Effect of depth and vent fluid composition on the carbon sources at two neighboring deep-sea hydrothermal vent fields (Mid-Cayman Rise)

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Abstract

In this study, we have used stable isotopes of megafauna, microbial mats and particulate organic matter to examine the effect of depth and vent fluid composition on the carbon sources at two proximal, chemically distinct hydrothermal vent fields along the Mid-Cayman Rise. The basalt hosted Piccard vent field (4980m) is twice as deep as the ultramafic hosted Von Damm vent field (2300m) and has very different faunal assemblages. Of particular note is the presence of seep-associated fauna, *Escarpia* and *Lamellibrachia* tubeworms, at the Von Damm vent field.

We identify a greater range of carbon sources and a suggestion of increased photosynthetic inputs to the Von Damm vent field compared to Piccard vent field. *Rimicaris hybisae* shrimp are the only abundant species shared between the two vent fields with $\delta^{13}\text{C}$ values ranging between -22.7 to -10.1‰. Higher concentrations of hydrogen sulfide in the vent fluids at Piccard is proposed to be responsible for varying the relative contributions of the carbon fixation cycles used by their epibionts. Seep-associated fauna at Von Damm rely on elevated, thermogenic hydrocarbon content of the vent fluids for their carbon source

($\delta^{13}\text{C}$ values ranging from -21.3 to 11.6‰). They also derive energy from hydrogen sulfide formed by the microbial reduction of sulfide ($\delta^{34}\text{S}$ values ranging from -10.2 to -6.9‰). The tubeworms have very short roots (buried at most a centimeter into rubble), suggesting that microbial sulfate reduction must be occurring either in the shallow subsurface and/or in the anterior part of the tube. Overall, megafauna at Von Damm vent field appear to have a smaller food chain length (smaller $\delta^{15}\text{N}$ range) but a greater breadth of trophic resources compared to the megafauna at the Piccard vent field.

Keywords: hydrothermal, seeps, food web, stable isotopes, Cayman

1. Introduction

In the late 1970's, discovery of dense communities of megafauna at deep-sea hydrothermal vents revolutionized our understanding of life on Earth and the potential for life to exist elsewhere in the universe (Lonsdale, 1977; Corliss et al., 1979; Chyba and Hand, 2001). In these complex ecosystems, chemoautotrophic bacteria provide primary production in the absence of sunlight (Jannasch and Wirsen, 1979). Both free-living and symbiotic bacteria harvest energy from oxidation of reduced chemicals coming from the seafloor to fix inorganic carbon, forming dissolved and particulate organic carbon (DOC and POC). This provides a food source to endemic consumers and occasional background fauna. Additional contributions to the food

web come from degradation of biomass of either chemosynthetic or photosynthetic origin, abiotic chemical processes and particulate organic matter (POM) from the subsurface or water column (Limen et al., 2007; Govenar, 2012).

The recent discovery of adjacent basalt- and ultramafic-hosted vent fields (21 km apart) on the Mid-Cayman Rise, provides us with a field opportunity to compare the megafauna and investigate carbon sources to two chemically distinct vent fields in close proximity to each other (German et al., 2010; Connelly et al., 2012; Kinsey and German, 2013). The basalt-hosted Piccard hydrothermal vent field (4987 m) in the rift valley of the Mid-Cayman Rise is the deepest vent field known to date. The shallower Von Damm ultramafic-hosted hydrothermal vent field (2300 m) is located 21 km south-southwest of Piccard, on the shoulder of an oceanic core complex (Figure 1A). The chemistry of hydrothermal fluids in ultramafic environments differs from that in basalt hosted mid-ocean ridge (MOR) settings, as a result of varying rock type (German and Von Damm, 2003). For example, ultramafic hydrothermal activity is generally associated with high concentrations of methane and hydrogen in the fluids (Charlou et al., 1998).

The Piccard hydrothermal field comprises seven sulfide mounds, three of which are actively venting (Figure 1B) (Kinsey and German, 2013). Two of the mounds, Beebe Vents and Beebe Woods, are venting high temperature black smoker vent fluids

rich in metals, hydrogen sulfide (12 mM) and hydrogen (21 mM) (max 398°C at Beebe Vents and 354°C at Beebe Woods) and the third mound, Beebe Sea, is venting cooler, diffuse flow fluids (max 111°C) (Figure 1B). The large metazoan species are arranged zonally, with dense swarms of *Rimicaris hybisae* in the warmest water and with peripheral anemones and gastropods (*Provanna* sp.) in cooler water (Nye et al., 2012; Kinsey and German, 2013; Plouviez et al., 2015). Exposed rocks are covered in white filamentous bacteria, reminiscent of sulfur oxidizing bacteria (Jannasch et al., 1989); squat lobsters (*Munidopsis* sp.) are occasionally observed interspersed with shrimp and anemones. Within 50 m of Beebe Woods, thick patches of orange sediment suggest the presence of iron-oxidizing bacteria (Emerson and Moyer, 2002).

The Von Damm vent field is a large conical mound on the edge of the Mt Dent oceanic core complex (Figure 1C)(Connelly et al., 2012). Von Damm vents emit cooler (max T: 226°C) clear fluids, which are very low in metals, and rich in hydrogen sulfide (3.2 mM), hydrogen (19 mM) and methane (2.8 mM). The fluids also have elevated ethane and propane concentrations relative to basalt hosted systems (German et al., 2010; Connelly et al., 2012; McDermott et al., 2012; Seewald et al., 2012; Bennett et al., 2013; Reeves et al., 2014). There are two distinct sites at Von Damm: the Spire and Shrimp Hole at Marker X18 (Mkr X18). At the Spire, clear fluids (max 226°C) are emitted from a large orifice at the top of the mound with smaller areas of focused, mixed flow on the flanks. The fauna are again dominated by dense swarms of *Rimicaris hybisae* around the high

temperature venting, along with white gastropods (*Itheyaspira bathycodon*) interspersed among the *R. hybisae* (Nye et al., 2012; Nye et al., 2013a; Plouviez et al., 2015). Two types of omnivorous shrimp (*Alvinocaris* sp., *Lebbeus virentova*), eelpout fish (*Thermarces* sp.), and squat lobsters (*Munidopsis* sp.) are also interspersed among the *R. hybisae*, but in much lower numbers (Nye et al., 2013b). At Shrimp Hole, on the plateau southeast of the Von Damm Spire, much cooler diffuse flow (<21°C) emanates from rubble. Two species of tubeworms (*Escarpia* sp., *Lamellibrachia* sp.) are aggregated at some areas of low-temperature diffuse flow (Connelly et al., 2012; Plouviez et al., 2015) and fields of empty mussel shells are present on these lower slopes. The tubeworms, *Escarpia* and *Lamellibrachia*, are typically seep associated (Levin, 2005). However, they have also been found in sedimented basins near hydrothermal vents and a whale carcass, demonstrating their opportunistic nature (Black et al., 1997; Feldman et al., 1998). This site included other, less abundant seep-associated taxa such as a mussel (within the *Bathymodiolus childressi* clade) and two clams (*Thyasira* sp. and *Pliocardiinae* sp.) (Plouviez et al., 2015).

The Von Damm and Piccard vent fields have very different faunal assemblages despite a geographical separation of only 13 km and it has been suggested that this results from depth and/or local conditions (Plouviez et al., 2015). *Rimicaris hybisae* is the only abundant species shared between Von Damm and Piccard, providing a second example of vent fields hosting dense populations of *Rimicaris* shrimp within close proximity but with different geological setting. Along the Mid-Atlantic Ridge,

Rimicaris exoculata has been found at several vent fields in the depth range of 2300 to 3900 m (Rainbow, Broken Spur, TAG, Snake Pit and Logatchev, 5S) (Schmidt et al., 2008). Broken Spur, TAG and Snake Pit are basalt hosted, whereas Rainbow and Logatchev are ultramafic. The other fauna at the Cayman vent fields are either unique to a particular vent site or present in much greater abundance at one site over another.

Empirical data have repeatedly shown that chemosynthesis at hydrothermal vents and cold seeps results in carbon, nitrogen and sulfur isotopic values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$) that are often distinct from those expected in photosynthetically based food chains in the deep sea (Govenar, 2012; Reid et al., 2013). Carbon isotope variations at the base of the food chain result from isotope variations in source dissolved inorganic carbon (DIC) and vent microbes adopting various metabolic/carbon fixation pathways that fractionate carbon to varying extents. Also at the base of the food chain nitrogen isotope variations reflect the nature of the local nitrogen source (Kennicutt et al., 1992; Bourbonnais et al., 2012). Sulfur isotope variation depends on the source of sulfur used in sulfur metabolism, either seawater sulfate or sulfide from the vent fluids, and the isotopic variability of the sulfur source (Fry et al., 1983).

Isotope source effects and biochemical fractionations are transferred through consumers, where further fractionation takes place. For carbon, the isotope composition increases by 0 to 1.5‰ per trophic level (Deniro and Epstein, 1978; Caut et al., 2009); for nitrogen, the isotope composition increases by 3 to 4‰ per trophic level (Minagawa and Wada, 1984; Macko et al., 1987; Lefebvre et al., 2009) and for sulfur by -1 to 2‰ during assimilation (Fry et al., 1983; MacAvoy et al., 2002).

In this study, we will examine the stable isotope composition of megafauna, microbial mats and POM at these two proximal, chemically distinct hydrothermal vent fields. We will examine the influence of depth on photosynthetic inputs and the unique characteristics of Von Damm that enable colonization of opportunistic seep fauna. Specifically, we will investigate 1) the source of organic carbon to each site, including photo- and chemo-synthetic inputs, 2) the specific conditions at Von Damm that enable survival of seep associated tubeworms, and 3) trophic relationships between consumers. These characteristics will then be compared to those at other systems.

3. Materials and methods

3.1 Collection methods

All samples were collected during R/V Atlantis Cruise AT 18-16 in January 2012 from the Von Damm and Piccard vent fields on the Mid Cayman Rise (German et al., 2010; Connelly et al., 2012; Kinsey and German, 2013). Representative individuals of the visually dominant megafauna were opportunistically collected at distinct locations within each vent field and are listed in Tables 1 and 2 with assemblage photos in Figures 2 and 3. Megafauna samples were collected using the Remotely Operated Vehicle (ROV) Jason and, depending on their size and mobility, the animals were either collected with the manipulator arm and deposited in bioboxes or sucked into a slurp chamber (a vacuum system typically used for shrimp sampling). Microbial mat samples were either sucked into the slurp chamber or collected attached to their rock substratum. Particulate organic matter was collected from the water surrounding the Von Damm hydrothermal vent field using an in-situ filtration device (Breier et al., 2014). Pre-combusted (450°C, for 14 hours) GF/F glass fiber filters (47 mm, 0.7 µm nominal pore size, Whatman) were loaded into the in-situ filtration device on the ROV to collect particulate matter. The inlet to the filtration device was attached to the manipulator of the ROV, enabling filtration of precisely selected volumes of fluid (ranging from 5 to 8 L, Table 3) within the vent field. After recovery of the ROV on board the ship, biological specimens were stored in seawater to allow them to void their gut contents. All the samples were sorted and the guts of the fish and squat lobsters were dissected. All samples were frozen at -20°C in glass containers.

3.2 Samples collected

Individuals of *Rimicaris hybisae* were collected from dense aggregations at Beebe Woods, Beebe Vents and Beebe Sea (Nye et al., 2012; Kinsey and German, 2013). Additional species, *Provanna* gastropods, anemones tentatively assigned to the genus *Maractis* [cf. *Maractis rimicarivora* of Mid-Atlantic Ridge hydrothermal vents (Fautin and Barber, 1999)], and *Munidopsis* squat lobsters, were collected from the diffuse flow (Table 1, Figure 2). A rock sample covered in white filamentous, potentially sulfur-oxidizing microbial mat (Jannasch et al., 1989) and an orange, potentially Fe-oxidizing microbial mat were collected from the surrounding area (Emerson and Moyer, 2002)(Table 1).

At Von Damm Spire, dense aggregations of *Rimicaris hybisae* were sampled from the edges of the large orifice (Table 2, Figure 3). Numerous *Itheyaspira bathycodon*, the white gastropod living interspersed among the shrimp, were sampled in the same slurp manipulations, as was an eelpout fish in the genus *Thermarces* and two types of putatively omnivorous shrimp, *Lebbeus virentova* and an *Alvinocaris* sp. (Table 2, Figure 3). A second discrete and dense patch of *R. hybisae* was sampled 30 m from the orifice, on the flanks of the Spire. At Shrimp Hole, two species of tubeworm (*Escarpia* sp., *Lamellibrachia* sp.) and a squat lobster (*Munidopsis* sp.) were sampled in an area of weak diffuse flow, together with additional *Alvinocaris* sp. shrimp and *I. bathycodon*.

3.3 Preparation of samples for isotopic analysis

In a land-based laboratory, organisms and microbial mat samples were freeze-dried. For the larger organisms (squat lobsters, fish, tubeworms) and shelled gastropods, muscle tissue was extracted for analysis. For tubeworms, this included samples from the trunk and vestimentum, and for squat lobsters and fish, muscle from the abdomen. For all other taxa, whole animals were homogenized individually. Initial analysis of carbon and nitrogen was carried out on samples without acid pre-treatment since this can prevent accurate nitrogen isotope determination (Brodie et al., 2011b). Representatives from each sample type were then acidified (5% HCl) within silver cups to remove inorganic carbonates (Brodie et al., 2011a). Sample types with more than 1% inorganic carbon were re-analyzed for carbon with an acid pre-treatment. Samples were run in triplicate, except when sample size was limited, i.e. gastropods and microbe samples.

GF/F filters were oven dried (60°C) and treated with concentrated HCl fumes under vacuum for 24 hours to remove the inorganic carbonates. Filters were redried (60°C), quartered, and packaged in tin cups. Two to three analyses were made from the same filter.

3.4 Sample analysis

Sample $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values were measured using a Costech Analytical Technologies, Inc. Elemental Analyzer, fitted with a Zero Blank Autosampler, and interfaced with a Thermo Scientific MAT 253 stable isotope ratio mass spectrometer in continuous flow mode. Isotope values were reported in the conventional delta (δ) notation (units of ‰) as relative differences between samples and standards. The standards were Vienna Pee Dee Belemnite, VPDB (for $\delta^{13}\text{C}$), air N_2 (for $\delta^{15}\text{N}$) and Vienna Canyon Diablo Troilite, VCDT (for $\delta^{34}\text{S}$). During instrument runs, isotopic compositions were measured relative to CO_2 , N_2 and SO_2 reference gases. Sulfanilamide and acetanilide were used throughout as laboratory standards, having been calibrated against certified reference materials (NBS18, NBS19 and USGS24), and were run as part of each sample set. The instrument had a precision (1σ) of $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$, $\pm 0.2\text{‰}$ $\delta^{15}\text{N}$ and $\pm 0.5\text{‰}$ $\delta^{34}\text{S}$ as calculated from repeat analyses of laboratory standards. The range in isotope values within a sample group was calculated by difference between the largest and smallest isotope value of the group.

3.5 Statistical analysis

Differences in faunal isotope signatures between and within sites were assessed using ANOVA or two tailed t-tests. Post-hoc comparisons for ANOVA were made using Tukey's HSD tests. If data sets failed to meet parametric assumptions (i.e. normality

and homogeneity variances), Kruskal-Wallis or Mann-Whitney tests were used and post-hoc comparisons for Kruskal-Wallis were carried out using Dunn's tests. An α level of 0.05 was chosen as the criterion for statistical significance. All data were analyzed in SigmaPlot software.

4. Results

4.1 Sulfur isotopes at both vent fields

At the Piccard vent field, $\delta^{34}\text{S}$ values for vent taxa fell within a narrow range (7.5‰ to 15‰; Figure 4A) but showed significant differences between megafauna groups across the three locations (Table 1, Kruskal-Wallis, $H(7) = 25.772$, $p < 0.05$). $\delta^{34}\text{S}$ values of megafauna collected around Beebe vents were similar (ANOVA, $F(2, 10) = 3.951$, $p = 0.054$), as well as *Rimicaris hybisae* (average $\delta^{34}\text{S} = 8.0 \pm 0.3$ ‰) and the orange microbial mat collected from Beebe Woods ($n=1$, $\delta^{34}\text{S} = 7.6$ ‰, statistical analysis not possible due to low n). In comparison, $\delta^{34}\text{S}$ values of megafauna collected around Beebe Sea were significantly different (ANOVA, $F(2, 8) = 16.338$, $p = 0.001$).

At the Von Damm vent field, the range of $\delta^{34}\text{S}$ values was much greater (Spire: 0.2‰ to 14.5‰; $\delta^{34}\text{S}$ range = 14.3‰, Shrimp Hole: -10.2‰ to 14.5‰; $\delta^{34}\text{S}$ range = 24.7‰; Figure 4B) and varied between vent species (Kruskal-Wallis, $H(9) = 29.890$, $p =$

<0.05). Tubeworms had the lowest $\delta^{34}\text{S}$ values; shrimp (*Rimicaris hybisae*) had the highest $\delta^{34}\text{S}$ values. $\delta^{34}\text{S}$ values of *R. hybisae* at Von Damm compared to those at Piccard were significantly different (ANOVA, $F(4, 25) = 82.306$, $\rho < 0.05$).

4.2 Carbon and nitrogen isotopes at Piccard

At the Piccard vents, the $\delta^{13}\text{C}$ values ranged between -27.1 and -10.1‰ ($\delta^{13}\text{C}$ range = 17.0‰) and megafauna fell into two groups; low $\delta^{13}\text{C}$ values for Group 1 with mean $\delta^{13}\text{C}$ values ranging between -27.1‰ and -22.6‰ (brown provannid gastropods, the orange and white microbial mats) and higher $\delta^{13}\text{C}$ values for Group 2 with mean $\delta^{13}\text{C}$ values ranging between -15.5‰ and -10.1‰ (*Rimicaris hybisae*, squat lobsters, anemones)(Figure 5A, Table 1). Higher $\delta^{13}\text{C}$ values were measured for *R. hybisae* from Beebe Sea compared to Beebe Vents and Beebe Sea (ANOVA, $F(2, 15) = 3.934$, $\rho = 0.042$), whereas similar $\delta^{13}\text{C}$ values were measured for *R. hybisae* from Beebe Vents and Beebe Woods (t-test, $t(10) = -1.048$, $\rho = 0.319$). Piccard $\delta^{15}\text{N}$ values ranged from 3.6‰ to 15.8‰ ($\delta^{15}\text{N}$ range = 12.2‰), with the orange microbial mat and brown gastropod *Provanna* sp. having the lowest $\delta^{15}\text{N}$ values (Figure 5A). Similar $\delta^{15}\text{N}$ values were measured for *R. hybisae* from all three Piccard sampling locations (Kruskal-Wallis, $H(2) = 1.499$, $\rho = 0.473$), but these values were significantly higher than those obtained from the gastropods (Kruskal-Wallis, $H(3) = 14.230$, $\rho = 0.003$). $\delta^{15}\text{N}$ values of the *Rimicaris* were 2 to 4‰ greater than the gastropods. Slightly higher, but not significant (Kruskal-Wallis, $H(3) = 6.033$, $\rho = 0.110$), $\delta^{15}\text{N}$ values were observed for the

squat lobster *Munidopsis* sp. (10.1 to 10.7‰). However, $\delta^{15}\text{N}$ values were higher for the anemones (11.5‰ to 15.8‰)(Kruskal-Wallis, $H(4) = 15.824$, $p = 0.003$).

4.3 Carbon and Nitrogen isotopes at Von Damm

The Spire had the narrowest range of $\delta^{13}\text{C}$ values between -26.0‰ and -12.5‰ ($\delta^{13}\text{C}$ range = 13.5‰), whereas the range of $\delta^{13}\text{C}$ values at Shrimp Hole (-28.3‰ and -11.6‰ ($\delta^{13}\text{C}$ range = 16.7‰)) were similar to the range at Piccard (Figure 5B, Table 2). The lowest $\delta^{13}\text{C}$ values (<-20‰) were observed in *Iheyaspira bathycodon*, *Alvinocaris* sp. and *Munidopsis* sp. and the highest $\delta^{13}\text{C}$ values (>-20‰) were those of *Lamellibrachia* sp., *Escarpia* sp., *Rimicaris hybisae*, *Lebbeus virentova* and *Thermarces* sp.. The $\delta^{13}\text{C}$ values for *I. bathycodon*, the only species sampled at both sites, were lower at Shrimp Hole relative to those at the Spire (t-test, $t(6) = -3.880$, $p=0.010$). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured for the two groups of *Rimicaris hybisae* at the Spire (at the orifice and on the flanks) were not significantly different (for $\delta^{13}\text{C}$ Mann-Whitney, $T(7, 11) = 69.00$, $p=0.856$, for $\delta^{15}\text{N}$ Mann-Whitney, $T(16, 8) = 76.00$, $p=0.150$). On the other hand, $\delta^{13}\text{C}$ values for *R. hybisae* at Von Damm were higher than *R. hybisae* at Piccard (Kruskal-Wallis, $H(4) = 27.540$, $p < 0.05$). Particulate organic matter collected at the Spire had $\delta^{13}\text{C}$ values ranging from -26.0 to -18.4‰ (mean = -21.5 ± 2.3 ‰)(Table 3).

The $\delta^{15}\text{N}$ values for the Von Damm samples were similar at the two sites, ranging between 4.6‰ and 11.5‰ ($\delta^{15}\text{N}$ range = 6.9‰) at the Spire and 2.8‰ and 9.2‰ ($\delta^{15}\text{N}$ range = 6.4‰) at Shrimp Hole (Figure 5B, Table 2). The range in values was half that of those at Piccard. At the Spire, similar low $\delta^{15}\text{N}$ values were measured for *Rimicaris hybisae*, *Alvinocaris* sp. and *Itheyaspira bathycodon* (Kruskal-Wallis, $H(2)=2.448$, $\rho = 0.329$). At Shrimp Hole, similar $\delta^{15}\text{N}$ values were measured for all of the species sampled (Kruskal-Wallis, $H(4)=5.384$, $\rho = 0.250$). At the Spire, the highest, significantly different (ANOVA, $F(3, 13) = 37.656$, $\rho < 0.05$) $\delta^{15}\text{N}$ values were observed in the eelpout *Thermarces* sp.. The greatest range of $\delta^{15}\text{N}$ values was observed in *Alvinocaris* sp. shrimp (*Alvinocaris* sp.; 2.9‰ to 7.6‰; $\delta^{15}\text{N}$ range = 4.7‰) and squat lobsters (*Munidopsis* sp.; 3.7‰ to 9.2‰; $\delta^{15}\text{N}$ range = 5.5‰). There was insufficient organic matter to measure nitrogen isotope compositions in particulate organic matter collected with the in-situ pump.

5. Discussion

5.1 Carbon sources to the Cayman vents

Chemoautotrophy at the base of a hydrothermal food chain fixes DIC from seawater and vent fluid to form complex organic molecules. In addition to chemosynthetically produced carbon, primary and secondary consumers graze on vent derived and photosynthetically produced organic matter. The Piccard vent field is twice as deep as the Von Damm vent field. Therefore

the potential for photosynthetically derived organic carbon input to the ecosystem should be less. Streit et al. (2015) found polyunsaturated fatty acids (PUFAs) possibly from a photosynthetic source (C20:5n3 and C22:6n3) in *Rimicaris* shrimp from both vent sites but could not determine whether photosynthetic POM contribution decreased with depth.

Large difference in $\delta^{34}\text{S}$ values exist between seawater sulfate compared to vent fluid sulfides (Fry et al., 1983). In previous studies, these differences have been used to discriminate between photosynthetic (~ 16 to 19‰) and chemosynthetic (-9 to 10‰) organic inputs (Erickson et al., 2009; Reid et al., 2013). The sulfur isotope composition of vent fluids is controlled by anhydrite precipitation during recharge of the hydrothermal system, where sulfate entering the high-temperature reaction zone is quantitatively reduced and mixed with H_2S hydrolyzed from the rock (Shanks, 2001). This anhydrite precipitation reaction results in vent fluid with $\delta^{34}\text{S}$ values typically between 6 and 14‰ .

At Piccard the $\delta^{34}\text{S}$ values of the fauna fell within a narrow range (Figure 4A, 7.5 to 15.0‰) and were lower than typical values for oceanic fauna (15 to 20‰ ; Kaplan et al., 1963; Fry et al., 1983). The orange microbial mat collected at Beebe Woods provides an example of a chemosynthetic primary producer. Warm fluids surrounding the mat would be expected to provide an inorganic sulfur source to the bacteria with a $\delta^{34}\text{S}$ value of $6 \pm 0.5\text{‰}$ (vent fluid value) (McDermott, 2015). This is indeed

the case since the orange microbial mat has a $\delta^{34}\text{S}$ value of 7.6‰. This is also true for the *Rimicaris* shrimp collected from the same location. The higher $\delta^{34}\text{S}$ values of the megafauna at Beebe Vents suggest a trophic level shift (-1 to 2‰) and/or an influence from other sulfur sources, such as a photosynthetic input. Average $\delta^{34}\text{S}$ values for megafauna at Beebe Sea fell within a small range (8.2 to 10.5‰, Table 1) indicating a vent fluid dominance of sulfur for samples with low $\delta^{34}\text{S}$ values (*Provanna* sp.), and trophic level shift/photosynthetic input for samples with higher $\delta^{34}\text{S}$ values (*R. hybisae* and *Munidopsis* sp.).

At Von Damm, $\delta^{34}\text{S}$ values of megafauna spanned a larger range, with higher values measured for *Rimicaris hybisae* (13.3 ± 0.8 ‰) compared to those measured for the same species at Piccard (8.0 ± 0.5 ‰). These higher values fall in the range typically expected for combined photosynthetic and chemosynthetic production sources (Reid et al., 2013). However, the $\delta^{34}\text{S}$ values for the vent fluid at the Von Damm Spire were also higher than those at Piccard, ranging between 10.3 and 10.6‰ (McDermott, 2015). The difference between the $\delta^{34}\text{S}$ values for the *Rimicaris* shrimp and the vent fluids at Von Damm (~ 2.9 ‰) was greater than that at Piccard (~ 0.4 ‰), suggesting additional input from photosynthetically derived organic carbon. This is not surprising considering the Von Damm vent field is much shallower than the Piccard Vent field.

5.2 Chemoautotrophy at the base of the food chain

5.2.1 Piccard vent field

The $\delta^{15}\text{N}$ vs. $\delta^{13}\text{C}$ plot of the Piccard vent fauna (Figure 5A) shows two narrow ranges of $\delta^{13}\text{C}$ values (Group 1 and Group 2) and a wide range of $\delta^{15}\text{N}$ values. This suggests that the organic carbon entering the food chain is derived from two dominant sources. In Group 1, the mean $\delta^{13}\text{C}$ values (-27.1‰ to -22.6‰) are consistent with the Calvin Benson Bassham (CBB) cycle with the Rubisco type I enzyme as the dominant carbon fixation pathway (Robinson and Cavanaugh, 1995). The CBB cycle is considered the principle pathway at temperatures $<20^\circ\text{C}$ and autotrophs supporting this group most likely derive their energy from sulfide and/or Fe oxidation (Hugler et al., 2011). Group 1 includes Provanna gastropods and two microbial mats, one of which is a white filamentous mat typical of sulfide oxidizers and the other is an orange mat typical of Fe oxidizers (Taylor et al., 1999; Emerson and Moyer, 2002).

A different chemoautotrophic carbon source for Group 2 taxa is inferred based on their higher $\delta^{13}\text{C}$ values. Within Group 2, shrimps belonging to the species *Rimicaris hybisae* have the lowest $\delta^{15}\text{N}$ values (with some site-specific variability) and along with their associated epibiotic microbes are at the base of the consumer food chain. *Rimicaris hybisae* is morphologically most similar to *R. exoculata*, *R. kairei* and *Chorocaris chacei* and they are endemic to hydrothermal vent systems (Martin and Haney,

2005; Nye et al., 2012). The carapace and mouth parts of *R. hybisae* are ornamented with setae bearing numerous bacteria-like structures. These bacteria are most likely epibiotic, 'syntrophic' bacterial communities, as observed within the carapace and on the mouth parts of *R. exoculata*, and *C. chacei* (Gebruk et al., 2000; Stams and Plugge, 2009). These bacteria are the dominant food source for the shrimp. It has been proposed that within the carapace, an internal sulfur cycle between sulfur-oxidizing ϵ - and γ -proteobacteria and sulfate-reducing δ -proteobacteria (using hydrogen as an electron donor) takes place (Ponsard et al., 2013). ϵ -proteobacteria found in association with *Rimicaris exoculata* have been shown to oxidize reduced sulfur compounds and hydrogen for energy generation and use reductive tricarboxylic acid cycle (rTCA) for carbon fixation, whereas γ -proteobacteria oxidize sulfur via the CBB cycle (Hugler et al., 2011). It is the combination of these two carbon fixation pathways that results in the higher $\delta^{13}\text{C}$ values.

5.2.2 Spire, Von Damm Vent field

As at Piccard, *Rimicaris hybisae* shrimp were abundant at Von Damm. At the Spire, this species had a narrow range of $\delta^{13}\text{C}$ values (-14.0 to -12.7‰, mean = -13.2 ± 0.4), compared with a wider range (-22.7 to -12.3‰, mean = -15.1 ± 3.5) 30 m away on the flanks of the Spire. Mobile species at other vent sites also exhibit spatial variability in $\delta^{13}\text{C}$ values. It has been suggested that this reflects higher concentrations of reduced compounds that are responsible for varying the balance of the two carbon

fixation pathways (De Busserolles et al., 2009; Reid et al., 2013). The wide range of $\delta^{13}\text{C}$ values for the *R. hybisae* on the flanks of the Spire also suggests alternative food sources for the shrimp from feeding on detritus and/or predation (Guri et al., 2012; Versteegh et al., 2014). Predation is suggested by a 3.8‰ difference between the highest and lowest $\delta^{15}\text{N}$ values for the flank shrimp, typical of a trophic level shift (Figure 5B). Shifts in $\delta^{13}\text{C}$ values without changes in $\delta^{15}\text{N}$ value could signify feeding on detritus (Figure 5B). As mentioned above, *R. hybisae* is morphologically similar to *R. exoculata*, *R. kairei* and *Chorocaris chacei* (Nye et al., 2012) but is genetically most closely related to *C. chacei* (S. Arnaud-Haond, pers. comm., Van Dover laboratory). Mature *C. chacei* get some of their food from grazing as well on their epibionts (Ramirez-Llodra and Segonzac, 2006).

Particulate organic matter collected from Von Damm is presumably composed of both chemo- and photo-synthetically produced carbon. This POM will include autotrophs, heterotrophs, as well as detritus from the vents and the water column. The $\delta^{13}\text{C}$ values of the POM ranged between -26.0 to -18.4‰, with an average value typical of photosynthetically derived carbon ($-21.5 \pm 2.3\text{‰}$). However, these samples were collected in warm (4 to 77°C) hydrothermal fluids and therefore the expectation is that they will be dominated by chemoautotrophs. One possible explanation is that the POM contains a combination of chemosynthetically produced organic matter that results from the CBB cycle as well as from the rTCA cycle.

Stable carbon isotopes cannot therefore be used to distinguish between photo- and chemosynthetically produced carbon in the POM.

5.2.3 Shrimp Hole, Von Damm

Shrimp Hole had a unique chemoautotrophic carbon source that was absent at both the Spire and Piccard, namely endosymbionts within the tubeworms. The tubeworms had $\delta^{13}\text{C}$ values ranging from -21.3 to -11.6‰ in *Escarpia* sp. and -21.1 to -13.3‰ in *Lamellibrachia* sp.. Seep tubeworms take up pore water DIC through their roots, part of which will be derived from microbial sulfate reduction coupled to hydrocarbon (including methane) oxidation (Becker et al., 2011). The $\delta^{13}\text{C}$ values of tubeworm tissues will therefore be influenced by the $\delta^{13}\text{C}$ values of the hydrocarbon. Seep fauna typically have much lower $\delta^{13}\text{C}$ values ($\delta^{13}\text{C} \sim -55$ to -26 ‰) indicative of a biogenic source of hydrocarbon (Becker et al., 2011), but the higher $\delta^{13}\text{C}$ values at Von Damm indicate a thermogenic source of hydrocarbon (i.e. methane, ethane and propane found in the vent fluids) (McDermott, 2014).

The range in $\delta^{13}\text{C}$ values is large, especially considering that tubeworms typically host a single type of γ -proteobacteria within their trophosome (Childress and Fisher, 1992). This could be a result of a mixed DIC source of seawater DIC and DIC from

hydrocarbon oxidation within the pore water fluids. In addition, endosymbionts have the potential to fix carbon by both the CBB and the rTCA cycle (Thiel et al., 2012) and they fractionate carbon by different amounts depending on the dominant carbon fixation pathway.

5.3 Seep fauna at Von Damm

The tubeworms, mussel and clams at Von Damm are typical of the seep environment. The low $\delta^{34}\text{S}$ values (-10.2 to -6.9‰) obtained from the tubeworms at Shrimp Hole are similar to those measured elsewhere in hydrocarbon seeps on the Louisiana Slope and the Florida Escarpment (Vetter and Fry, 1998). These values are indicative of a biological source of hydrogen sulfide from the microbial reduction of sulfate (Kim et al., 1989; Miura et al., 2002) and sulfate reduction, often coupled to methane oxidation, typical of seep environments. Tubeworms at Shrimp Hole (Von Damm) have very short roots (buried at most a centimeter into rubble), suggesting that microbial sulfate reduction must be occurring either in the shallow subsurface and/or in the anterior part of the tube (Duperron et al., 2014).

Cold seep tubeworms, mussels and clams have been found at other hydrothermal vent fields, e.g., sediment hosted sites where hydrocarbon concentrations are elevated in vent fluids as a result of organic decomposition (Valu Fa Ridge, Lau Back-Arc

Basin; Southward, 1991; Middle Valley, Juan de Fuca Ridge; Juniper et al., 1992; TOTO Caldera, South Mariana Volcanic Arc, DESMOS, Manus Basin and Brothers Caldera, Kermadec Arc; Kojima et al., 2006; Palinuro volcanic complex, Western Mediterranean Sea; Thiel et al., 2012). The elevated hydrocarbon concentrations within their fluids enable sulfate reduction to hydrogen sulfide, providing chemical energy to the tubeworms (Levin, 2005) and methane to the methanotrophic endosymbionts in the mussels and clams (Fisher et al., 1987). Levin et al. (2012) introduced the idea of 'hydrothermal seeps' as represented by the Jaco Scar site on the subductive seamount of the Costa Rica margin. The fauna at Jaco Scar are found at vents and/or seeps and have stable isotope signatures intermediate between sedimented vents and seeps. Using this model, Shrimp Hole has a closer relationship to a hydrothermal vent system with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the tubeworms falling within the same range as those measured for the fauna at the Spire (Figure 5B).

It is striking that the tubeworms use hydrogen sulfide sourced from microbial sulfate reduction rather than geothermal hydrogen sulfide in vent fluids yet their carbon originates from a thermogenic source. This could be because the tubeworms produce their own hydrogen sulfide in the anterior part of their tube (Duperron et al., 2014). Nevertheless, anaerobic oxidation of methane coupled to sulfate reduction may be essential for the existence of seep-like tubeworms at a vent field. Other chemical processes normally associated with seeps could also be responsible for the occurrence of tubeworms in this

area. At Piccard, the lack of sediment cover or reduced concentrations of methane/hydrocarbons in the vent fluids must make the vent field uninhabitable to tubeworms. Hydrocarbons therefore appear to exert an important control on the faunal diversity in these two vent fields.

5.4 Trophic relationships between consumers and comparison with other vent fields

5.4.1 Species found at both vent fields

Rimicaris hybisae was the only abundant species shared between Von Damm and Piccard vent field. The lack of genetic differences between the two populations suggests effective dispersal both geographically and in the water column through larval, juvenile and/or adult stages (Plouviez et al., 2015). However, the stable carbon isotope values of *R. hybisae* were lower at Von Damm (mean $\delta^{13}\text{C}$ -15.1 to -13.2‰) compared to Piccard (mean $\delta^{13}\text{C}$ -11.4 to -10.5‰). Stable carbon isotope values of *Rimicaris* shrimp on the MAR also show variability, ranging from -14.6 to -10.1‰ (Gebruk et al., 2000). This range of values is similar for both ultramafic and basalt hosted vent fields and is most likely the result of a varying contribution from the two carbon fixation pathways (De Busserolles et al., 2009; Reid et al., 2013). Streit et al. (2015) suggest that at Piccard, compared to Von Damm, carbon fixation by ϵ - and γ -proteobacteria is more important than fixation by the rTCA cycle, leading to an

increase in $\delta^{13}\text{C}$ values. This could reflect the higher H_2S concentrations at Piccard (12 mM vs 3.2 mM at Von Damm) rather than the H_2 concentrations, which are similar.

Along the MAR, *Rimicaris* shrimp compete with *Bathymodiolus* mussels for habitat, but this was not the case at these two sites along the Mid-Cayman Rise (Desbruyeres et al., 2000). At Von Damm, live *Bathymodiolus* mussels were scarce yet there was an abundance of empty mussel shells. This is most likely a result of localized temporal changes in temperature/chemistry in these areas (Plouviez et al., 2015). Filter feeding by the mussels means that the surrounding vent fluids must have low particulate loading in order for the mussels to survive. It is therefore not surprising that mussels were absent at Piccard.

In addition to *Rimicaris hybisae*, the squat lobster *Munidopsis* sp. was present at both vent fields. This is likely the result of a non-specialized diet (Limen and Juniper, 2006) as suggested by their range in $\delta^{13}\text{C}$ values. These squat lobsters are likely to have a mixotrophic diet, grazing off surfaces and decaying matter (e.g. shrimp exuviae; (Soto, 2009)). Their $\delta^{15}\text{N}$ values are consistent with their role as secondary consumers (Figure 2a and b). *Munidopsis* is the most widespread of all vent-associated taxa and has been reported at both hydrothermal vents and cold seeps (Stevens et al., 2008).

5.4.2 Species unique to Piccard

Provannid gastropods were found in and around the rocks covered with white microbial mat at Beebe Sea. Similar $\delta^{13}\text{C}$ values were measured for the gastropods (-26.9‰ to -24.7‰) and the white microbial mats (-25.5‰), consistent with grazing by snails on microbial mat as well as an additional carbon source with lower $\delta^{13}\text{C}$ values. These gastropods could harbor their own symbionts as demonstrated for the hydrothermal vent gastropod *Cyathernia naticoides* (Zbinden et al., 2015)

The anemones were unique to Piccard and based on $\delta^{15}\text{N}$ values (11.5 to 15.8‰), they are at the top of the Piccard food chain. The Piccard anemones are visually reminiscent of *Maractis rimicarivora*, a morphologically similar vent species found at Mid-Atlantic Ridge vents in close association with dense shrimp aggregations (Fautin and Barber, 1999). These anemones appear to be endemic to hydrothermal vent systems. *Maractis rimicarivora* preys on shrimp, stunning the victim with toxins and ingesting the shrimp whole (Van Dover, 2000). If *Rimicaris hybisae* shrimp were the sole diet of these anemones, we would expect the carbon and nitrogen isotope composition of the anemones to be 0 to 1.5‰ (carbon) and >3‰ (nitrogen) greater than the values measured for the *R. hybisae* sampled in this study. Instead, the anemones $\delta^{13}\text{C}$ values are less than the *R. hybisae* and their $\delta^{15}\text{N}$ values are 6.1‰ greater, suggesting an additional nutritional source that is currently unknown.

5.4.3 Species unique to Von Damm

There were a further four unique consumers at Von Damm; *Itheyaspira bathycodon* gastropods, two omnivorous shrimp (*Lebbeus virentova* and *Alvinocaris* sp.) and the *Thermarces* eelpout fish. The more complicated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plots for both the Spire and Shrimp Hole (Figure 5B) compared to Piccard reflect the greater variability in carbon sources and/or carbon fixation pathways, both of which will increase the diversity of the trophic resources available to particular species. (Section 5.2). The smaller range in $\delta^{15}\text{N}$ values indicates a smaller food chain length (Perkins et al., 2014). Consumers may be migratory and source their food from both the Spire and Shrimp Hole or other localized sites of venting at Von Damm. In addition, microbial subsurface processes affecting the vent fluids at Shrimp Hole may also be present at the Spire and the surrounding mixed fluids.

The fact that POM and *Itheyaspira bathycodon* gastropods yield similar $\delta^{13}\text{C}$ values (-26.0 to -18.4‰ and -28.4 to -20.9‰, respectively) is consistent with a snail grazing diet of POM. The lower $\delta^{13}\text{C}$ values of *I. bathycodon* at Shrimp Hole relative to those at the Spire suggest a different combination of food sources at each site. This could include chemosynthetic microbial assemblages that utilize different carbon fixation pathways and/or a photosynthetic input.

Isotope values indicate that *Alvinocaris* sp. ($\delta^{15}\text{N} = 2.9$ to 7.6‰ , $\delta^{13}\text{C} = -27.8$ to -18.3‰ , $\delta^{34}\text{S} = 1.1$ to 4.5‰) has a mixed diet, feeding on POM, *I. bathycodon* gastropods, *R. hybisae* and tubeworms, the latter exhibiting the lowest $\delta^{13}\text{C}$ values ($\delta^{15}\text{N} \sim 4.8\text{‰}$, $\delta^{13}\text{C} \sim -21\text{‰}$). This is consistent with evidence that other *Alvinocaris* species are opportunistic grazers (Gebruk et al., 2000; Stevens et al., 2008). In comparison, *Lebbeus virentova* shrimp ($\delta^{15}\text{N} = 6.3$ to 7.6‰ , $\delta^{13}\text{C} = -19.4$ to -12.5‰) had similar nitrogen and carbon isotope values to *R. hybisae*. *Lebbeus virentova* do not harvest their own epibionts, instead they graze on bacteria and detritus. Their location at the Von Damm Spire would provide them with a large source of vent derived organic carbon i.e. bacteria and decaying matter. *Lebbeus* sp. are not restricted to areas of venting and are found throughout the deep ocean, unlike *Alvinocaris* shrimp, which are endemic to hydrothermal vents and seep environments (Martin and Haney, 2005). Therefore migration from the Spire to Shrimp Hole to gain nutrition from the tubeworms would be feasible and result in the lower $\delta^{34}\text{S}$ values ($\delta^{34}\text{S} = 3.5$ to 13.3‰) compared to *R. hybisae*.

The eelpout *Thermarces* sp. has the highest $\delta^{15}\text{N}$ values at Von Damm and must therefore be at the top of the food chain. Even though whole *Rimicaris hybisae* shrimp were found within the guts of these fish, $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values of the fish ($\delta^{13}\text{C} \sim -15.4 \pm 1.8\text{‰}$, $\delta^{34}\text{S} \sim 9.1 \pm 0.6\text{‰}$) suggest a mixed diet, which may include *Alvinocaris* sp. and *Lebbeus virentova*.

Conclusions

In this study we have compared two proximal vent fields (21 km apart) and used stable isotopes to examine and compare the fauna. We have identified a greater range of carbon sources to the fauna at the Von Damm vent field compared to Piccard, providing a greater breadth of trophic resources. This is possibly the result of distinct chemistry in the vent fluids and the shallow depth, which would result in a higher input of photosynthetically-derived photodetritus. In particular, it is the presence of thermogenic hydrocarbons in the vent fluids at Von Damm that enable survival of the seep-associated tubeworms.

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Figure Legends

Figure 1 – (A) map of the Mid-Cayman Rise, (B) map of the Piccard vent field with Beebe Vents, Beebe Woods and Beebe Sea and (C) map of the Von Damm vent field with the Spire and Shrimp Hole

Figure 2 – Assemblages of megafauna at Piccard as photographed during sample collection (Table 1) A) High temperature chimneys at Beebe Vents B) *Rimicaris hybisae*, *Provanna* sp. and anemones collected from the base of the chimneys C) High temperature chimneys at Beebe Woods covered in *Rimicaris hybisae* D) *Rimicaris hybisae*, *Provanna* sp. and anemones collected from the chimneys E) Orange microbial mats F) Overview of the diffuse flow at Beebe Sea G) White microbial mat

Figure 3 - Assemblages of megafauna at Von Damm as photographed during sample collection (Table 2) A) The large venting orifice at the Von Damm Spire, surrounded by *Rimicaris hybisae* B) *R. hybisae*, *Itheyaspira bathycodon* and *Thermarces* sp. on the edges of the large orifice C) *R. hybisae* and *I. bathycodon* on the flanks of the Spire D) Overview of the diffuse flow at the Shrimp Hole with microbial staining, tubeworms, *R. hybisae*, and *I. bathycodon* E) A closer view of Shrimp Hole, including *Munidopsis* sp. as well as tubeworms and *I. bathycodon*

Figure 4 – $\delta^{34}\text{S}$ plots of individual species at each vent field A) Piccard vent field B) Von Damm Shrimp Hole and Spire. Vertical dashed line indicates the $\delta^{34}\text{S}$ of the vent fluid (McDermott, 2014).

Figure 5 – $\delta^{15}\text{N}$ vs. $\delta^{13}\text{C}$ plots of vent fauna on the Mid-Cayman Rise. Samples identifying the base of the food chain are highlighted with solid symbols. (A) Piccard vent taxa, with $\delta^{13}\text{C}$ values falling into two groups. Nitrogen content of rock covered in white filamentous microbial mat with $\delta^{13}\text{C}$ values of -25.5 and -24.3‰ was below detection limit (Table 1). Therefore a range of expected $\delta^{15}\text{N}$ values is indicated, with low $\delta^{15}\text{N}$ values typical of the base of the food chain (B) Von Damm vent taxa at the Spire and Shrimp Hole

Highlights

1. A greater range of carbon sources have been identified at the shallower Von Damm vent field compared to the deeper Piccard vent field.
2. Seep associated tubeworms rely on a thermogenic hydrocarbon source from the vent fluids

3. Microbial sulfate reduction at Von Damm either occurs in the shallow subsurface and/or in the anterior part of the tubeworm

4. Von Damm appears to have a smaller food chain length but a greater breadth of trophic resources compared to Piccard

Table 1 – Samples collected from Piccard vent field, including average $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values for 'n' number of samples analyzed.

Sample no.	Species	Date	Latitude	Longitude	Depth (m)	Location	Temp (°C)	n	Av. $\delta^{13}\text{C}$ (‰)	Av. $\delta^{15}\text{N}$ (‰)	Av. $\delta^{34}\text{S}$ (‰)
J2-613-19	Rimicaris hybisae	1/11/12	18 32.8185	81 43.1004	4972.11	Beebe Vents	8.8 to 12.6	7	-11.4 ±0.8	7.7 ±2.0	11.1 ±0.4
J2-613-18	Provanna sp.		18 32.8183	81 43.1005	4971.91		8.8 to 12.6	3	-25.6 ±1.5	4.3 ±0.7	9.5 ±0.9
J2-613-21	Anemones		18 32.8176	81 43.0994	4971.53		8.8 to 12.6	5	-13.2 ±0.4	13.8 ±1.6	12.1 ±2.0
J2-613-24	Rimicaris hybisae		18 32.7709	81 43.0852	4966.17	Beebe Woods		7	-11.0 ±0.4	7.6 ±1.9	8.0 ±0.5
J2-619-27	Orange mat	1/21/12	18 32.7703	81 43.0770	4969.06		10.6	1	-24.5	4.4	7.6
J2-620-27	Orange mat	1/23/12	18 32.7937	81 43.0929	4961.59			1	-22.6	4.0	

J2-619-15	Rimicaris hybisae	1/21/12	18 32.7730	81 43.0870	4967.09	Beebe Sea	6	-10.5 ±0.5	6.5 ±0.9	10.5 ±0.6
J2-620-30	Provanna sp.	1/23/12	18 32.7944	81 43.0669	4945.11	<43	4	-25.7 ±0.8	4.2 ±0.1	8.2 ±0.5
J2-620-31	Munidopsis sp.		18 32.8159	81 43.0803	4976.65	<43	2	-15.1 ±0.5	10.4 ±0.4	9.5 ±0.1
J2-618-16	White mat	1/20/12	18 32.7939	81 43.0618	4939.53	<38	1	-25.5		
J2-613-17	White mat	1/11/12	18 32.8191	81 43.1021	4973.59		1	-24.3		

n = number of samples analyzed

Table 2 - Samples collected from Von Damm vent field.

Sample no.	Species	Date	Latitude	Longitude	Depth (m)	Location	Temp (°C)	n	Av. $\delta^{13}\text{C}$ (‰)	Av. $\delta^{15}\text{N}$ (‰)	Av. $\delta^{34}\text{S}$ (‰)
Spire											
J2-617-05	Rimicaris hybisae	1/19/12	18 22.6148	81 47.8802	2293.6	Spire - on edges of large orifice		8	-13.2 ±0.4	5.9 ±0.6	13.3 ±0.8
J2-617-06	Iheyaspira bathycodon	1/19/12	18 22.6142	81 47.8794	2293.6			3	-21.7 ±0.9	5.0 ±0.3	10.1 ±0.3
	Thermarces sp.							2	-15.9 ±2.7	10.7 ±1.1	9.9
J2-617-07	Thermarces sp.	1/19/12	18 22.6140	81 47.8783	2293.2			2	-14.5 ±1.5	9.9 ±0.0	8.9 ±0.4
J2-617-08	Iheyaspira bathycodon	1/19/12	18 22.5963	81 47.8868	2295.9			3	-24.4 ±3.4	5.3 ±0.5	
	Thermarces sp.							1	-16.2	9.2	8.7
	Alvinocaris sp.							2	-22.2 ±5.4	5.9 ±1.9	

	Lebbeus virentova							6	-15.0 ±2.4	6.9 ±0.4	8.0 ±4.3
J2-616-44	Rimicaris hybisae	1/18/12	18 22.5982	81 47.8835	2290.7	On flanks of Spire		16	-15.1 ±3.5	6.4 ±1.0	12.8 ±0.5
Shrimp Hole											
J2-616-25	Escarpia sp.	1/18/12	18 22.4797	81 47.8408	2375.1	Interspersed shrimp and gastropods	<50.5	17	-16.4 ±3.3	4.2 ±0.7	-8.5 ±1.5
	Lamellibrachia sp.							8	-15.7 ±2.5	4.4 ±0.8	-8.0 ±1.5
J2-616-28	Alvinocaris sp.	1/18/12	18 22.4806	81 47.8406	2374.9			7	-22.6 ±3.1	5.2 ±1.5	3.3 ±1.9
	Itheyaspira bathycodon							3	-25.8 ±2.0	4.8 ±0.5	
J2-621-15	Munidopsis sp.	1/24/12	18 22.4839	81 47.8417	2374.8			1	-26.7	3.7	0.4
J2-621-19	Munidopsis sp.	1/24/12	18 22.5079	81 47.8154	2387.3			1	-22.0	9.2	9.3

n = number of samples analyzed

Table 3 - $\delta^{13}\text{C}$ values of the particulate organic matter at Von Damm. Due to the low concentrations of particulate organic matter, it was only possible to measure $\delta^{13}\text{C}$.

Sample no.	Species	Date	Latitude	Longitude	Depth (m)	Location	Temp (°C)	n	Av $\delta^{13}\text{C}$ (‰)	Seawater filtered (L)
J2-614	Particulate organic matter	1/13/12	18 22.5833	81 47.8829	2290	Hot vent	77	1	-19.4 ±0.1	5
J2-614	Particulate organic matter	1/13/12	18 22.5999	81 47.8871	2296	Cooler vent	64	1	-19.8 ±0.1	5
								1	-20.0 ±0.4	
J2-614	Particulate organic matter	1/13/12	18 22.5999	81 47.8871	2296	Background	4	1	-22.2 ±0.2	8
								1	-22.5 ±0.3	

J2-614	Particulate organic matter	1/13/12	18 22.5999	81 47.8871	2288	8 m in the hydrothermal plume	18	1	-26.0 ±0.2	6
								1	-18.4 ±0.5	
								1	-22.1 ±0.2	
								1	-22.7 ±0.2	

n = number of samples analyzed. Error on isotope value propagated from blank correction of filter.

Figure 1

Figure 2

Beebe Vents

Beebe Woods

Beebe Sea

Figure 3

Figure 4

Figure 5

(A) Piccard vent field

(B) Von Damm vent field