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Pre- and post-eruption diffuse flow variability among tubeworm habitats at 9°50′ north on the East Pacific Rise

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ABSTRACT

A seafloor eruption at 9°50′N East Pacific Rise (EPR) in 2005–2006 fundamentally changed the fluid chemical and biological community composition throughout the region. Prior to the eruption (in 2004 and 2005), this region of the EPR was dominated by siboglinid (*Riftia pachyptila*) tubeworms and bathymodiolin (*Bathymodiolus thermophilus*) mussels. Following the eruption, the tubeworm, *Tevnia jerichonana*, was the first observed sessile megafauna to have colonized nascent vent openings. The eruption provided the unique opportunity to compare species-specific habitat chemistry and address previously documented differences in the colonization order of tubeworm species hypothesized to be due to the different physiological tolerances to changing vent fluid chemistry. We coupled *in situ* electrochemical measurements of free sulfide (S_{free}), Σ total sulfide, O_2, Fe(II), Mn(II), and other S(-II) species with the occurrence of tubeworm colonies to document and compare, for the first time, the chemical habitats of the dominant tubeworm fauna on the East Pacific Rise, and the pre-and post-eruptive diffuse fluid chemistry in the region.

Median sulfide concentrations increased two to four fold from 2004–2005 when *R. pachyptila* were dominant to 2006–2008 when *T. jerichonana* were dominant, and median oxygen conditions decreased from 40–58 μM to below the detection limit of 3–5 μM over the same period. These data suggest fundamental differences between these tubeworm habitats, as well as the possibility of increased tolerance for microaerophilic conditions in *T. jerichonana*. Sulfide-to-Temperature (*S/T*) ratios increased from before (2004) to after the eruption (2006–2007). However, *S/T* ratios at two of the sites in 2005 increased from 2004 indicating that a part of the hydrothermal vent field may have been "heating up" prior to the eruption. The results of diffuse flow habitat chemistry provide data for the first time that *R. pachyptila* and *T. jerichonana* tubeworms may preferentially inhabit different chemical habitats.

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1. Introduction

The hydrothermal vent biology and chemistry of 9°50′N East Pacific Rise (EPR) has been extensively studied since the 1991–1992 seafloor eruption (e.g., Shank et al., 1998; Lutz et al., 1994; Von Damm, 2000; Le Bris et al., 2006; Scheirer et al., 2006). Biological succession and annual chemical changes following the 1991 eruption were studied by Shank et al. (1998), in which temperature and total sulfide (Σ total sulfide = $H_2S+HS^-+FeS+S_x^{2-}$, denoted as S_{total}) concentrations decreased annually among diffuse flow sources from April 1991 (55 °C and 1900 μM S_{total}, two weeks after the 1991 eruption) to November 1995 (24 °C and 300 μM S_{total}, 55 months after the 1991 eruption). The initial appearance of the vent-endemic tubeworms in discrete and mono-specific colonies began with the "pioneer" and foundation species, *Tevnia jerichonana* (Jones, 1985) within 11 months of the eruption (March 1992). Colonization by *T. jerichonana* was followed by the subsequent colonization of another tubeworm, *Riftia pachyptila* (Jones, 1981), within 32 months of the 1991 eruption (December 1993, 35 °C and 979 μM S_{total}). Through documented changes in community structure and fluid chemistry (and in the absence of *in situ* measurements of diffuse fluid habitat chemistry directly within *T. jerichonana* colonies), Shank et al. (1998) hypothesized that the differences in the colonization order of these foundation species were due to the different physiological capacities and tolerances to the changing chemical environment.

Subsequent findings that different chemical habitats are correlated with the presence of different vent faunal species, including *R. pachyptila* and alvinellid polychaetes (Luther et al., 2001a) and *R. pachyptila* and bathymodiolin mussels (Le Bris et al.,

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2006), help to explain the microhabitats in which organisms reside and over time, the sequence of megafaunal colonization observed at 9°50′N EPR, as temperature and sulfide concentrations decrease (Shank et al., 1998). While *T. jerichonana* and *R. pachyptila* sequentially dominate post-eruptive vent habitats, they both thrive in diffuse flow fluids where mixing occurs at the interface between oxygenated seawater and reduced vent fluid rich in sulfide. In this sulfide-rich vent fluid, they utilize the free sulfide (Σ free sulfide = H_2S+HS^-, denoted as S_{free}) as opposed to S_{total} (Childress et al., 1984; Luther et al., 2001a).

In 2005–2006, another volcanic eruption in the 9°50′N region (Rubin et al., 2006; Tolstoy et al., 2006; Cowen et al., 2007) initiated venting activity, providing the unique opportunity to determine whether or not fundamental chemical differences in *T. jerichonana* and *R. pachytila* habitats exist. Prior to the eruption, the dominant siboglinid tubeworm was *R. pachyptila* with a notable absence of *T. jerichonana*. However, following the eruption, *T. jerichonana* was again the first siboglinid tubeworm to colonize nascent vent openings. In this paper, we utilize *in situ* electrochemical data, pre- and post-eruption, to comparatively reveal fundamental differences between these tubeworm habitats, as well as the possibility of increased tolerance for microaerophilic conditions in *T. jerichonana.*

2. Methods

2.1. Study sites

In situ voltammetry measurements were conducted at 9°50′N EPR (9°46′N to 9°52′N) in April 2004 (*Alvin* Dives 3996–4012, April 8–24), April–May 2005 (*Alvin* Dives 4099–4113, April 24–May 10), June 2006 (*Alvin* Dives 4201–4207, June 25–July 1), January 2007 (*Alvin* Dives 4297–4318 from January 13–February 3), and June 2008 (*Alvin* Dives 4400–4408, June 6–13). Study sites (Fig. 1), where chemistry measurements on and near tubeworms were taken, included Alvinella Pillar (2005), Bio 9 (2005, no S_{free} data available due to noisy electrochemical scans), East Wall (2004, 2005), Hobbit Hole (2007), L Vent (2007), Marker 15/141 (2007, 2008), Marker 19 (2007), Marker 26/Arches (2007), Marker 28 (2007), Marker 35 (2007, 2008), Marker 61 (2005), Tamtown (2006, 2007), and Tica (2004, 2005, 2007, 2008). To fully characterize the potential differences in microhabitats of the two tubeworms species, and taking the different tube lengths within a given assemblage, we collected all electrochemical data immediately adjacent to the base, middle (approximately half the distance between the distal and proximal ends of the tube), or at the location of the plume of *R. pachyptila* and *T. jerichonana.*

2.2. Data collection

Data collection (as described by Nees et al., 2008) was conducted using *in situ* voltammetry using solid state gold-amalgam (Au/Hg) working microelectrodes. Briefly, these electrodes consisted of a 100-μm gold wire housed inside polyethylether ketone (PEEK) tubing and plated with mercury (Brendel and Luther, 1995; Luther et al., 1999). They were operated within the DSV *Alvin* through the use of Analytical Instrument Systems, Inc. (AIS) DLK-SUB analyzer (AIS-ISEA I) connected to a laptop computer (Nuzzio et al., 2002). A solid state reference (Ag/AgCl) electrode and counter (Pt) electrode were attached to the *Alvin* basket in ambient seawater, while the working (Au/Hg) electrodes and temperature probe were housed inside a Delrin or titanium wand, along with a thermocouple (Luther et al., 2001a, b). Due to a failure with the electrochemical analyzer's thermocouple in 2008,

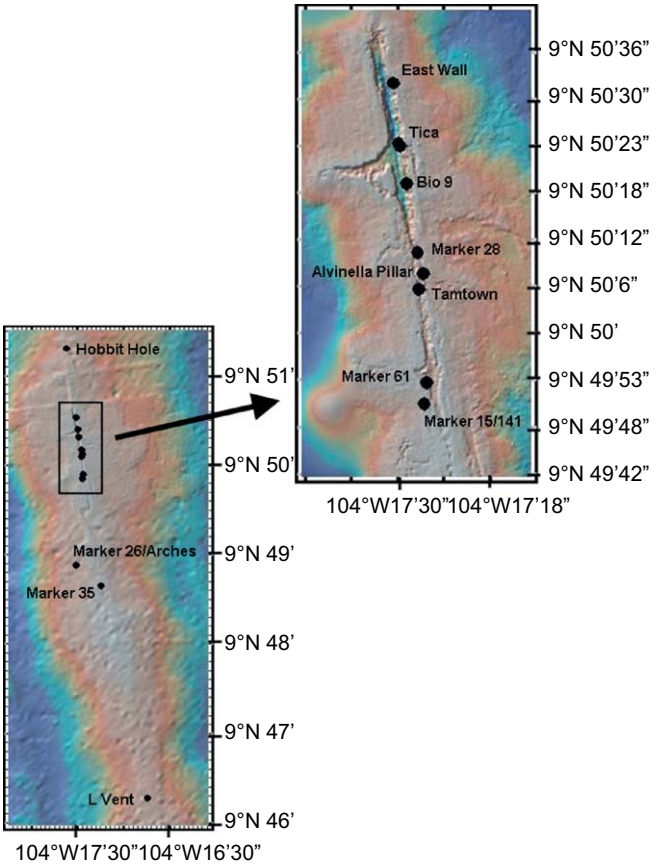

Fig. 1. Map of study sites from 2004, 2005, 2006, 2007, and 2008 where S_{free} and O_2 measurements and temperatures were collected within in the vicinity of *R. pachyptila* and *T. jerichonana*. The figure on the left displays all 12 sites with a filled circle representing each site. The figure on the right displays an enlarged image (of the box outlined in the left figure) of the eight northern locations. Pre-eruption sites include Alvinella Pillar (2005), Bio 9 (2005), East Wall (2004, 2005), Marker 61 (2005), and Tica (2004, 2005). Post-eruption sites include Hobbit Hole (2007), L Vent (2007), Marker 15/141 (2007, 2008), Marker 19 (2007), Marker 26/Arches (2007), Marker 28 (2007), Marker 35 (2007, 2008), Tamtown (2006, 2007), and Tica (2007, 2008).

temperature was measured with a second external probe supplied by the DSV *Alvin* during that year.

In situ electrochemical scans were collected in a program of up to 10 individual scans lasting 1.5–2 min and later analyzed onboard ship. Cyclic voltammetry, at a scan rate of 2000 mV s^{-1}, was used for all measurements. Each scan process consisted of an electrode cleaning step with a holding potential of −0.9 V or −1.0 V for 5 s (depending upon the year of data collection), a conditioning step where the initial potential (−0.05 V for 2007 and −0.10 V for all other years) was held for 2 s, and the measurement step where the electrochemical scan was collected (from −0.05 V to −1.8 V to −0.05 V in 2007 and from −0.10 V to −1.8 V to −0.10 V in all other years). The forward scan gives the S_{free} concentration, whereas the reverse scan gives the Σ total sulfide. In some cases the current for the S_{free} signal was off scale due to very high sulfide concentrations (>200 μM). Because the tubeworm sites showed no signal or only a very small signal for iron bound to sulfide and no polysulfide signal, the peak for Σ total sulfide was used to measure sulfide in those cases and reported as S_{free}. Detection of multiple analytes included O_2 (detection limit, denoted as DL = ~3–5 μM), H_2S (DL = 0.2 μM), Fe(II) (DL = 10 μM), Mn(II) (DL = 5 μM), and other S(-II) species such as polysulfides (S_x^{2-}, DL = 0.2 μM) and thiosulfate ($S_2O_3^{2-}$, DL = ~30 μM) (Brendel and Luther, 1995; Luther et al., 2001b,