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Microbial biofilms associated with fluid chemistry and megafaunal colonization at post-eruptive deep-sea hydrothermal vents

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ABSTRACT

At deep-sea hydrothermal vents, reduced, super-heated hydrothermal fluids mix with cold, oxygenated seawater. This creates temperature and chemical gradients that support chemosynthetic primary production and a biomass-rich community of invertebrates. In late 2005/early 2006 an eruption occurred on the East Pacific Rise at 9°50′N, 104°17′W. Direct observations of the post-eruptive diffuse-flow vents indicated that the earliest colonizers were microbial biofilms. Two cruises in 2006 and 2007 allowed us to monitor and sample the early steps of ecosystem recovery. The main objective of this work was to characterize the composition of microbial biofilms in relation to the temperature and chemistry of the hydrothermal fluids and the observed patterns of megafaunal colonization. The area selected for this study had local seafloor habitats of active diffuse flow (in-flow) interrupted by adjacent habitats with no apparent expulsion of hydrothermal fluids (no-flow). The in-flow habitats were characterized by higher temperatures (1.6–25.2 °C) and H_2S concentrations (up to 67.3 μM) than the no-flow habitats, and the microbial biofilms were dominated by chemosynthetic *Epsilonproteobacteria*. The no-flow habitats had much lower temperatures (1.2–5.2 °C) and H_2S concentrations (0.3–2.9 μM), and *Gammaproteobacteria* dominated the biofilms. Siboglinid tubeworms colonized only in-flow habitats, while they were absent at the no-flow areas, suggesting a correlation between siboglinid tubeworm colonization, active hydrothermal flow, and the composition of chemosynthetic microbial biofilms.
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1. Introduction

Studies of diffuse-flow hydrothermal vents at 9°50′N on the East Pacific Rise (hereafter referred to as EPR) following seafloor volcanic eruptions (in 1991 and 2006) have provided information about processes controlling the initial colonization by microbial biofilms and subsequent succession of vent metazoans (Shank et al., 1998; Govenar, 2012; Sievert and Vetriani, 2012). While, in general, metazoan colonization correlates with temperature and hydrothermal fluid chemistry (Shank et al., 1998; Luther et al., 2001; Luther et al., 2012), biological interactions may also play a role in colonization patterns (*e.g.*, Mullineaux et al., 2003; Govenar et al., 2012). Many vent invertebrates rely on chemosynthetic microorganisms that convert the energy of the reduced chemical species dissolved in the hydrothermal fluids into biochemical energy (ATP) to fix carbon dioxide. Also, in other marine habitats, microbial cues of metazoan settlement are critically important. Dispersive larvae respond not only to the texture and composition of microorganisms in biofilms, but also to chemicals produced by microbial consortia or individual microbial species (reviewed by Underwood and Keough, 2001; Hadfield, 2011). In addition, metamorphosis from the free-swimming larval stage to the sessile adult stage can be initiated by a different composition of the biofilms (Tebben et al., 2011; Yang et al., 2013).

Hence, chemosynthetic microorganisms may provide useful cues that indicate habitat quality for metazoan colonizers. Indeed, biologists have long hypothesized that microbial biofilms at deep-sea hydrothermal vents may interact with vent larvae to induce settlement and metamorphosis (Van Dover, 2000; Adams et al., 2012). However, this hypothesis remains largely untested.

Direct observation of the colonization of diffuse-flow vents following a volcanic eruption on the EPR has shown that microbial

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biofilms are the pioneer colonizers of newly-formed vents (Lutz et al., 2001; Sievert and Vetriani, 2012). Further, small subunit rRNA gene surveys of vent microbial communities indicated that *Epsilonproteobacteria* were the dominant microorganisms associated with the colonization of substrates, as well as the most abundant primary producers at diffuse-flow hydrothermal vents (Lopez-Garcia et al., 2003; Alain et al., 2004; Campbell et al., 2006; Sievert and Vetriani, 2012).

In December 2003, we initiated colonization studies at diffuse-flow vents located on the EPR to examine the correlation between microbial and megafaunal colonizers. In late 2005/early 2006, a volcanic seafloor eruption buried many of the pre-existing benthic communities in fresh lava (Cowen et al., 2007). The eruption also created more than 20 nascent vent habitats, establishing a time-zero for subsequent biological colonization and community development. While previous studies have documented post-eruptive changes in the chemistry of diffuse-vent fluids (Shank et al., 1998; Von Damm and Lilley, 2004), an integrated investigation that simultaneously examined the structure of early microbial colonists, megafaunal colonization and fluid chemistry in diffuse-flow vents had not been conducted.

Here we conducted time-series *in situ* experiments to examine patterns of microbial community structure and composition, fluid temperature and chemistry and megafaunal colonization at various post-eruptive diffuse-flow vents on the EPR. The goal of this study was to examine for the first time co-located linkages between hydrothermal fluid chemistry, microbial biofilms and megafaunal colonization. Specifically, amongst newly-formed, post-eruptive vents, we aimed to: (1) characterize the composition of microbial colonizers; (2) correlate patterns of microbial colonization in response to different geochemical regimes; and (3) examine patterns of megafaunal colonization. Our findings revealed marked differences in the composition of microbial biofilms and vent-endemic megafaunal colonization at hydrothermally active (in-flow) and inactive (no-flow) areas.

2. Materials and methods

2.1. Site description and sampling strategy

To investigate patterns of microbial and megafaunal colonization at post-eruptive hydrothermal vents in relationship to different thermal and geochemical regimes, we designed and deployed experimental colonization substrates that allow the coordination and integration of these data. The substrates, hereafter referred to as TAMS (Temporal Autonomous Multi-disciplinary Substrates), were designed to allow hydrothermal fluids to pass through the colonization surface. Each surface was constructed from a 4″ × 4″ polyethylene frame holding two layers of 1 mm wide polyester mesh to facilitate permeability and one 100 μm layer in the middle to provide substrate for microbial colonization. Each TAMS was equipped with a VEMCO temperature data logger for continuous monitoring of the temperature throughout the deployment.

TAMS were deployed on the EPR at either visible diffuse-flow (position designated as in-flow) or onto basalt where there was no visible diffuse-flow or evidence of exposure to hydrothermal fluids (position designated as no-flow). For the purpose of the present study, eight TAMS were deployed in in-flow and four in no-flow positions (Table 1). Nearly all of the TAMS were deployed ~6 months after the eruption for 196–202 days, at a site named "Tamtown" (Marker 8/11, 9°50.09′N 104°17.46′W, 2503 m). In this study, we also included two TAMS that were deployed ~12 months after the eruption for 49 days, at a site named "Marker 19" (9°47.44′N 104°16.97′W, 2510 m). We found no substantive differences in the fluid chemistry, microbial composition, or megafaunal colonization between duration length, deployment time, or sites, so the analyses presented here focus on the differences between in-flow and no-flow habitats.

Table 1
Summary of TAMS deployed during the study and presence/absence of colonization.

Position	TAMS	QI	QII	QIII	QIV
In-flow	8	+	+*	−	−*
In-flow	9	+	−*	+	+*
In-flow	11	+	−*	0	+*
In-flow	12	+*	+	+*	+
In-flow	13	−	+*	−	−*
In-flow	16	+	+	+*	+*
In-flow	20	+*	+	+*	+
In-flow	21	+*	+*	+*	+*
No-flow	4	−	−	−	−*
No-flow	5	−*	−	−	−
No-flow	22	−	−	−*	−
No-flow	29	−	−*	−	−

Quadrants (QI, QII, QIII, QIV) of TAMS colonized (+) or uncolonized (−) by siboglinid tubeworms. TAMS quadrants selected for microbial diversity analyses (DGGE and/or clone libraries) are marked with a *.

The sites were established during Alvin dives 4203, 4207 and 4282. TAMS were transported to the seafloor in filtered seawater to prevent contamination by surface-water microbial and metazoan populations and were recovered in individual temperature-insulated containers (bioboxes). Upon recovery, TAMS were immediately transferred into the shipboard 4 °C cold room. TAMS were divided into quadrants (I, II, III, IV), inspected and documented using digital imaging. The TAMS were disassembled in either cold sterile seawater or preservative (depending on the method of recovery), and both sides of the mesh were carefully examined for megafaunal colonists, which were documented using high-quality digital imaging at 10× magnification, physically removed from the mesh, measured (for body length), and frozen individually. After removal of all megafaunal colonists, the mesh was stored for microbial diversity analyses.

2.2. In situ fluid chemistry

Fluid chemistry measurements were conducted by voltammetry using both submersible-mounted and autonomous solid-state microelectrodes (Luther et al., 2008). Measurements of sulfide (H_2S/HS^-), oxygen (O_2) and temperature (°C) on each TAMS were taken at deployment and recovery using microelectrodes operated by the *DSV Alvin* manipulator as previously described (Luther et al., 2008). Detection limits (dl) are 0.2 μM for H_2S and 3 μM for O_2. TAMS-associated VEMCO data loggers recorded *in situ* temperatures every 15 s.

Fluid chemistry measurements were performed using an *in-situ* electrochemical analyzer (AIS-ISEA™-III) operated manually by an operator within the *DSV Alvin*. Temperature and cyclic voltammetry (CV) electrochemical scans (7–10) were collected at the same point using a wand, which encased 4 Au/Hg micro-electrodes (Luther et al., 2008) and a thermocouple. VEMCO temperature loggers were used instead of thermocouples as they are smaller, allowing for easier positioning of the electrodes. For a detailed description of the operation of the ISEA, see Luther et al. (2001, 2008) and Moore et al. (2009).

Gold amalgam micro-electrodes, as described in Brendel and Luther (1995) and Luther et al. (2008) were used for all experiments. Electrodes were sanded, polished and then plated with Hg by reducing Hg(II) from a 0.1 N $Hg(NO_3)_2$ in a 0.05 N HNO_3 solution for 4 min at a potential of −0.1 V, while purging with Ar. The mercury/gold amalgam interface was conditioned using a 90 s −9 V polarization procedure in a 1 N NaOH solution. The solid state Ag/AgCl reference and Pt counter

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