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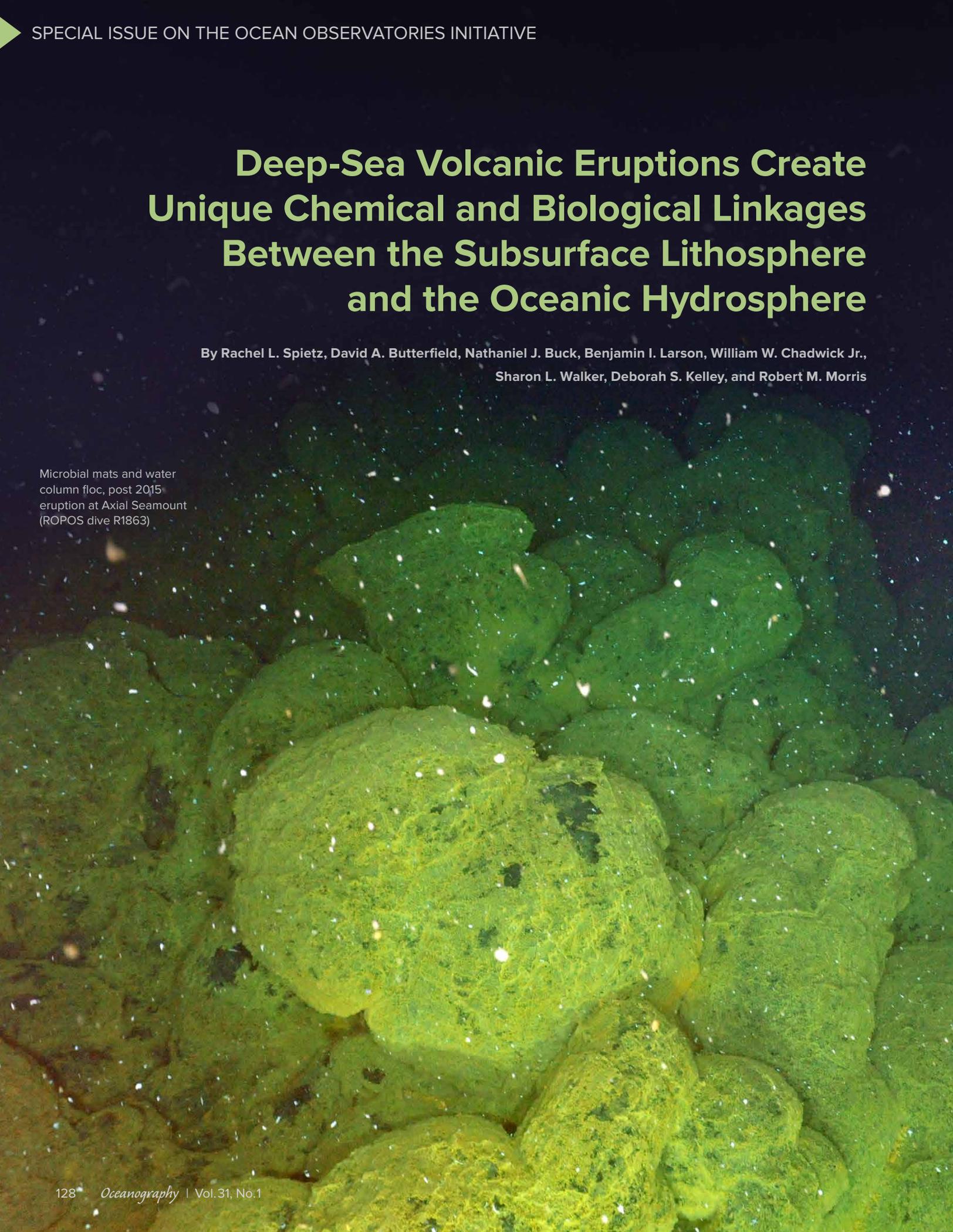
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Deep-Sea Volcanic Eruptions Create Unique Chemical and Biological Linkages Between the Subsurface Lithosphere and the Oceanic Hydrosphere

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Microbial mats and water column floc, post 2015 eruption at Axial Seamount (ROPOS dive R1863)



ABSTRACT. In April 2015, pressure recorders, seismometers, and hydrophones attached to the Ocean Observatories Initiative (OOI) Cabled Array on Axial Seamount detected, in real time, a volcanic eruption predominantly located along the north rift zone (NRZ). Real-time detection enabled a rapid response cruise to augment OOI data with ship-based physical, chemical, and biological sampling of the eruption and the new lava flows. The combined data set demonstrates the synergistic value of real-time monitoring combined with rapid response efforts that sample beyond the boundaries of a fixed cabled array. These combined data show that the 2015 eruption gave rise to chemically and microbiologically variable hydrothermal plumes over new NRZ lava flows, reflecting chemical and biological linkages between the subsurface lithosphere and the oceanic hydrosphere. The warmest and least diluted plume near the new lava flows was 0.119°C above background seawater and hosted thermophilic and hyperthermophilic taxa that are typically identified in hydrothermal fluids emanating from the warm subsurface. Cooler and more diluted hydrothermal plumes farther from a hydrothermal fluid source were 0.072°–0.078°C above background seawater and hosted mesophilic and psychrophilic taxa that are typically identified in neutrally buoyant plumes at persistent hydrothermal venting sites. Potentially chemosynthetic microbial lineages, including Epsilonproteobacteria, Gammaproteobacteria, and Methanococcales, were positively correlated with elevated temperature anomalies. These data suggest that hydrothermal fluid flow through new lava flows on the NRZ supported diverse microbial communities for several months following the 2015 eruption and that subsurface heterogeneity contributed to the structure of unique hydrothermal-plume-hosted microbial communities.

BACKGROUND

Axial Seamount is the largest and most active volcano on the Juan de Fuca Ridge spreading center. Annual research cruises have collected chemical, geological, and biological data at Axial Seamount for more than three decades, making this one of the longest time series for a deep-sea volcanically driven hydrothermal system. In 1998, an eruption on Axial's south rift zone was remotely detected by US Navy hydrophones (Dziak and Fox, 1999; Chadwick et al., 2013). Axial Seamount erupted again in 2011 along the south rift zone, resulting in lava flows inside and outside the caldera with numerous “snow blower” vents that emitted white floc from dense eruption-associated microbial mats (Caress et al., 2012; Meyer et al., 2013; Kelley et al., 2014). In 2014, the Ocean Observatories Initiative (OOI) completed installation of a regional cabled observatory that spans the Juan de Fuca Plate with nodes at Axial Seamount

that include over 20 cabled instruments within the caldera (Kelley et al., 2016).

The OOI Cabled Array detected in real time the most recent eruption, which started on April 24, 2015, and lasted for several weeks (Nooner et al., 2016; Wilcock et al., 2016). These data were critical for identifying new lava flows, capturing for the first time the locations and timing of earthquakes and explosive events as they occurred. The data suggest that activity was focused along Axial's north rift zone (NRZ), and this location was confirmed by depth changes detected by bathymetric resurveys and remotely operated vehicles in July and August 2015 (Chadwick et al., 2016; Kelley et al., 2016). The thickest new lava flows were covered by microbial mats, and there were numerous sites of hydrothermal flow (Chadwick et al., 2016; Kelley et al., 2016). The bathymetric and visual observations detected 11 new lava flows from at least 13 new fissures along the NRZ and within Axial

caldera (Chadwick et al., 2016), with a combined volume of $1.48 \times 10^8 \text{ m}^3$, making the 2015 eruption the largest volume of lava documented since data collection began in the mid-1980s. The morphology and chemical composition of separate lava flows varied from thin sheet flows within the caldera to much thicker and more evolved (lower MgO) pillow lava along the NRZ (Chadwick et al., 2016).

Eruptive events at mid-ocean ridges are responsible for high fluxes in heat, chemicals, and biological matter from the subsurface (Baker et al., 1987; Butterfield et al., 1997; Delaney et al., 1998). Previous studies show that abrupt changes in the seafloor's physical and chemical environment and the overlying water column follow eruptive events and influence the structure and activity of local microbial communities (Huber et al., 2002, 2003). For example, fresh basalt in areas of hydrothermal flow after eruptive events is rapidly colonized by microbes (Gulmann et al., 2015). These benthic biofilms are dominated by chemolithoautotrophs (Meyer et al., 2013) that support seafloor communities at hydrothermal systems for months to years following eruptions (Tunnicliffe et al., 1997).

Eruptions can produce new venting of hydrothermal fluids due to increased permeability of the crust and new heat sources such as subseafloor magma and freshly erupted lava fields that are still cooling (Baker, 1998; Baker et al., 2004). Neutrally buoyant hydrothermal plumes from long-lived vents are a mixture of entrained background seawater and <0.01% of subsurface-derived hydrothermal fluid (Lupton et al., 1985). A recent high-resolution spatial study of hydrothermal vent plumes along the Eastern Lau Spreading Center suggests that ubiquitous deep-sea microbes populate plume microbial communities, while the contribution of subsurface microbial taxa to plume communities is secondary as

a result of extreme dilution within the hydrothermal plume (Sheik et al., 2015). Yet, some subsurface bacteria, such as sulfur-oxidizing Epsilonproteobacteria, demonstrate strong distance-decay relationships within plumes, with high abundances near the source of hydrothermal flow, and they can be considered indicators of hydrothermal activity (Djurhuus et al., 2017). While distance-decay relationships and high rates of entrainment of background deep-sea microbial communities primarily structure plume microbial communities, the geochemical and physical environment of the subsurface source fluids also impose selective pressures on microbial community composition over time (Huber et al., 2007; Opatkiewicz et al., 2009; Anderson et al., 2013).

Newly established links between the seafloor and subsurface magma sources,

as the result of a deep-sea eruption, have the potential to create variable subsurface hydrothermal conditions that alter overlying seawater non-uniformly, which may be reflected in the structure of microbial communities in newly formed eruptive hydrothermal plumes. We use physical, chemical, and biological data to characterize hydrothermal plume heterogeneity above new lava flows along the NRZ at Axial Seamount. Our data indicate that differences in subsurface environments associated with new lava flows can create geochemically unique hydrothermal plumes that harbor distinct microbial communities comprised of both deep-ocean and subsurface lineages. This has the potential to significantly impact deep-ocean microbiology, as mid-ocean ridges span 65,000 km of Earth's surface and are responsible for approximately 70% of the volcanic activity on Earth.

RESULTS AND DISCUSSION

Physical and Chemical Characterization of Distinct Post-Eruption Hydrothermal Plumes

A rapid response cruise was added to the previously planned R/V *Thompson* TN327 expedition to survey the geology, chemistry, and microbiology of new lava flows. CTD tow-yo surveys above the new NRZ lava flows collected continuous measurements for depth, temperature, salinity, and turbidity. Potential temperature and turbidity anomalies verified the presence of near-seafloor hydrothermal plumes 50–100 m thick extending horizontally several kilometers over the northernmost new lava flows (Methods in online Supplementary Materials, Figure 1A, Table 1). It is estimated that 92% of the erupted volume was accounted for in the three northernmost lava flows (#8–#10 using the numbering scheme

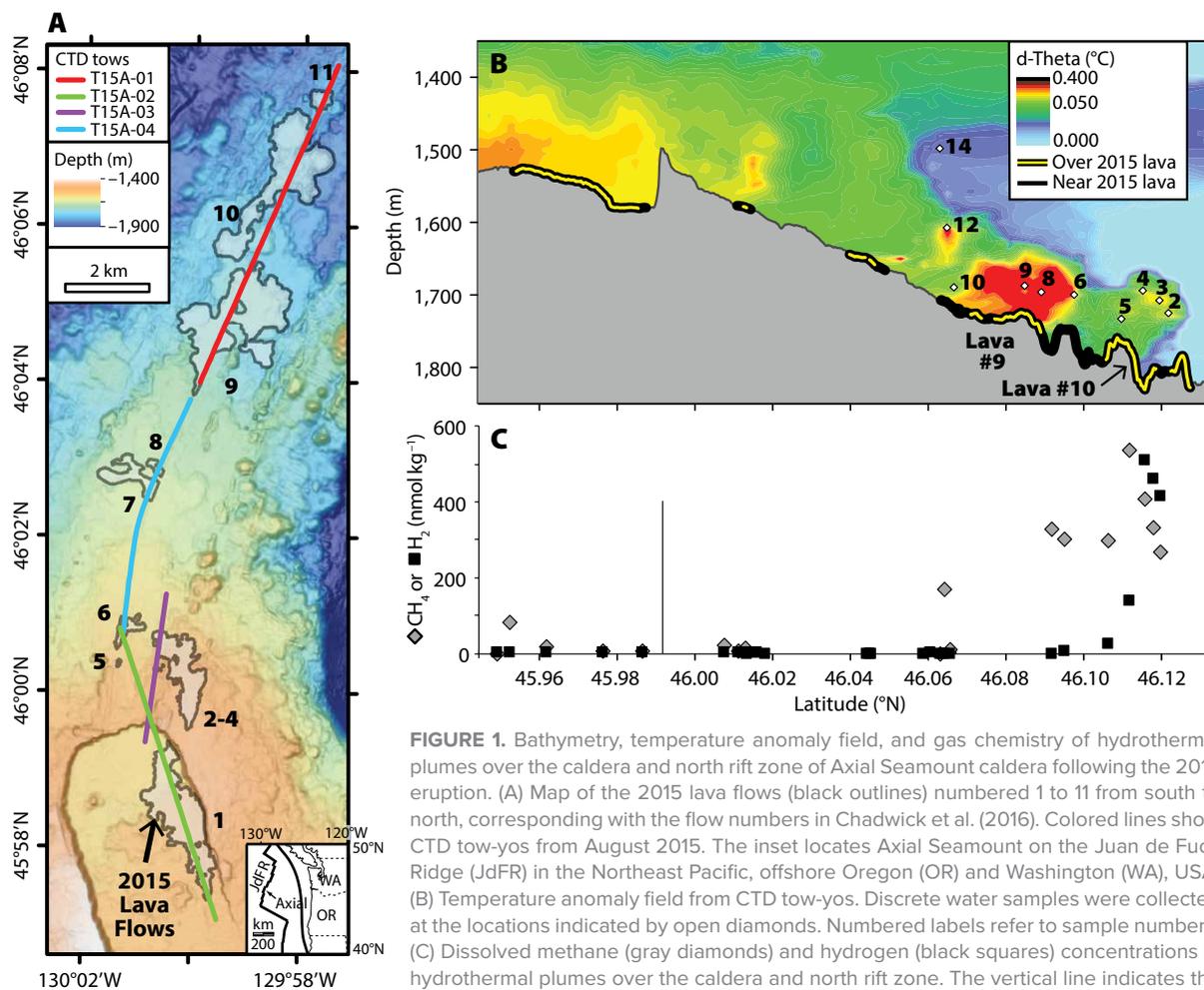


FIGURE 1. Bathymetry, temperature anomaly field, and gas chemistry of hydrothermal plumes over the caldera and north rift zone of Axial Seamount caldera following the 2015 eruption. (A) Map of the 2015 lava flows (black outlines) numbered 1 to 11 from south to north, corresponding with the flow numbers in Chadwick et al. (2016). Colored lines show CTD tow-yos from August 2015. The inset locates Axial Seamount on the Juan de Fuca Ridge (JdFR) in the Northeast Pacific, offshore Oregon (OR) and Washington (WA), USA. (B) Temperature anomaly field from CTD tow-yos. Discrete water samples were collected at the locations indicated by open diamonds. Numbered labels refer to sample numbers. (C) Dissolved methane (gray diamonds) and hydrogen (black squares) concentrations in hydrothermal plumes over the caldera and north rift zone. The vertical line indicates the northern boundary of Axial caldera.

from south to north following Chadwick et al., 2016). Hydrothermal plumes above these thicker northern flows had higher temperature anomalies than plumes overlying thinner new flows within Axial caldera or elsewhere along the NRZ. The plumes over new lava flows #9 and #10 (46.08°N and 46.11°N, respectively) were sampled for further characterization of plume chemistry and microbial microbiology. A total of 44 water-column samples from the caldera, NRZ, and background seawater were analyzed shipboard for methane and hydrogen concentrations. DNA was extracted from a subset of 12 water-column samples, and the microbial community was characterized by 16S rRNA gene sequencing (Methods in online Supplementary Materials).

Temperature and turbidity anomalies, as well as methane and hydrogen concentrations, were not uniform along the NRZ (Figure 1B,C) and showed regions of variability above lava flows #9 and #10 (Table 1). The hydrothermal plume above lava flow #9 (samples 6, 8, and 9) had the highest temperature and turbidity anomalies, measured as Δ NTU (nephelometric turbidity units; Figure 1B, Table 1). The plume over lava flow #10 (samples 2, 3, 4, and 5) was characterized by the highest hydrogen and methane concentrations compared to any other plume along the NRZ or within Axial caldera but had lower temperature and turbidity anomalies than in the plume over lava flow #9 (Figure 1B,C, Table 1). Two samples (10 and 12) were collected within the broader plume, not above a new lava flow, to compare lava-associated plumes with the non-lava associated plume (Figure 1B). Non-lava temperature anomalies were similar to those over lava flow #10 (average 0.078°C), but turbidity anomalies were lower than in both lava-associated plumes (Δ NTU = 0.024 vs. >0.039). Similarly, methane concentrations in the non-lava plumes were lower than in the lava-associated plumes, and hydrogen concentrations were near zero (Table 1). One background sample was collected at the

NRZ (sample 14) where temperature and turbidity anomalies were not detected. Two additional background samples were collected 24 km northeast of Axial Seamount and at depths corresponding to plume samples above lava flows #9 and #10 (1,500 m and 1,700 m).

Differences in plume conditions above the two NRZ lava flows indicate variability in the subsurface geology, chemistry, and microbiology. While no obvious differences in lava morphology or composition were detected between flows #9 and #10 (Chadwick et al., 2016), the microbial mats covering lava flows were thicker and more orange in color on lava flow #9 relative to lava flow #10. Additionally, the sharp increase in plume hydrogen and methane concentrations over lava flow #10 indicates differences in the chemistry, and possibly microbiology, over the two flows.

Hydrothermal fluids enriched in reduced chemical species fuel high rates of microbial productivity, which are commonly more productive than photosynthetically driven parts of the ocean (Lutz et al., 1994; McCollom and Shock, 1997; Shock and Holland, 1997; McCollom, 2000). Geochemical models predict that most chemosynthetic primary production within vent plumes occurs when

concentrations of hydrogen and sulfide are highest. This condition can occur in the early stages of hydrothermal plume development (McCollom, 2000). Microbial characterization of persistent vent plumes shows that sulfur- and hydrogen-oxidizing autotrophic bacteria dominate vent fluids at their source and are present in diffuse-flow fluids (Sunamura et al., 2004; Anantharaman et al., 2013; Anderson et al., 2013; Mattes et al., 2013). Understanding the heterogeneity in the hydrothermal plumes associated with new lava flows from the 2015 eruptive event is important when considering biogeochemical models of deep-sea eruptions.

Microbiological Characterization of Distinct Post-Eruption Hydrothermal Plumes

To understand how microbial community structure relates to environmental heterogeneity within post-eruptive hydrothermal plumes, we characterized microbial communities in discrete samples collected from the plumes over lava flows #9 and #10, in non-lava associated samples, and in background seawater. Non-metric multidimensional scaling of microbial operational taxonomic units derived from 16S rRNA gene sequence

TABLE 1. Physical and chemical measurements. Discrete samples are categorized by region and match sample numbers as indicated in Figure 1.

Region	Sample (ID)	Depth (m)	Temperature anomaly (°C)	Turbidity anomaly (Δ NTU)	CH ₄ (nmol kg ⁻¹)	H ₂ (nmol kg ⁻¹)
Lava flow #10	2	1,725	0.070	0.057	333	461
	3	1,708	0.082	0.054	406	508
	4	1,694	0.081	0.039	536	140
	5	1,733	0.054	0.035	297	25
Lava flow #9	6	1,700	0.113	0.134	301	4
	8	1,696	0.121	0.202	NA	NA
	9	1,687	0.122	0.241	NA	NA
Non-lava	10	1,689	0.059	0.024	8	0
	12	1,607	0.096	0.024	168	0
Background	14	1,498	0.012	0.005	NA	NA
	1500	1,500	-0.012	0.001	BDL	1
	1700	1,700	0.000	0.001	1	1

NA = not available (data not collected). BDL = below detection limit. Δ NTU = turbidity anomaly in nephelometric turbidity units.

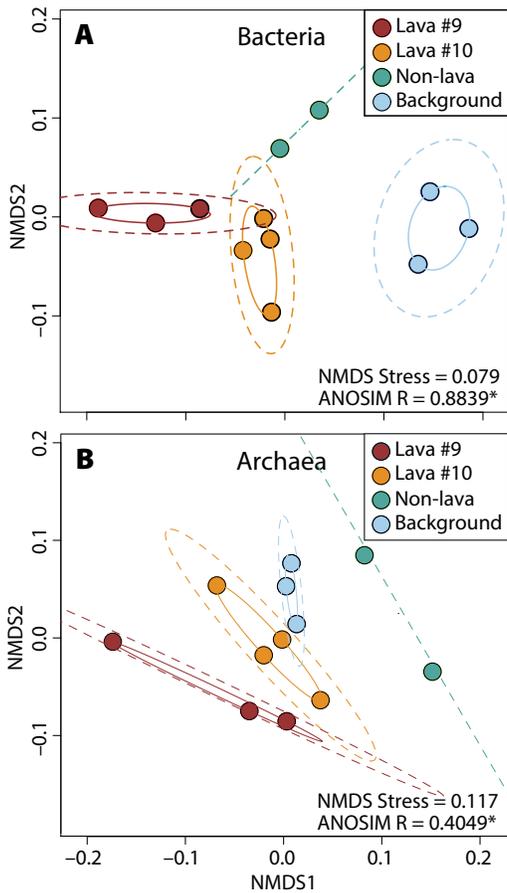


FIGURE 2. Non-metric multidimensional scaling plot of the differences between microbial communities across sampling regions at Axial Seamount following the 2015 eruption. Microbial communities were assessed for (A) bacterial and (B) archaeal composition. Points represent individual samples, and the colors of points represent four distinct sampling regions (above lava flow #10, lava flow #9, or non-lava seafloor, and background seawater not influenced by hydrothermal activity). Solid lines define a convex hull of the set of samples within a group while the dashed-lines show a dispersion ellipse using the standard deviation of sample point scores under a 95% confidence limit. An asterisk indicates $p < 0.01$.

analyses indicates that bacterial community composition was unique within each region (Figure 2A, ANOSIM global $R = 0.8839$, $p < 0.01$). The four regions sampled were also significantly distinct in terms of their archaeal communities (Figure 2B, ANOSIM global $R = 0.4049$, $p < 0.01$). Dispersion ellipses demarcating the standard deviations of sample points within each region indicate that microbial community composition was distinct in each of the four regions sampled.

Distinct bacterial communities were identified over the four different sampling regions even at a broad taxonomic level (Figure 3, Figure S1). The most abundant classes of bacteria were Alphaproteobacteria, Gammaproteobacteria, and Epsilonproteobacteria (Figure 3A). Gammaproteobacteria were dominant in plume regions (40.0% to 49.3%). Alphaproteobacteria dominated communities in background seawater, averaging 45.5% of the bacterial 16S rRNA gene sequences recovered from these samples. Many of the top bacterial classes were strongly correlated with temperature and turbidity anomalies, both indicators of hydrothermal input (Table S1). The Gammaproteobacteria and Epsilonproteobacteria had strong normal relationships with anomalies of temperature (adjusted R^2 : 0.63 and 0.67, respectively) and turbidity (adjusted R^2 : 0.57 and 0.96, respectively) across all 12 samples, while the Alphaproteobacteria had a strong inverse relationship with temperature and turbidity anomalies (adjusted R^2 : 0.78 and 0.74, respectively; Table S1).

Shifts in archaeal communities were also evident, though patterns in distribution were most noticeable among three low abundance orders: Methanococcales, Methanomicrobiales, and Cenarchaeales (Figure 3B). Methanococcales were most abundant in the near-seafloor plume over lava flow #9 (average 1.8%), where temperature anomalies were highest and where there were elevated methane and hydrogen concentrations, and over lava flow #10 (average 1.4%) where temperature anomalies were lower but methane and hydrogen concentrations were highest. Their contribution to archaeal communities decreased significantly in non-lava samples (average 0.8%) and in background seawater (0.2%). The Methanococcales also had the highest correlations with temperature and turbidity anomalies (adjusted R^2 : 0.82 and 0.55, respectively; Table S2). Cultivation-based studies have isolated thermophilic and

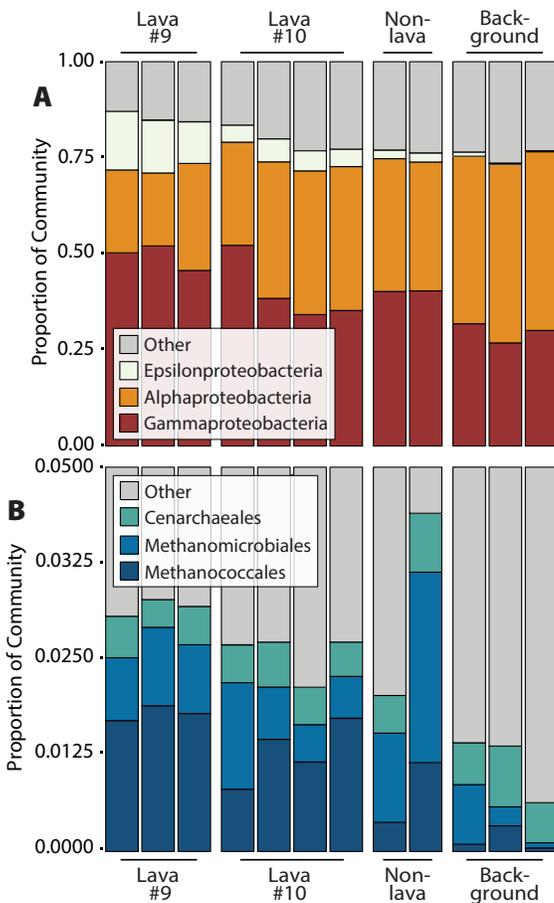


FIGURE 3. Proportions of key (A) bacterial classes and (B) archaeal orders detected along the north rift zone of Axial Seamount following the 2015 eruption. Samples are ordered by decreasing turbidity anomaly, a proxy for hydrothermal circulation, from left to right. Samples are classified into four distinct sampling regions: above lava flow #9, lava flow #10, non-lava, and background samples not influenced by hydrothermal activity.

hyperthermophilic hydrogen-consuming Methanococcales with temperature requirements well above the temperature of the hydrothermal plume fluids from which they were sampled (Holden et al., 1998; Summit and Baross, 1998; Topcuoglu et al., 2016). The implication from these studies is that mesophilic and thermophilic microorganisms in the heated subsurface environment are released into seawater (Delaney et al., 1998; Holden et al., 1998; Summit and Baross, 1998).

Strictly methanogenic Methanomicrobiales were most abundant in the non-lava associated samples and least abundant in background seawater. Most members of the Methanomicrobiales are psychrophilic or mesophilic and can use either hydrogen or formate as

electron donors for methanogenesis and acetate as a carbon source (Liu, 2010). It is important to note that while the Methanomicrobiales were most numerous in the non-lava region, their relative abundance compared to other archaeal orders was low (1.82% of archaeal sequences) and that the detection of a 16S rRNA gene sequence in the environment does not imply activity. Therefore, Methanomicrobiales may persist longer than thermophilic and hyperthermophilic methanogens in hydrothermal plumes that cool and become more dilute with entrained seawater, but are likely not contributing as much to methanogenesis within the plume, as indicated by the lower concentrations of methane in mid-plume samples. Methane-oxidizing microbes are known to dominate hydrothermal

plumes at Axial Seamount (Mattes et al., 2013), suggesting that they may contribute to the drawdown in methane in the non-lava associated samples. These data suggest that temperature-dependent niche partitioning among subsurface methane-producing Methanococcales and Methanomicrobiales is evident in newly formed lava-associated plumes.

Indicator analyses of bacterial taxa detected over new lava flows and in background seawater also suggest that there are detectable differences in species adapted to differences in subsurface temperatures. There were significant increases in the relative abundance of Epsilonproteobacteria in hydrothermal plumes (Figure 4). On average, they accounted for 13.2% of the bacterial community in the higher-temperature

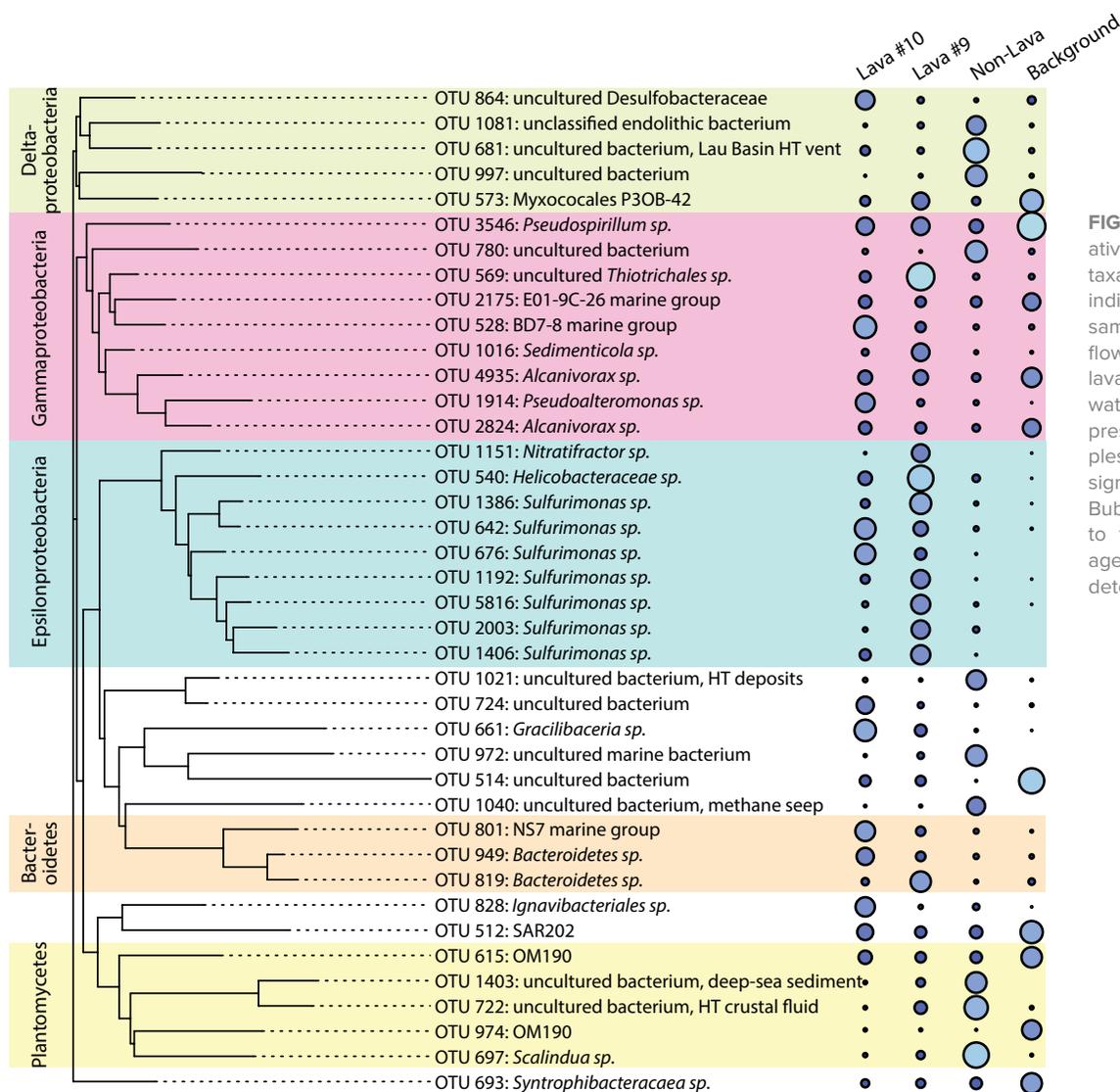


FIGURE 4. Phylogeny and relative abundances of bacterial taxa identified as significant indicators for each distinct sampling region: above lava flow #9, lava flow #10, non-lava, and background seawater. All indicator taxa were present in at least three samples, and indicator values were significant at alpha <0.05. Bubble size is proportional to the log-transformed average abundance of sequences detected within a region.

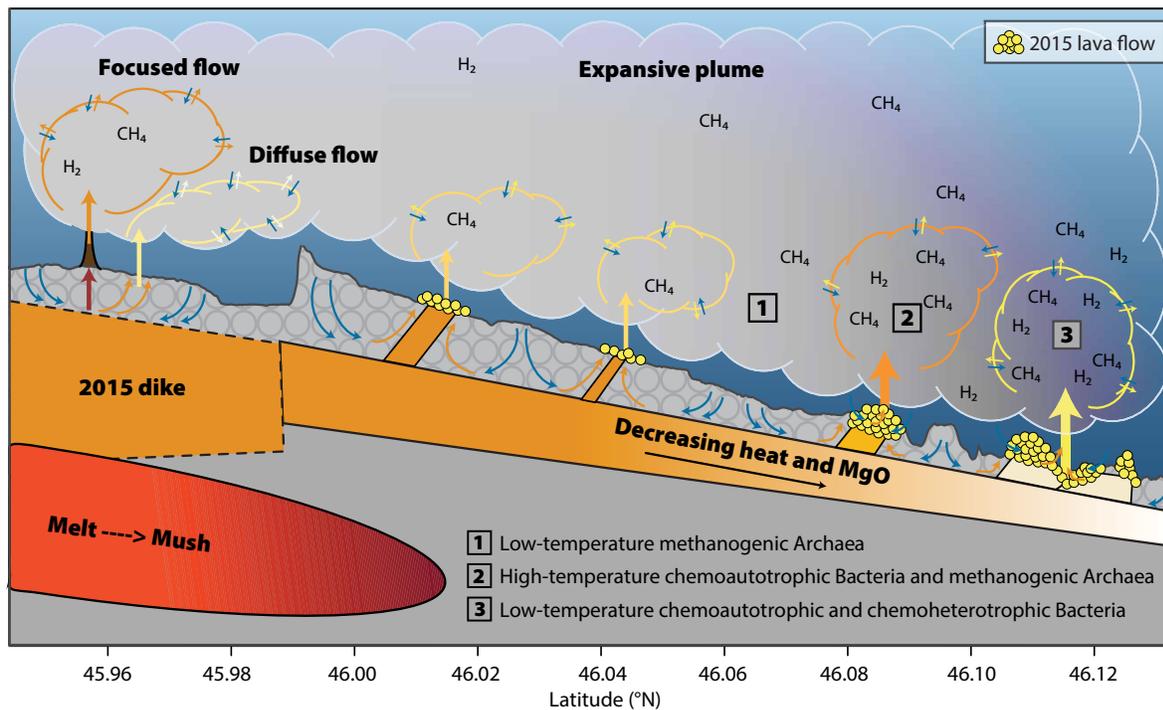


FIGURE 5. Conceptual model showing the different sources of hydrothermal plumes and the implications for overlying sea-water microbial communities and chemistry, with interpretation of subsurface processes modified from Chadwick et al. (2016). The weight of arrows corresponds to the estimated relative magnitude of hydrothermal input to plumes. Colors outlining distinct plumes correspond to the relative temperature of the plume, with white being cool and orange being hotter. Lines outlining non-buoyant plumes are theoretical boundaries that are not necessarily distinct but rather gradients between regions of hydrothermal input from the subsurface and background seawater. Numbered boxes indicate microbial functional groups strongly associated with each plume region. Note that the vertical axis is exaggerated to show detail.

plume over lava flow #9 and only 0.6% in background seawater. Indicator analyses suggest that thermophilic taxa from the Epsilonproteobacteria, including *Sulfurimonas* sp., are significant indicators in these plumes. These data support the hypothesis proposed by Djurhuus et al. (2017) that members of the mesophilic/thermophilic sulfur-oxidizing Epsilonproteobacteria are strong indicators of hydrothermal activity. We add that individual taxa within the Epsilonproteobacteria demonstrate preferences for different temperature ranges or subsurface geochemistry, which affects the distribution of different taxa across plumes of varying origin (Figures 3 and 4).

CONCLUSIONS

Real-time data from the OOI Cabled Array at Axial Seamount enabled a rapid response expedition to characterize the geochemistry and microbiology of

post-eruptive hydrothermal plumes overlying new lava flows from the 2015 eruption. Our results suggest that differences in the hydrothermal sources associated with distinct lava flows and their subsurface feeder dikes create near-seafloor plume environments that are chemically and microbiologically distinct from upper, non-buoyant hydrothermal plumes. We present a conceptual model that incorporates different hydrothermal venting sites over new lava flows to highlight differences in plume chemistry and microbiology at Axial Seamount (Figure 5). In the model, we attribute differences in microbiology to differences in subsurface microbial communities injected into the water column, differences in the degree of mixing due to seawater entrainment, and differences in residence time in the plume. These findings extend our knowledge, indicating that post-eruptive hydrothermal output over new lava flows can continue to influence

deep-sea processes for months following an eruption and that the influence on deep-sea chemistry and microbiology is heterogeneous.

SUPPLEMENTARY MATERIALS

Methods, Figure S1, and Tables S1 and S2 are available online at <https://doi.org/10.5670/oceanog.2018.120>.

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