, low pH or high iron at Riftia Field at the time
of this study. Like vestimentiferans, *Bathymodiolus
thermophilus* relies primarily on sulfur-oxidizing symbi-
ons for nutrition (Fisher 1990, Nelson et al. 1995). Low
sulfide concentrations could have limited individ-
ual and population growth of *B. thermophilus* (Smith
however, *B. thermophilus* can also supplement its diet
by filter-feeding (Page et al. 1991). High iron concen-
trations may signify high levels of other metals and
mineral particulates. At another hydrothermal vent
field on the Mid-Atlantic Ridge, the presence of mus-
sels (*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 col-
lected (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 bet-
ter physiological condition at Riftia Field in the late
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 *Branchi-
plicatus 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 sam-
ples aggregations at Riftia Field in 1999, 2001 and
and the dominance of *P. grasslei* in 1999 and later in
2001 and 2002, after the chemical composition of hydro-
thermal fluids appears to have changed, also reflects
the importance of larval dispersal and biological inter-
actions in the distribution of hydrothermal vent fauna.

The high similarity in the structure and the composi-
tion of the community associated with *Riftia pachyptila*
is primarily due to 9 common species that dominated
the epifaunal density and biomass. Some of the com-
mon 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 spe-
cies included the polychaetes *Amphisamytha galapa-
gensis* and *Ophryotrocha akessoni*, the gastropod
*Lepelodrilus elevatus*, and the amphipod *Ventilla
sulfuris*. Some other species, including the polychaetes
*Paralvinella grasslei* and *Galapagomystides aristata*
and the gastropods *Cyatherna naticoides*, *Rhyncho-
pelta 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 asso-
ciated 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*<sub>log</sub>, 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.

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