



Living on the edges of diffuse vents on the Juan de Fuca Ridge

Jean MARCUS and Verena TUNNICLIFFE
 Department of Biology, University of Victoria, P.O. Box 3020, STN CSC,
 Victoria, British Columbia,
 Canada V8W 3N5
 Fax 250-721-7120 – E-mail: jmarcus@uwic.ca

Introduction

The first ecological studies at the Galapagos Rift vents invoked the concept of species zonation around diffuse vent openings (Hessler & Smithey, 1983). Assemblages changed with increasing distance from hydrothermal influence: the direct flow dominated by vestimentiferans, clams, polynoids and limpets; mussels, serpulid worms and anemones in the next zone; and, a third peripheral zone dominated by siphonophores and ophiuroids. Other studies also relate patterns of species distributions to varying intensities of fluid flow properties (Fustec et al., 1987; Desbruyères et al., 1994; Sarrazin et al., 1999; Gebruk et al., 2000; Micheli et al., 2002).

Zonation is less visually evident at vents on the Juan de Fuca Ridge (JdFR). Species richness on the JdFR is lower compared to the East Pacific Rise and Galapagos Rift (Tunnicliffe et al., 1998); comparable megafaunal peripheral species such as suspension-feeding serpulids are absent. Nonetheless, hydrothermal influence decreases with increasing distance from the vent. Tubeworm clusters diminish and disappear, but many of the same species are present on adjacent rocks. We hypothesize that, with distance, faunal assemblages shift from a typical vent composition towards an assemblage less tolerant of vent conditions and less dependent on high rates of primary production. Our objectives are to determine whether vent assemblages are distinguishable from peripheral assemblages and, if so, to document the major differences.

Methods

The 1998 eruption on Axial Volcano, Juan de Fuca Ridge, created numerous low temperature vents (Embley & Baker, 1999). For this study, we sampled in July 2000 with the remotely-operated vehicle *ROPOS*. Two locations at each vent were targeted: within shimmering flow ('Flow' samples) and at distances of 0.5 to ~6 m from the vent where no flow was evident ('Periphery' samples). 'Flow' samples were coupled with one 'Periphery' sample, except one vent where three Periphery samples were taken; three other collections were only Flow samples (Table 1). The distance of Periphery samples from venting was estimated by video with scale indicators and cruise notes. Flow samples were

Table 1. Collection listing; X denotes a sample. Distance from flow is given for Periphery samples. ID is the vent label, and * denotes a subsample from a complete collection.

Vent	ID	Flow	Periphery		
			Near 0.5 m	Mid. 1-3 m	Far 5-6 m
Cloud	A	X	X	X	X
Mkr 33	B	X		X	
Mkr 113	C	X		X*	
Bag City	D	X		X	
Joystick	E	X	X		
Snail	F	X			
Nascent	G	X			
Bag City	H	X			

tubeworm (*Ridgeia piscesae*, Jones 1985) grabs, sometimes coupled with suction samples; Periphery samples were suctions. We justify the mixed methods by a requirement for maximal assemblage representation.

Samples in 7% formalin were sorted to the lowest possible taxonomic rank; although picked to 64 µm, only species whose adults would be retained on a 1 mm sieve are reported. Species evenness was calculated for Flow samples combined and Periphery samples combined using the Hurlbert's PIE measure (EcoSim 6.0, Acquired Intelligence Inc. & Kelsey-Bear). Body weight data are reported for two species, *Lepetodrilus fucensis* McLean, 1988 and *Depressigyra globulus* Warén & Bouchet, 1989; bulk wet weight was measured for combined individuals from each microhabitat sampled at Cloud vent. Similarity among samples was investigated by cluster analysis using species presence/absence data (Jaccard similarity coefficient, flexible method, $\beta = -0.25$); only complete samples were included (see Table 1). Clustering was preformed in NTSYS 2.0 (Exeter Software).

Results

1. Composition and distribution

The average relative abundances of taxa collected from the eight Flow samples and the seven Periphery samples are listed in Table 2. More species were collected on the Periphery (n=36) than in Flow (n=31). All but 4 species sampled in Flow were also present in Periphery samples, while 9 species occurred exclusively in Periphery samples (Table 2). Overall, species evenness is higher in Periphery samples: the probability that two randomly selected individuals are two different species is 0.75 for Periphery samples and 0.62 for Flow samples.

A striking similarity of the habitats is the abundance of two gastropods: the limpet, *Lepetodrilus fucensis*, and the snail, *Depressigyra globulus* (Table 2). The limpet ranks as the first or second most abundant species in every Periphery sample (range from 23.5% to 55.1% relative abundance) except in the farthest Cloud sample (2.5% relative abundance). Several differences occur between the Flow and Peripheral locales. First, the alvinellid polychaete, *Paralvinella pandorae* Desbruyères & Laubier, 1986 shifts

Table 2. The average relative abundances of taxa from Flow and Periphery samples. *Ridgeia piscesae* is not included. * indicates species only found at Joystick Flow vent which is likely waning. ARA = average relative abundance, SP = sites present, NP = not present, P = present.

Taxon	Species	Flow		Periphery	
		% ARA	# SP (of 8)	% ARA	# SP (of 7)
Gastropoda	<i>Lepetodrilus fucensis</i>	45.805	8	41.211	7
Polychaeta	<i>Paralvinella pandorae</i>	35.508	8	0.309	4
Gastropoda	<i>Depressigyra globulus</i>	10.938	8	11.487	7
Polychaeta	<i>Ophryotrocha globopalpata</i>	2.466	8	12.662	7
	<i>Amphisamytha galapagensis</i>	1.830	8	9.345	7
	<i>Paralvinella palmiformis</i>	0.924	5	NP	-
	<i>Branchinotogluma</i> sp.	0.675	8	0.537	2
	<i>Parougia wolffi</i>	0.671	7	5.697	6
	<i>Lepidonotopodium piscesae</i>	0.319	8	0.171	3
	<i>Hesiospina vestimentifera</i>	0.198	6	9.375	7
Ostracoda	<i>Euphilomedes climax</i>	0.152	1	0.105	3
Gastropoda	<i>Provanna variabilis</i>	0.147	5	1.234	6
Polychaeta	<i>Paralvinella sulfincola</i>	0.067	1	NP	-
	<i>Prionospio</i> sp.	0.064	3	1.554	6
	<i>Opisthotochopodus tunnicliffeae</i>	0.058	5	0.407	2
	<i>Hesiodaira glabra</i>	0.045	4	0.006	1
Pycnogonida	<i>Ammothea verenae</i>	0.038	3	0.004	1
Polychaeta	<i>Levensteiniella kincaidi</i>	0.032	4	0.417	6
	<i>Protomystides verenae</i>	0.029	4	NP	-
	<i>Amphiduropsis axialensis</i>	0.019	4	0.421	3
	Unknown spionid	0.009	2	0.109	3
Aplacophora	<i>Helicoradomenia juani</i>	0.008	1*	0.048	3
Gastropoda	<i>Pyropelta musaica</i>	0.007	1*	0.242	3
	<i>Lacunoides vitreus</i>	0.007	1	0.021	1
	<i>Hyalogyrina globularis</i>	0.006	2	NP	-
Polychaeta	<i>Nereis piscesae</i>	0.006	3	0.079	2
Nemertea	<i>Thermanemertes valens</i>	0.006	3	0.142	3
Bivalvia	Vesocomyid clam	0.005	3	0.040	2
Amphipoda	Amphipod sp.	0.005	1*	0.117	3
Ophiuroidea	Ophiroid sp.	0.003	1*	0.019	1
Polychaeta	<i>Vampiropolynoe embleyi</i>	0.001	1	0.021	1
	Unknown polychaete #1	NP	-	2.978	4
	Unknown polychaetes mixed	NP	-	0.476	3
Gastropoda	<i>Provanna laevis</i>	NP	-	0.227	1
Bivalvia	Juvenile clams	NP	-	0.215	3
Polychaeta	Unknown orbiniid	NP	-	0.123	2
	Unknown nereid?	NP	-	0.082	3
	<i>Nicomache venticola</i>	NP	-	0.045	1
?	Unknown psuedocoelomate?	NP	-	0.032	1
Polychaeta	<i>Leitoscoloplos pachybranchiatus</i>	NP	-	0.014	1
	<i>Harmothoe macnabi</i>	NP	-	0.013	1
Ciliata	Folliculid sp.	NP	-	P	1
Hurlbert's PIE		0.62		0.75	

from ubiquity and high abundance (35.5%) in Flow to lower occurrence and lower abundance (under 1%) on the Periphery. Its congener, *Paralvinella palmiformis* Desbruyères & Laubier, 1986 is absent in Periphery samples. Second, four polychaete species are relatively more abundant on the Periphery than in Flow: *Amphisamytha galapagensis* Zottoli, 1983, *Ophryotrocha globopalpata* Blake & Hilbig, 1990, *Parougia wolffi* Blake & Hilbig, 1990 and *Hesiospina vestimentifera* Blake, 1985

(Table 2). *A. galapagensis*, an ampharetid, forms a conspicuous Periphery “belt” of tubes covering the basalt. Third, the polynoid polychaete *Levensteiniella kincaidi* Pettibone, 1985 typically rare in visible flow (JM unpub. data) occurs in all complete Periphery samples (Table 2; missing from Mkr 113 Periphery sample, Table 1).

2. Size structure

Individuals of the dominant gastropod species display marked size differences between the Flow and Periphery areas. The body sizes of *Lepetodrilus fucensis* and *Depressigyra globulus* at Cloud Vent decrease with increasing distance from vigorous flow. Average wet weight for the former species drops by three orders of magnitude and the latter by two orders (Table 3). This trend was observed for both species in all Periphery samples.

Table 3. Average wet weight (g) of *Lepetodrilus fucensis* and *Depressigyra globulus* individuals from Cloud vent. For both species there is a trend of decreasing size with increasing distance from visible flow. n = number of individuals used for bulk measurements.

Species	Flow	Near	Mid.	Far
<i>L. fucensis</i>	0.1153 n=100	0.0721 n=100	0.0002 n=100	0.0002 n=7
<i>D. globulus</i>	0.0215 n=46	0.0244 n=69	0.0007 n=75	0.0002 n=25

3. Sample similarity

A cluster analysis of presence/absence data of all collections groups Periphery samples and visible Flow samples separately (Fig. 1). The one Periphery collection that clusters with Flow samples is the closest peripheral sample from Cloud vent taken only ~ 0.5 m away from the visible flow (Fig. 1). One Flow collection (Joystick) clusters with Periphery samples; visual observations suggest that this vent was waning at the time of sampling: the maximum

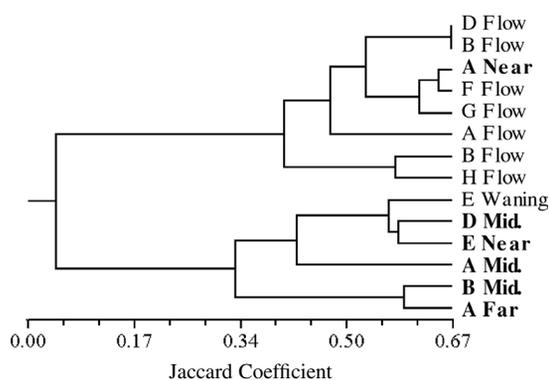


Figure 1. Cluster diagram of species occurrences in collections. Font indicates sample type: normal are Flow and bold are Periphery samples. Table 1 gives vent name labels and Periphery distances from vent.

temperature detected was 4°C, the thin tubes of *Ridgeia piscesae* held shriveled trophosomes, and alvinellid polychaetes were low in relative abundance (3.5%). Table 2 indicates that, of the Flow samples, only Joystick hosts four species that are otherwise found on the Periphery.

Discussion

The assemblage sampled beyond the edges of visible vent flow differs from vent openings where temperatures ranged between 13 °C and 39 °C (excluding waning Joystick vent). The Flow samples retrieved over 85% of the macrofauna recorded from a larger study of Axial vent fauna (Tsurumi, 2001). At the scale of this study, cluster analysis identifies a peripheral fauna. However, that fauna retains a ‘vent’ character: over 75% of the species are known from active vents and *Lepetodrilus fucensis* dominates both habitats.

The physico-chemical attributes of the habitat are likely key factors. Although water characteristics were not measured until the following summer, we detected no temperature or sulphide anomalies at any peripheral sites. The close Cloud periphery may be an exception as fluid was advecting over the adjacent substratum during sampling. This moderate environment likely facilitates the occupation of peripheral areas by species precluded from the harsher vent habitat. Conversely, the disappearance of alvinellid polychaetes in the periphery may be in part due to loss of tubeworm substratum, changing resources, and increased competition from ampharetids.

Two and a half years post-eruption may not be enough time for encroachment by the normal deep-sea fauna to vents. There is no evident reason why they are not more abundant. We assume that the major food source is organic detritus from nearby vents. The most abundant animals are grazers/deposit feeders. However, the average relative proportion of potentially predatory and scavenging worms (polynoids, hesionids, dorvilleids, nereids and nemerteans) is greater from Periphery (29.9%) than Flow (4.5%) samples. A large nereid or polynoid predator may have a substantial influence on community structure. Apart from localized mats of folliculid protozoans, we find no suspension feeders.

The limpet, *Lepetodrilus fucensis*, is the most abundant animal in all collections except the most distal Cloud sample. This animal has multiple food gathering strategies and ranges from vent periphery to high temperature smoker habitats. It is ubiquitous on the Juan de Fuca Ridge (Tsurumi & Tunnicliffe, 2001). The marked size differences in *L. fucensis* and *Depressigyra globulus* between Flow and Periphery may reflect the different habitat. Abundant small individuals of these species are uncommon in Flow samples (JM pers. obs.); juveniles may be excluded from Flow areas by predation or active venting conditions, or the small stage is very transitory. Low spatial variability in limpet larval arrival to the bottom (Metaxas, pers. comm.) implies that recruit supply is similar. However, size differences may also be due to stunted growth or predation of larger adults on the periphery. Sizes of mytilid bivalves from the Mid-Atlantic Ridge may also be related to flow proximity (Comtet & Desbruyères, 1998).

At ~6 m from Cloud, the number of vent obligate animals decreased. While vent larvae may be arriving over wide spatial ranges, they are not surviving in large numbers. Tsurumi (2001) examined suction samples of surfaces beyond vent influence (~20-30 m away) to verify the absence of the Flow species listed here. She also found animal assemblages similar to the Periphery among tubeworm collections from failing vents where fluid flow is not visible and vestimentiferans are in poor condition. These waning vents also have higher species richness and evenness, fewer vent obligate species, the presence of deep-sea taxa, and a lower density of individuals. The vent temporal sequence may have some analogy in the spatial array.

The vent peripheral assemblage has many of the same species found in venting fluids. However, the small size and low abundance of these animals form a poorly visible band around the vents on Axial Volcano although patches of ampharetids and ciliates occur. There appears to be some incursion from the ambient deep-sea fauna. Spatial competition at the vents may relegate some individuals to this peripheral zone while other species may find it an optimal zone for foraging. Further comparative work on size and maturity characteristics of select species should better define the role of this habitat.

Acknowledgements

We thank R. W. Embley and the NOAA Vents Program and the logistical support of the *Ronald H. Brown* and the ROV *ROPOS*. This study was supported by NSERC Canada.

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