



Post-eruption succession of macrofaunal communities at diffuse flow hydrothermal vents on Axial Volcano, Juan de Fuca Ridge, Northeast Pacific

Jean Marcus^{a,*}, Verena Tunnicliffe^{a,b}, David A. Butterfield^c

^a Department of Biology, University of Victoria, PO Box 3080, Victoria, BC, Canada V8W 3N5

^b School of Earth & Ocean Sciences, University of Victoria, Canada V8W 3P6

^c Joint Institute for the Study of the Atmosphere and Oceans, University of Washington, Box 354925, Seattle, WA 98115, USA

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ABSTRACT

Hydrothermal vents harbor dense aggregations of invertebrate fauna supported by chemosynthesis. Severe tectonic events and volcanic eruptions frequently destroy vent communities and initiate primary succession at new vents on ridge-crest submarine lava flows. An eruption on Axial Volcano (~1500 m depth), a seamount on the Juan de Fuca Ridge (JdFR) in the northeast Pacific Ocean, occurred in January 1998, which created new substratum and vents. This study examines the development of the macrofaunal vent assemblages associated with tubeworms (*Ridgeia piscesae*) at eight diffuse flow vents over the following 3 years. Biological collections by suction of lava surfaces also characterized “pre-tubeworm assemblages”. Coupled fluid sampling showed an overall decrease in temperature, sulphide, and sulphide-to-heat ratios over 3 years as well as large spatial variability across the new vents. We examined collections of pre-eruption diffuse flow vent assemblages at Axial Volcano to compare the stages of new community development to “mature” vents. Mature vent assemblages are characterized by two major community types dominated by limpets (*Lepetodrilus fucensis*) and alvinellid polychaetes (*Paralvinella pandorae* and/or *P. palmiformis*).

The following post-eruption succession patterns emerged. First, *R. piscesae* tubeworms took up to 3 years to establish aggregations at the new vents, and the majority of pre-tubeworm assemblages were dominated by grazing polychaetes. Second, species colonized quickly and by 30 months after habitat creation >60% of Axial's species pool had arrived at the new vents; abundance at mature vents predicted colonization success with some notable exceptions. Third, shifts in species dominance occurred rapidly and by Year 3 new vent assemblages resembled mature, pre-eruption communities. In general, tubeworm assemblages were dominated by alvinellid polychaetes (*P. pandorae* and *P. palmiformis*) in the first 2 years post-eruption, with limpets (*L. fucensis*) becoming more numerous in Year 3. Fourth, successional trajectories corresponded to four habitat variables: the timing of *R. piscesae* recruitment, vent age, maximum vent fluid sulphide-to-heat ratios, and maximum vent fluid temperatures. The two mature community types (dominance by limpets or alvinellid polychaetes) seem to relate in part to vent differences in fluid properties, with limpets more prevalent than alvinellids at diffuse vents with lower maximum sulphide-to-heat ratios and temperatures.

We present a general model of post-eruption succession for Juan de Fuca Ridge diffuse flow vents. The model incorporates potential abiotic and biotic drivers of community development and identifies six successional stages: a pre-tubeworm assemblage, four tubeworm assemblage states determined by the relative dominance of alvinellid polychaetes and the limpet, and a final senescent stage when venting wanes. Future eruptions will allow for this model to be tested through direct observation and experimentation.

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1. Introduction

Low-temperature or “diffuse” vents occur intermittently along the volcanically active mid-ocean ridge system. These habitats may experience episodic eruptions that destroy vent-associated fauna and create multiple new diffuse vents along large tracks of pristine lava. Vent ecosystems along ridges with medium to fast seafloor spreading rates, such as the East Pacific Rise (EPR), may

* Corresponding author. Present address: Fisheries Centre, University of British Columbia, 2202 Main Mall, Vancouver, BC, Canada V6T 1Z4. Tel.: +1 604 827 5476; fax: +1 604 737 1905.

E-mail address: jean.marcus@ubc.ca (J. Marcus).

see repeated primary successions as community development is reset by eruptive and/or tectonic events on a decadal time scale (Embley et al., 1998; Soule et al., 2007). Frequent and severe eruptive disturbances may create a spatiotemporally shifting mosaic of available vent habitats in a region (Nees et al., 2008) set within a suite of more stable vent fields.

Succession at vents can be tracked from colonization through to older, well-established stages since communities change over time scales of months to years (Tunnicliffe et al., 1997; Shank et al., 1998; Marcus, 2003). This rapid rate of change facilitates understanding of the organization of vent communities as succession can be documented in conjunction with measurement of the predicted drivers of spatial and temporal community dynamics. Such a direct observational method is impossible for tracking succession on terrestrial lava flows (Cutler et al., 2008) or at other reducing habitats such as cold seeps (Bergquist et al., 2003), where slow rates of change necessitate a chronosequence approach.

In this paper, we document the vent community response to an eruption on Axial Volcano on the Juan de Fuca Ridge (JdFR) which has been the site of sustained venting within the caldera since discoveries in 1983 and 1984 (Embley et al., 1990). Two other studies document primary succession on diffuse flow vents from the onset of habitat creation: 9°N on the East Pacific Rise (Shank et al., 1998) and CoAxial Segment on the JdFR (Tunnicliffe et al., 1997). Both sites were characterized by the creation of numerous diffuse flow vents on the new lava and by the similar patterns of colonization and subsequent community development across new vents. At 9°N, all nascent vents were successively dominated by three megafaunal species: two vestimentiferan tubeworm species (*Tevnia jerichonana* and *Riftia pachyptila*) in the first 2 years, and a mussel (*Bathymodiolus thermophilus*) in the next 3 years (Shank et al., 1998). At CoAxial, all nascent vents were colonized by the vestimentiferan tubeworm, *Ridgeia piscesae* (Siboglinidae, Polychaeta), and the alvinellid polychaete, *Paralvinella pandorae*, at 1 year post-eruption (Tunnicliffe et al., 1997). Proposed mechanisms responsible for observed species shifts include species responses to predictable post-eruption fluid changes (Shank et al., 1998) and strong facilitating and competitive interactions (Fustec et al., 1987; Hessler et al., 1988; Mullineaux et al., 2000). Tunnicliffe et al. (1997) also invoked the concept of stochastic events affecting colonization.

Tsurumi and Tunnicliffe (2001) also documented the characteristics of tubeworm-associated communities at diffuse vents 2–8 years following the eruption of Cleft Segment on the Juan de Fuca Ridge. At 2 years post-eruption *R. piscesae* aggregations occurred at all sites and *P. pandorae* was abundant, constituting 20–98% of the tubeworm-associated assemblages. In contrast, from 4 to 7 years post-eruption (no observations in Year 3) less than 1% of animals were *P. pandorae*, which had shifted to a smaller body size, and the limpet *Lepetodrilus fucensis* numerically dominated most vents. By 5 years most diffuse venting had waned and by 8 years all were extinct. Despite these taxonomic shifts, and concurrent changes in fluid properties (Butterfield and Massoth, 1994), the tubeworm-associated assemblages did not differ statistically among years. Though this lack of difference may be attributable to sampling design, Tsurumi and Tunnicliffe (2001) proposed that a study of less than a year is needed to observe successional patterns at new vents.

Our Axial Volcano study is based on biological collections of diffuse flow vent communities at 7, 18, 30 and 42 months post-eruption. We interpret the patterns of community development by assessing the structure of pre-eruption diffuse flow communities on Axial, estimating the available species pool, and assessing vent fluid properties coupled with the collections. This study is based in observation. Ecological observations and pattern

detection are essential, especially during the early stages of understanding the ecology of a system, as they form the basis of explanatory models and forestall experimental analyses of improbable processes (Underwood et al., 2000).

Our goal was thus pattern detection in order to generate probable hypotheses of the processes that drive the development of diffuse flow communities at Axial Volcano. However, our comprehensive knowledge of the Axial communities prior to the eruption, as well as the results of previous eruptions on the JdFR (CoAxial and Cleft Segments), allowed us to also test two hypotheses. First, we predicted that initial colonization would parallel that pattern observed at CoAxial: all new vents would be colonized by the tubeworm *R. piscesae* and the polychaete *P. pandorae* within one year. Second, we predicted that within 3–5 years new vents would be dominated by the limpet *L. fucensis* and resemble the pre-eruption diffuse flow communities at Axial.

2. Methods

2.1. Study site

Axial Volcano lies on the central segment of Juan de Fuca Ridge approximately 400 km west of Oregon, USA. In the summit caldera around 1500 m depth, sustained hydrothermal activity is largely restricted to three “fields” (Fig. 1): ASHES, CASM and SRZ (Embley et al., 1990). The SRZ was visited in five summers between 1985 and 1997 when discrete concentrations of diffuse venting with tubeworms and other vent fauna were recorded (Embley et al., 1990; Butterfield et al., 2004). On January 28 1998, intense earthquakes began on Axial and lasted 11 days as the seismic swarms migrated 50 km south from the SRZ. Submersible investigations on the SRZ in summer 1998 encountered a new lava flow that paved over animal assemblages observed the previous year in the vicinity of the Mkr 33 site (Fig. 1) (Embley et al., 1999). All new venting emanated from cracks in basalt and was low-temperature (maximum recorded at 55 °C in 1998).

We studied development of the biological communities by sampling vents concurrently for fauna and fluid characteristics each year wherever possible. The age of vents on the new flow is well constrained. Three vents on adjacent older lava (Fig. 1) were included as “nascent” because they were not previously seen and their features were consistent with 1998 flow initiation: dense microbial mats and high sulphide-to-heat ratios between 5.3 and 7.6 nmol J⁻². This study does not examine fauna from sulphide chimneys, which are absent from the new lava flow.

Community structure data exist for 21 low-temperature vents sampled from all Axial fields in 1986–88 and 1997–1999 (Table 1). Their absolute ages are unknown, but we consider them examples of mature (well-established) diffuse flow communities because they are characterized by a similar set of species and many size classes are present. In addition, observed variability among mature vent communities is unrelated to vent field location or sampling year (Tsurumi and Tunnicliffe, 2003), and the Axial caldera experienced no major perturbations (i.e. a seafloor eruption or the cessation of fluid flow in the vent fields) from the discovery of venting in the mid-1980s to the 1998 eruption (Embley et al., 1990).

2.2. Biological sampling and processing

Faunal assemblages were sampled from nine new vents over 4 years (Table 2). Years 1 through 4 refer to sampling dates of 7, 18, 30 and 42 months after the January 1998 eruption. We grabbed tubeworms (*R. piscesae*) and associated fauna with the

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