



Mosaic community dynamics on Juan de Fuca Ridge sulphide edifices : substratum, temperature and implications for trophic structure

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Introduction

Ecological studies at hydrothermal vents often emphasize the importance of spatio-temporal heterogeneity in organism distribution within individual sites (Sarrazin et al., 1997) but the relative roles of environmental conditions, biological interactions and/or random processes in structuring hydrothermal communities remain poorly understood (Sarrazin & Juniper, 1999). A model of community succession developed by Sarrazin et al. (1997, 1999) proposed that a series of faunal assemblages form a mosaic community that colonizes hydrothermal edifices of the northeast Pacific vents. This paper further develops the succession model by incorporating new observations.

At the core of the model is the recognition of distinct faunal assemblages that characterize each of 6 (occasionally 3, see below) successional stages. Assemblage I is the first to colonize newly-formed chimney surfaces and is principally composed of the alvinellid polychaete *Paralvinella sulfincola* Desbruyères & Laubier, 1993 and the copepod *Stygiopontius quadrispinosus* Humes, 1987. The formation of a marcasite (FeS₂) crust beneath *P. sulfincola* tubes facilitates colonization of the substratum by the less tolerant alvinellid *Paralvinella palmiformis* Desbruyères & Laubier, 1986, forming Assemblage II. As the substratum stabilizes and flow intensity decreases, other macrofaunal species progressively appear. Assemblage III is dominated by *P. palmiformis*, high gastropod densities (*Lepetodrilus fucensis* McLean, 1988, *Provanna variabilis* Warén & Bouchet, 1986 and *Depressigyra globulus* Warén & Bouchet, 1989), and a few polynoid polychaetes. These species are joined by the vestimentifera *Ridgeia piscesae*

Jones, 1985 in Assemblage IV, and the growth of *R. piscesae* leads to the complex and diverse Assemblage V (low-flow). Assemblage VI represents a senescent phase where *R. piscesae* gradually die and associated species disappear. The presence of scavengers and detritivores in Assemblage VI may be related to decreased hydrothermal flux and to the accumulation of detrital organic matter. Occasionally, another mature vestimentiferan assemblage (Assemblage V high-flow) can develop directly from Assemblage I or II under intense fluid flow rates. As in Assemblage V low-flow, Assemblage V high-flow is dominated by *Ridgeia piscesae* but gastropods and polynoids are rare and species diversity is considerably lower (Sarrazin & Juniper, 1999). These assemblages are typical of hydrothermal edifices throughout the northeast Pacific spreading ridges.

Changes from Assemblages II through IV are mostly driven by reduction in hydrothermal fluid flow, while between Assemblage IV and V low-flow, biological processes such as tube worm growth initiate succession. The influence of environmental factors, such as H₂S concentrations, fluid flow intensity and substratum type, on species distribution was confirmed from in situ measurements on two Juan de Fuca Ridge sulphide edifices by Sarrazin et al. (1999). Their data also indicated a relationship between flow intensity and mineralization of the substratum, suggesting that different areas of the edifice are progressively mineralized in parallel with faunal succession. Other habitat factors such as dissolved oxygen concentration and nutritional resources were also proposed to influence species distribution.

Here we build upon the Sarrazin et al. (1999) model by incorporating preliminary analyses of substratum mineralogy and porosity, and temperature time series within different faunal assemblages. We also include a first consideration of food availability for deposit and suspension feeding invertebrates by biochemical characterization of particulate organic matter sampled from two early successional assemblages (II and V high-flow).

Methods and Results

Substrata

Mineral substrata underlying the different faunal assemblages were collected during two cruises to the Endeavour Segment of the Juan de Fuca Ridge. Most substratum samples were taken from the Gwenen edifice in the Mothra vent field (Kelley et al., 2001). One further sample (transitional high-flow Assemblage V) was collected from the top of the S&M edifice complex (Main Endeavour vent field). Samples were carefully dried, and polished thin sections were made for microscopic (reflected and transmitted light) characterization of porosity, mineralogy and texture. Observations on substratum samples beneath Assemblage I were taken from an earlier study by Juniper et al. (1992).

Macroscopic examination of the substrata showed that the substratum under Assemblage I (early colonization) was friable, porous and soft, with little silicification, while beneath low-flow Assemblage V (mature tube worm community) the substratum was hard and exhibited conchoidal fractures, together indicative of high silica content. Under the microscope, Assemblage I (Hell), transitional high-flow V (S&M) and III (Gwenen) substrata showed features characteristic of early, rapid mineral accretion. Substrata from beneath these assemblages were more porous and less silica-rich than substrata collected beneath Assemblage IV and V (low- & high-flow). In particular, the abundance of heterogeneous Fe-sulphide crystals, the presence of Zn-sulphides in both inner and outer zones, and limited pore infilling by amorphous silica were noticeable (Table 1). The texture of the substratum under Assemblage III was more heterogeneous. Abundant very small vestimentiferan tubes were mineralized and incorporated into the vent structure, providing further evidence of rapid accretion. Fine-scale mineralogical differences between the interior and exterior of the incorporated worm tubes, indicate an influence of the tubes on mineralization processes (Zbinden et al. 2001).

There were no pronounced differences in substratum mineralogy between Assemblages IV and V (low- & high-flow) and all showed features typical of more advanced stages of edifice mineralization. In particular, there was distinct zonation of both texture and mineralogy (barite dendrites and Fe-sulphides versus Cu-, Fe-, Zn- and Pb-sulphides). Outer zones, and inner zones of some samples, contained mineralized worm tubes coated with a variable thickness layer of amorphous silica. In general, a decrease in porosity and an increase in the amount of pore infilling by amorphous silica was observed from Assemblage I to V (Table 1).

The outer zone of the substratum from the transitional high-flow V Assemblage exhibited a distinct mineralogy and texture, dominated by marcasite with minor barite and an absence of amorphous silica, consistent with observations of mineralogy beneath *Paralvinella sulfincola* tubes by Juniper et al. (1992). In fact, a time-series study showed that this particular faunal assemblage took over a site previously colonized by an alvinellid assemblage (I or II, Sarrazin et al. 1997).

The extreme degree of silicification of the substrata beneath Assemblages IV and V (low-flow) suggests that the substrata were less permeable than substrata beneath assemblages I through III and that instead of exiting through the structure, fluid flow inputs could come from nearby sources. In addition, no statistical difference in porosity was observed between substrata from high-flow and low-flow Assemblage V (Table 1). The observed differences in flow rates between these two assemblages could be related to differences in lateral fluid flow inputs rather than from fluids coming through the substratum. This hypothesis needs further attention.

Temperature

Recording temperature probes (Vemco) were deployed in 4 different assemblages (I, III, V low-flow and VI) colonizing high-temperature sulphide structures located on the Endeavour segment of the Juan de Fuca Ridge in June-July 2000. Three probes per assemblage were deployed. The probes were left for about 3 months and recovered during a later cruise.

Preliminary analyses of these recordings reveal that, unlike what is predicted by our model, mean temperatures in the different assemblages did not decrease from Assemblage I through V low-flow but were rather similar (~11.8 °C [I], 12.2 °C [III], 14.9 °C [V low-flow]). Only senescent Assemblage VI showed lower temperatures (~5 °C), consistent with the model. On the other hand, the variations between individual probes were higher in earlier successional stages. For example, in Assemblage I, mean temperatures measured by the two Vemco probes (the third overheated and failed) were markedly different (5.87 °C versus 17.65 °C) while in Assemblage V low-flow, both mean measured temperatures were similar (15.93°C versus 13.81°C). Point temperature data from other sources for Assemblages I and V high-flow reinforce the notion of a broader range of habitat temperatures earlier in the faunal succession process (Table 1). This is consistent with in situ measurements of Sarrazin et al. (1999) that showed that species characteristic of earlier assemblages tolerate a more extreme habitat and are present over a broader range of temperature and chemical conditions. More detailed statistical analyses of the temperature recordings are ongoing, with emphasis on understanding habitat stability at different successional stages. The absence of significant temperature variations at the substratum level further underlines the need to address lateral fluid flow inputs when measuring temperatures in vent faunal assemblages. The incorporation of measurements at different vertical levels within the studied assemblages (substratum versus surface) should be considered.

Table 1. Substratum mineralogy and porosity (by visual estimate) for sulphide edifice faunal assemblages from Endeavour Segment, Juan de Fuca Ridge, along with means and standard deviations (in parentheses) from 3-month continuous (5-minute interval) temperature records and other temperature data. Temperature records and substratum samples for each assemblage type are not necessarily from the same location. AmSi—amorphous silica; Ba—barite; Cp—chalcopyrite; Ga—galena; Mc—marcasite; Po—pyrrhotite; Py—pyrite; Sp—sphalerite; Wtz—wurtzite.

Faunal assemblage	Substratum mineralogy, outer zone	Substratum mineralogy, inner zone	Substratum porosity	3-month T°C records	Other T°C data
I Hell edifice, Axial Volcano	Spongy Mc and Py, minor Sp, Ga and intergrown Ba ¹ .	Sphalerite infilling and overgrowing pyritic dendrites and bladed anhydrite ¹	Up to 90% in outer crust ¹	5.87 (2.78) 17.65 (7.36)	5.1 - 35.6 ² 2.6 - 88.5 ³
Transitional high-flow V S&M edifice, Endeavour Segment	Mc/Py with minor interstitial Wtz or interstitial and included Ba	20 x 300 µm and 5 x 60 µm Po grains and 50 - 75 µm Wtz grains and minor Py	80-85 % inner, 30-60% outer	No data	No data
III Gwenen edifice, Endeavour Segment	Abundant 2 mm diameter worm tubes, most empty, some partially filled with small grains of Ba, Po/Mc and strands of AmSi. Ba dendrites with minor amounts of Po/Mc at ends of dendrites, extend from exterior of tubes and are coated with 30 µm thick layer of AmSi. Areas between tubes exhibit 10-100 µm grains of Wtz, Ga and Mc, coated with 30 µm thick layer of AmSi	No zonation	5 to >70%, varies locally (overall ~45%)	20.81 (4.74) 11.25 (2.80) 13.77(3.28) 3.19 (3.18)	No data
IV Gwenen edifice, Endeavour Segment	Ba dendrites and minor Py/Mc, some pieces of mineralized worm tubes, coated with <5-20 µm thick layer of AmSi	50 to 200 µm Wtz grains with inclusions of Cp and Ga coated with <5-30 µm thick layer of AmSi	10 -50 %, varies locally	No data	No data
V low-flow Gwenen edifice, Endeavour Segment	Ba dendrites and rosettes with minor Py/Mc and mineralized worm tubes coated with 10-20 µm thick layer of AmSi	50-200 µm Wtz grains with inclusions of Cp and Ga coated with 10-30 µm thick layer of AmSi	5-50 %, varies locally	15.93 (5.40) 13.81 (3.34)	No data
V high-flow Gwenen edifice, Endeavour Segment	Ba and minor Py/Mc and mineralized worm tubes coated with <10-30 µm thick layer of AmSi	20-35 µm thick layer of AmSi coating either Py/Mc and minor Wtz ± mineralized worm tubes OR Wtz with minor Cp, Ga, Py	5-20 % inner, 10-80% outer; varies locally	No data	24.2 - 41.9 ⁴
VI	No data	No data	No data	9.10 (3.72) 3.77 (3.62) 2.16 (2.23)	No data

¹ From Juniper et al. (1992)

² From Grelon (2001) - range of mean temperatures for 6 separate Assemblage I habitats on Phoenix-Hillock, Medusa and Hell sulphide edifices, Axial Volcano, Juan de Fuca Ridge, in 1997 & 1998

³ From Morineaux (unpubl. data) - range of 18 point temperature measurements taken with 6-point 'Spider' temperature probe array, one measurement at each of 3 Assemblage I habitats on Mushroom and Hell sulphide edifices, Axial Volcano, Juan de Fuca Ridge, in 2000.

⁴ From Butterfield (unpubl. data) - range of 4 point temperature measurements taken within high-flow Assemblage V at the T&S edifice, Axial Volcano, Juan de Fuca Ridge, in 1998 & 1999.

Food availability

In a preliminary characterization of the particulate organic

matter (POM) available at different successional stages, we analysed POM from the polychaete-dominated Assemblage

II (Pork Chop, ASHES vent field) and the immediately following tube worm stage (Assemblage V high-flow; T&S, CASM vent field), both located in the caldera of Axial Volcano, Juan de Fuca Ridge.

Two samples were collected in 1999 from each assemblage using a suction-sampling device mounted on the remotely-operated vehicle ROPOS. The hydraulic manipulators of the vehicle were used to position the intake of a sampling hose within the faunal assemblages, and water was pumped through 2 l acrylic jars equipped with 2 layers of 200mm Nitex nylon mesh at the outlet, to concentrate particles within the jars. Samples were kept at ambient bottom temperature ($\sim 2^{\circ}\text{C}$) until they were brought to the surface where subsamples were frozen (-80°C) for biochemical analysis and preserved in seawater-buffered formalin (7‰ final concentration) for DAPI staining and cell counts. Organic carbon and nitrogen contents were determined on freeze-dried material using a Carlo-Erba CN analyser. Available protein content was measured in triplicate as in Mayer et al. (1986). Total lipid content was determined in triplicate using the sulphophosphovanillin method of Barnes & Blackstock (1973). Formalin-preserved samples were stained with DAPI and DAPI-staining cells were counted in replicate by epifluorescence microscopy.

Compared to Assemblage II, particulate matter from Assemblage V high-flow (HF) had a higher organic content (6.2%C and 1.4%N for Assemblage V-HF versus 1.3%C and 0.3%N for Assemblage II; Table 2). However, the organic matter from Assemblage V-HF was of lower nutritional quality, containing fewer bacteria (7×10^{10} cells g^{-1} C versus 15×10^{10} cells g^{-1} C for Assemblage II), less protein (103 mg g^{-1} C versus 213 mg g^{-1} C for Assemblage II), and less lipid (42 mg g^{-1} C versus 193 mg g^{-1} C for Assemblage II). A similar accumulation of organic matter with lower nutritional quality was observed at nascent basalt-hosted vents on Axial Volcano following colonization by tube worm assemblages (Levesque & Juniper, this volume). The latter evidence led the authors to propose that particulate matter, in early-successional basalt-hosted polychaete and gastropod assemblages, is dominated by local free-living microbial primary production, whereas later-successional tube worm assemblages accumulate detritus both from local and sedimentary sources (Levesque & Juniper, this volume).

Table 2. Biochemical composition (organic carbon and nitrogen contents, available protein content, DAPI-staining cell counts and lipid content) of the particulate matter from Assemblage II (Pork Chop) and Assemblage V high-flow (T&S). Values are mean and (range). A single sample from each assemblage was analysed for lipid content, thus the range could not be calculated.

Assemblage	%C	%N	Cell counts 10^{10} cells gC^{-1}	Proteins mg gC^{-1}	Lipids mg gC^{-1}
Pork Chop (II)	1.3 (2.3)	0.3 (0.4)	15 (20)	213 (199)	193
T&S (V-HF)	6.2 (1.2)	1.4 (0.1)	7 (8)	103 (136)	42

The results presented in Table 2, albeit preliminary and incomplete, support the extension of the detrital accumulation hypothesis to sulphide edifice assemblages. As faunal biomass builds during succession ($>500\times$ increase from Assemblage I through to Assemblage V low-flow; (Sarrazin & Juniper, 1999)) a greater amount of detritus will be produced, and three-dimensional structures created by tubeworm aggregations should favour the accumulation of particulate material within the assemblage. Through succession, food available to suspension- and deposit-feeders will tend to diversify from microbial mats and biofilms to a more heterogeneous particulate matter pool containing microbial biomass and organic detritus.

A diversification of food resources should therefore be accompanied by a diversification of nutritional strategies. This can be seen in assemblage composition data (Sarrazin & Juniper, 1999) and descriptions of the feeding modes of the faunal groups (see Sarrazin et al., 1999). Early-successional assemblages are composed almost exclusively of suspension- and deposit-feeders (mainly alvinellid polychaetes), while later-successional assemblages include endosymbiotic-containing fauna (*Ridgeia piscesae*), predators (e.g. polynoid polychaetes), as well as suspension- and deposit-feeders (e.g. alvinellids and gastropods). This should increase the complexity of the food web, possibly through a larger number of trophic levels and the exploitation of more trophic niches. This hypothesis is currently being tested on a broader scale (C. Levesque, in preparation).

Conclusions

The substratum analysis indicates a trend of decreasing porosity from Assemblage I through to Assemblage V, consistent with present models of the progressive mineralization of massive sulphides. This observation supports the idea that faunal succession proceeds as the substratum matures. Our data also suggest that as porosity significantly decreases beneath the different assemblages, the influence of lateral fluid flow inputs from nearby sources could become important. Therefore, the environmental conditions experienced by vent assemblages may be more influenced by fluid coming through the substratum in early-successional assemblages, and by lateral inputs from adjacent sources in later-successional assemblages. Faunal colonization stages may also affect early mineralization stages, as proposed by Juniper et al. (1992) for tube building by Assemblage I sulphide worms (*Paralvinella sulfincola*), and as observed here, beneath Assemblage III.

Theoretically, a decrease in substratum porosity should reduce direct flow of hydrothermal fluids to overlying faunal assemblages. Flow reduction need not directly affect measured temperatures. Mean temperatures in the 3-month records varied little from Assemblages I through to V low-flow, although there was a noticeable temperature decrease for senescent Assemblage VI. This observation emphasizes the need to directly measure fluid flow rates, in addition to other environmental variables, when investigating the relationship between vent faunal succession and habitat dynamics. We have begun using a quantitative flow

visualization tool, developed during a post-doctoral fellowship (J. Sarrazin) at the Woods Hole Oceanographic Institution, to measure flow rates within different faunal assemblages. Data provided here showed that lateral flow should also be taken into account, particularly in later-successional assemblages.

We summarize the points discussed in an updated version (Fig. 1) of the Sarrazin et al. (1999) model of community succession. Biotic factors (diversification of particulate food resources and trophic complexity) are now considered separately and given greater prominence. The driving abiotic processes are the decrease in substratum porosity and the stabilization of the habitat. As mineralization and succession progress on the sulphide edifice, the influence of other biotic factors, such as predation and competition, should become apparent. In parallel, suspension- and deposit-feeders will exploit a more 'detrital' food supply and should play a greater role in organic matter recycling. Abiotic factors still appear to predominate the passage through earlier-successional stages, perhaps up to Assemblage III. Habitat severity also appears to be critical to the maintenance of high-flow Assemblage V, where predatory and grazer species are rare. McDonald et al. (this volume) point out the critical importance of grazer-free

vestimentiferan assemblages to the reproductive potential of local and regional populations. An improved understanding of the importance of biological interactions in relation to the physico-chemical driving forces awaits further study of vent community ecology.

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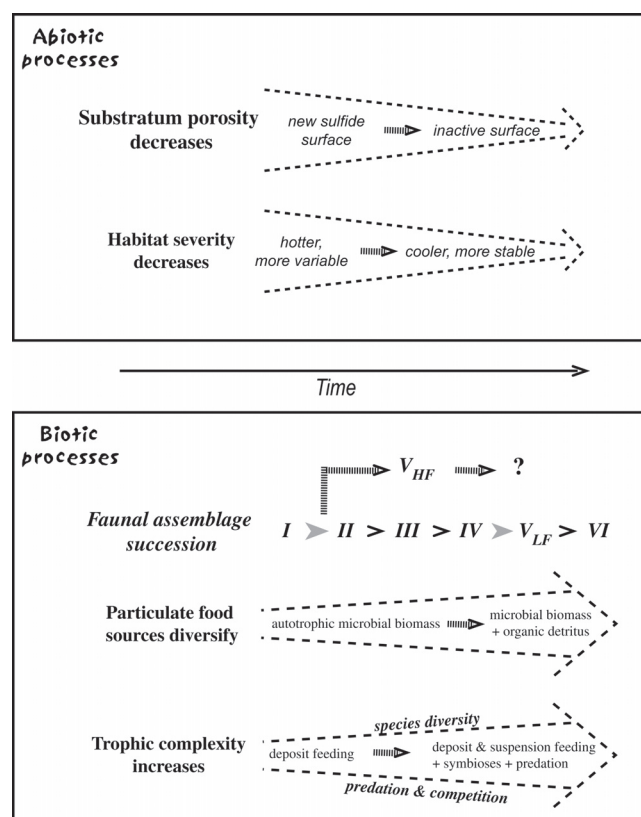


Figure 1. Summary model of abiotic and biotic factors influencing faunal community succession on Juan de Fuca Ridge sulphide edifices (modified from Sarrazin et al., 1999).