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## Biological colonization of new hydrothermal vents following an eruption on Juan de Fuca Ridge

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**Abstract**—A recent eruption on CoAxial Segment of Juan de Fuca Ridge initiated hydrothermal conditions with rapid changes in water chemistry and growth of microbial communities. Vent animals recruited from distal sources within a year. One site with newly erupted lava attracted no animals to high-iron and low-sulphide conditions. However, sustained release of flocculent material at a second site suggests extensive subterranean microbial production; here, the dissolved sulphide/heat ratio peaked during the first year. The first larval recruits included vestimentiferans, alvinellid polychaetes and nemerteans; despite the small areal extent of venting, one-third of the regional vent species pool had arrived by 2 years. Near-optimal growth conditions and recruitment by many species continued in the centre of the system but several habitats went extinct within 2 years. Rapid response and exploitation by vent animals must be an important adaptation to such ephemeral conditions. © 1997 Elsevier Science Ltd

### INTRODUCTION

The responses of communities to the formation, stabilization and destruction of habitat are important issues in the study of community development. Hydrothermal vent communities experience a wide range of conditions, varying in time and space, that influence development of the fauna. Whereas some sites have been hydrothermally active for hundreds or thousands of years (Kapell and Franklin, 1989; Lalou *et al.*, 1995), recent work has identified highly dynamic magmatic activity on several ridge crests such as Juan de Fuca (Chadwick and Embley, 1994), northern East Pacific Rise (Haymon *et al.*, 1993) and southern East Pacific Rise (Urabe *et al.*, 1995; Auzende *et al.*, 1996). Eruption frequency is probably related to seafloor spreading rate (Fornari and Embley, 1995).

It is rare to record an eruptive event on a ridge crest. Such events were observed in April 1991 on East Pacific Rise near 9°N (9N EPR) (Haymon *et al.*, 1991) and July 1993 on CoAxial Segment, Juan de Fuca Ridge. At 9N EPR, a robust animal assemblage was mostly destroyed. Survivors nearby (within 1.5 km) apparently supplied scavengers within days

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(Haymon *et al.*, 1993); it is likely that the larvae settling within a year (Lutz *et al.*, 1994) recruited from these survivors or even from pre-eruption larval releases in the water. The CoAxial eruption provides the first case of *de novo* community development: to the best of our knowledge, no vents existed within 18 km immediately preceding the eruption. Here, we integrate observations on geological conditions, water chemistry and microbial characteristics, and examine the dynamics of the colonizing community in the evolving conditions of the habitat. Complementary information on the CoAxial eruption has been given by Fox (1995), Holden (1996) and Butterfield *et al.* (1997). Information repeated here is necessary for the animal colonization story.

#### Study site

The eruption event occurred on Juan de Fuca Ridge on "CoAxial Segment", which overlaps the northern rift of Axial Volcano. The neovolcanic of CoAxial Segment occupies the central 1 km of the axial valley, where the lavas are the youngest. The CoAxial event is the first mid-ocean ridge accretion episode to be documented at inception. It was recorded remotely by the US Navy's SOSUS system (Fox *et al.*, 1995). In late June 1993, swarms of earthquakes began just north of Axial Volcano and rapidly migrated northward about 40 km before localizing at a site centred around 46°30'N, 129°35'W (Fig. 1). Here, a lava flow was found within days of eruption (Embley *et al.*, 1995). Earthquakes continued for several weeks. Because spatial and temporal seismicity patterns resembled those of Icelandic fissure eruptions, this event is interpreted as an upper crustal dyke injection with a large lateral component (Dziak *et al.*, 1995). Water column surveys in 1990 and 1991 in the vicinity of Floc Site detected no anomalies related to hydrothermalism (E. Baker, personal communication, 1996). Mullineaux *et al.* (1995) reported the lack of any hydrothermal vent larvae in 1990 plankton tows that went over the major post-eruption venting sites. It is difficult to prove an absence, but we believe there were no extant vents or "seed" populations in the vicinity (within 15 km) of the new vents.

## METHODS

Primary vent sites were located using stationary CTD casts and "Tow-yos" (CTD casts while steaming) in July and October 1993 (Baker *et al.*, 1995b; Embley *et al.*, 1995). Table 1 lists the research visits to CoAxial. The remote vehicle *ROPOS* operates on a fibre optic cable with video feed; it uses two manipulators for sampling and can be wired for real-time data collection. *ROPOS* dives mapped the lava flow ("Flow Site" at 46°32'N in Fig. 1) immediately after the eruption. The vehicle also located a site of intense flocculate release

Table 1. Timing of investigations relative to the eruption event on CoAxial Segment

Date	Event	Sites visited
26 June–17 July 1993	Eruption	Northward migration
17 July–1 August 1993	<i>ROPOS</i> vehicle	Flow Site; near Floc Site
11 October–24 October 1993	<i>Alvin</i> submersible	Flow, Floc and Source Sites
30 June–8 July 1994	<i>Alvin</i> submersible	Flow, Floc and Source Sites
1 July–7 July 1995	<i>Alvin</i> submersible	Flow, Floc and Source Sites

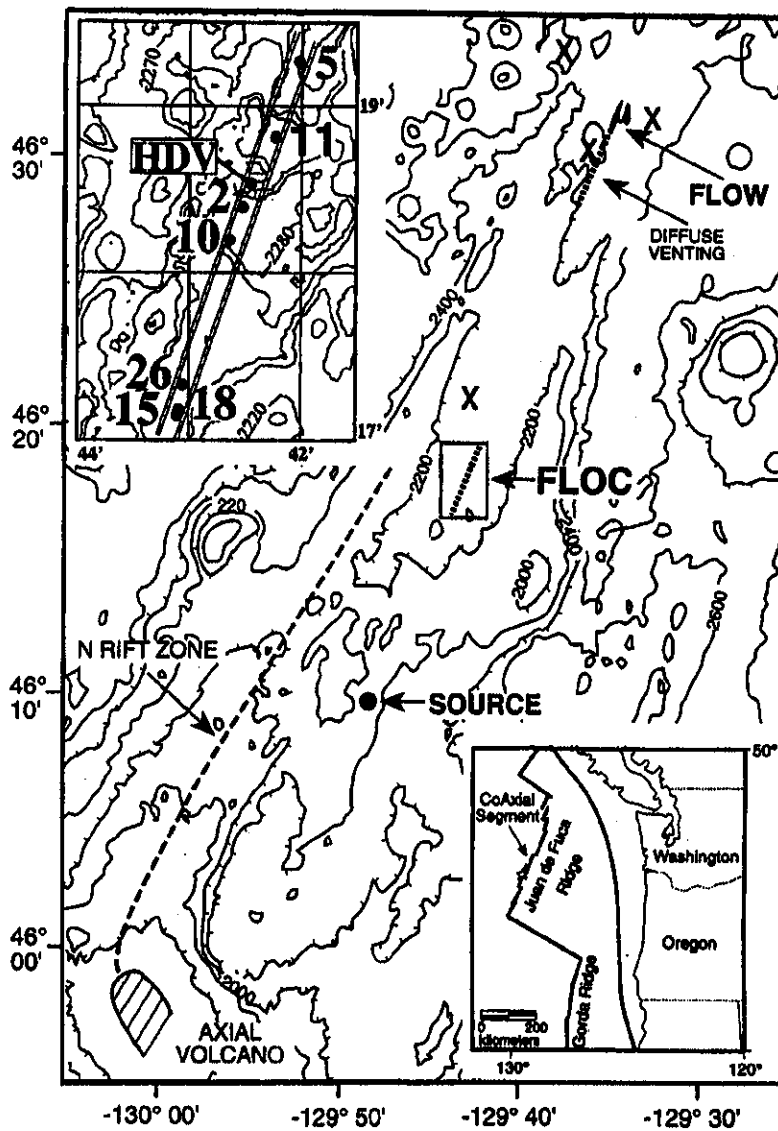


Fig. 1. Location of the July 1993 dyke injection event on CoAxial segment, Juan de Fuca Ridge. Lava erupted at Flow Site; colonization occurred at Floc Site. Source Site was an extant vent at the time of eruption. The crosses indicate locations of the current meters (Cannon *et al.*, 1995; R. E. Thomson, personal communication, 1996). The dotted line on the North Rift Zone indicates the presumed spreading locus propagating north of Axial Seamount; this axis may continue on the same trend further north and perhaps support vents in an unexplored area north of Floc Site. Upper inset shows major sampled vents at Floc Site. Marker 15/18/26 site visited only in 1995.

("Floc Site", 46°17') 20 km to the southwest although the actual vents there were not found. In October 1993, the submersible *Alvin* reoccupied Flow Site and pinpointed the new venting at Floc Site along a fissure swarm cutting through older basalts (Fig. 1). A high-temperature site ("Source Site") was discovered 18 km southwest of Floc (46°09'N); the name reflects an initial supposition that a subsurface magma source may be located here. The venting deposits and fauna here clearly predated the eruption judging by the alteration and oxidation of parts of the deposit, partly entombed worm tubes in the oxidized deposits and the presence of juveniles and adults of a diverse range of species. All these marked sites were revisited in summers of 1994 and 1995 by *Alvin*. In 1995, exploration extended the known venting area further south to Marker 18 area (Fig. 1). Towed camera and CTD tow-yo surveys of CoAxial's neovolcanic zone in 1993 and 1994 have revealed no additional venting sites, new or old (Fig. 2).

Vent fluids were collected in 750 ml titanium major samplers (Von Damm *et al.*, 1995) and processed immediately after recovery. A description of methods used and the details of CoAxial vent fluid chemistry have been given by Butterfield *et al.* (1997). Magnesium is nearly removed from seawater during water-rock interaction at temperatures above 150–200°C (Bischoff and Dickson, 1975). On-axis diffuse venting typically results when fluids from a high-temperature reaction zone mix with cold, seawater-like fluid below the seafloor, yielding a mixture depleted in Mg. Further mixing with ambient bottom seawater inevitably occurs during sampling. For this reason, the most Mg-depleted diffuse fluids sampled are considered the best samples and are chemically most representative of what is leaving the seafloor. Therefore, we report maximum or extreme values of extensive chemical properties for each vent site. Likewise, the highest measured temperatures are most representative of the actual exit temperatures.

A new submersible-mounted instrument, SUAVE (Massoth *et al.*, 1991), allowed real-time assessment of dissolved Mn, Fe (II + III), and H<sub>2</sub>S every 5 s during precise positioning of the sample intake; a high-resolution temperature sensor is coupled to the intake. This system uses flow analysis-colorimetric detection. The upper limit of determination for H<sub>2</sub>S concentrations was 110 µmol kg<sup>-1</sup>; unexpectedly, these concentrations were exceeded in July 1994 fluids from Floc Site.

Microbial samples came from the titanium samplers and from suction samplers used to retrieve the matted substance on the rock surfaces. Fluid and "mat" samples were preserved in 1–2% glutaraldehyde. For estimates of concentrations, cells were filtered onto Iralgan Black prestained 0.22 µm filters, stained with DAPI and counted under epifluorescence. Viable thermophiles and hyperthermophiles were cultured using enrichment techniques of Holden (1996). SEM, X-ray microanalysis, phase-contrast and light microscopy imaged microbial mat characteristics. Frozen mat samples were assayed for CO<sub>2</sub> fixation potential and heat labile sulphide oxidation activity (Juniper and Martineu, 1995; Juniper *et al.*, 1995) as well as for total sulphur, organic carbon and nitrogen. Metal and metalloid analyses were performed by ICP-MS (inductively coupled plasma mass spectrometry).

Most animals were collected when *Alvin's* manipulator grabbed clumps of tubeworms, which were placed in sealed boxes for transit. Additional specimens came from suction samples of mat and Niskin bottles triggered over the vents. It was not possible to take quantitative samples with the manipulator; thus this work is limited by the lack of rigour in duplication of sampling effort. We believe, however, that the samples are reasonable representations of the species associated with vestimentiferans. Samples were preserved for later complete sorting on shore where collections were picked, and all washings examined

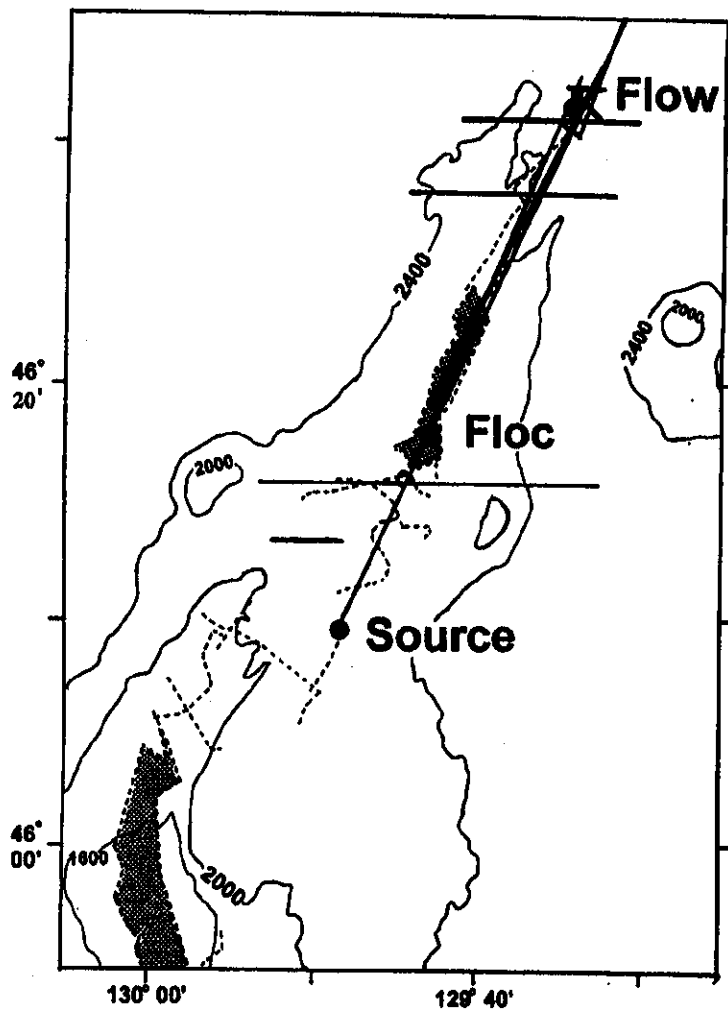


Fig. 2. Locations of CTD "tow-yos" and camera tows from 1993 to 1995, to illustrate the area of coverage seeking other vents. Straight continuous lines are CTD tows. Dotted lines are camera tows; hatched areas indicate saturated coverage by many overlapping camera tows.

down to the scale required to observe recent settlement stages (to 100  $\mu\text{m}$ ). Close *in situ* and image examination of the colonized sites could detect no uncollected species but did reveal that relative abundances of species differed on microbial mats and among tubeworms.

## RESULTS

### July 1993

As the seismic signals subsided, we explored Flow Site (Table 1) and found a cooling lava flow about 300 m by 2.5 km in area. Diffuse venting was nearly continuous with

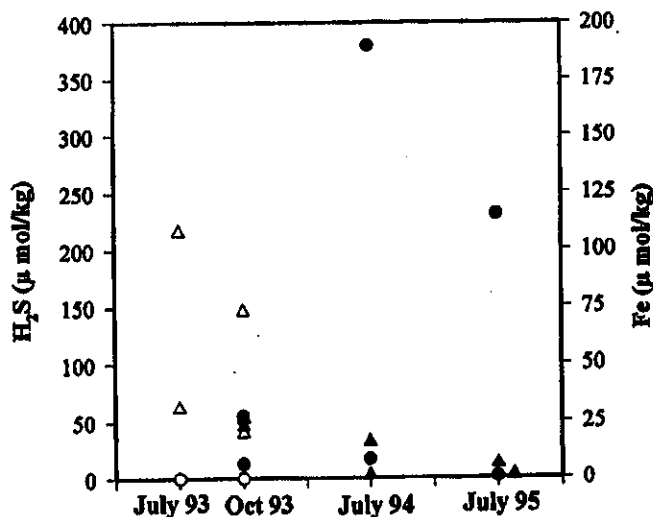


Fig. 3. Time series of ranges in Fe (triangles) and H<sub>2</sub>S (circles) concentrations in diffuse vent fluids: open symbols for Flow Site, closed for Floc Site. Pairs of like symbols show minimum and maximum measured values for all samples from each site.

temperatures to 51°C (Embley *et al.*, 1995). Contemporaneous water column work located plumes over Flow and Floc Sites (Baker *et al.*, 1995b; Lupton *et al.*, 1995; Massoth *et al.*, 1995). *ROPOS* was not correctly positioned to locate Floc venting, but it encountered dense clouds of white flocculated matter from this nearby source. As water samples collected from ventlets in the new lava flow (1 August 1993) differed from seawater Mg by less than 0.5%, it is difficult to identify major element trends. Fluids were slightly higher than seawater in chlorinity, hydrogen sulphide was not measurable (below 0.5 μmol kg<sup>-1</sup>) and total dissolvable iron was enriched in major and SUAVE samples (Fig. 3). Bright orange deposits consisting of up to 25% iron covered as much as 14% of the new lavas. The loose flocculated matter seen "blowing" from cracks accumulated in drifts on the lavas; this material showed low CO<sub>2</sub> fixation activity (from D-ribulose-1,5-biphosphate carboxylase activity—RubCase) and an origin below the seafloor appears more likely than *in situ* growth (Juniper *et al.*, 1995). The morphological diversity present (filaments, cocci and bacilli), in addition to some detectable RubCase and sulphide oxidation activity, suggests the presence of autotrophic processes other than iron oxidation. This observation is supported by low Fe:Org C ratios (8:1) compared with growth efficiency studies of iron chemoautotrophs that yield 1 mol carbon per 50–100 mol of iron oxidized (Juniper and Tebo, 1995).

#### October 1993

Shimmering venting had visibly diminished at Flow Site and the extensive bright orange deposits of the previous July were now brown. Pervasive venting was no longer visible but discrete flows were located (to 36°C) near previous sample locations. Fluid samples now had Mg depletions up to 4–5% relative to seawater and chlorinities higher than seawater. Iron

concentrations remained high (30–70  $\mu\text{mol kg}^{-1}$ ) and  $\text{H}_2\text{S}$  undetectable. Microbes found in Flow fluids were almost exclusively iron-oxidizers as determined from morphology (Juniper *et al.*, 1995), and mat subsamples contained only 1% ( $n = 10$ ) DAPI-staining cells compared with 22% ( $n = 10$ ) in July, indicating an activity decline (Fig. 4a–d).

At Floc Site, extensive venting of low-temperature fluids occurred along a fissure swarm that cut through pillow and sheet flow lavas near the centre of the axial valley. Although there was no evidence of 1993 eruptive lavas, the extensive microbial mats and lack of macrofaunal colonization indicated venting was very recent. Floc Site fluid samples were lower than seawater in chloride, had iron concentrations below 30  $\mu\text{mol kg}^{-1}$  and hydrogen sulphide up to 60  $\mu\text{mol kg}^{-1}$ . These characteristics are consistent with dilution of a slightly vapour-enriched high-temperature endmember fluid. Lithium concentrations were up to twice ambient seawater at both sites, indicative of high-temperature water–rock reaction. SUAVE measured  $[\text{H}_2\text{S}]$  at Marker 11 (later colonized) to be less than 3  $\mu\text{mol kg}^{-1}$ . Clouds of flocculates rose from venting along fissures at Floc Site, creating white drifts on the seafloor. Both sulphur- and methane-oxidizing microbes were isolated from fluids. Hyperthermophilic sulphur-reducers and methanogens were isolated from fluids at temperatures 30–50°C below optimum growth temperatures of the microbes (Holden, 1996). Visual observations from divers and cameras located no macrofauna at Floc Site. No macrofaunal larvae were detected in mat samples from a 6°C vent although some mat was bound in faecal pellets, suggesting arrival of a grazer such as a benthic copepod.

The four sparsely colonized chimneys at Source Site appeared unaffected by the eruption event. The 1993 animal collections represented a mature community with a few recent recruits. As this site was considered to have great potential to provide larvae to the new vents, it was revisited in subsequent years. Although relative abundance of species varied among the chimneys, the same suite of species (Table 2) was found each year. Dense populations of deep-sea suspension feeders growing on nearby rocks imply that long-term hydrothermal flow here may have encouraged colonization in response to greater suspended matter flux.

#### July 1994

At Flow Site, only one vent was located (9°C) and fluid samples were indistinguishable from seawater. Vents visited at Floc Site occurred at five locations along a strike of 7 km length. Maximum temperatures measured were 12°C (Marker 2). The two Floc Site vents sampled in 1993 were diminished in temperature, areal extent and floc emission (Marker 11 from 22°C to 7°C and Marker 3A, near HDV, from 18°C to 8°C). Magnesium depletion was 2–3% relative to seawater but now  $\text{H}_2\text{S}$  was enriched to 380  $\mu\text{mol kg}^{-1}$ . Iron concentrations had dropped markedly; peak concentrations for both SUAVE and discrete samples ranged from 11 to 16  $\mu\text{mol kg}^{-1}$ , and concentrations of less than 5  $\mu\text{mol kg}^{-1}$  were determined for several sites. SUAVE scans around vestimentiferans were made at two vents: four times, the detector intake was placed within a centimetre of the worm plumes then among their bases, holding for several minutes for each scan. The 110  $\mu\text{mol kg}^{-1}$  upper limit of determination for  $\text{H}_2\text{S}$  was exceeded each time at both plumes and bases in these 4–12°C fluids.

Two mat types were observed around the venting at Floc Site. Four locations were coated with continuous sheets of white mat extending hundreds of square metres. This white flocculated mat showed little cellular structure (Fig. 4e) and minimal enzyme activity was recorded, but was probably of microbial origin and appeared identical to matter produced

Table 2. Taxa identified from CoAxial vent collections

Group	Family	Species	Floc 1995		Source
			Floc 1994	Active	
Stauromedusa <sup>a</sup>	unknown	unknown		x	
Vestimentifera	Ridgeiidae	<i>Ridgeia piscesae</i>	xxx	xxxx	xx xxxx
Polychaeta <sup>a</sup>	Spionidae	<i>Prionospio</i> sp.		x	xx
Polychaeta <sup>b</sup>	Phyllodocidae	<i>Protomystides verenae</i>			x
Polychaeta	Polynoidae	<i>Branchinotoglumina grasslei</i>		xx	xx
Polychaeta	Polynoidae	<i>Branchinotoglumina sandersi</i>	x	xx	xx
Polychaeta	Polynoidae	<i>Lepidonotopodium piscesae</i>		x	x
Polychaeta	Polynoidae	<i>Levensteiniella kincaldi</i>	x		xx
Polychaeta <sup>b</sup>	Polynoidae	<i>Opisthotrochopodus tunnicliffeae</i>			x
Polychaeta <sup>a</sup>	Polynoidae	<i>Harmothoe</i> cf. <i>globosa</i>	x	x	x
Polychaeta	Hesionidae	<i>Amphiduros axialensis</i>			x
Polychaeta	Hesionidae	<i>Hesioptna vestimentifera</i>		x	x
Polychaeta	Hesionidae	<i>Hesiodelta glabra</i>		x	x
Polychaeta	Orbiniidae	<i>Letoscoloplos pachybranchiatus</i>			x
Polychaeta	Dorvilleidae	unknown		x	
Polychaeta	Ampharetidae	<i>Amphisamytha galapagensis</i>	x	x	x xxx
Polychaeta	Alvinellidae	<i>Paralvinella sulficola</i>			xx
Polychaeta <sup>a</sup>	Alvinellidae	<i>Paralvinella pandorae</i>	xxx	xxxx	
Polychaeta	Alvinellidae	<i>Paralvinella palmiformis</i>		xx	xxx
Solenogaster	Simrothiellidae	<i>Helicoradomenia juani</i>			x
Gastropoda	Scissurellidae	<i>Temnocinelis euripes</i>			x
Gastropoda	Clypeosectidae	<i>Clypeosectus curvus</i>			x
Gastropoda	Lepetodrilidae	<i>Lepetodrilus fucensis</i>	x	xxx	xx xxxx
Gastropoda	Peltopiridae	<i>Depressigyra globulus</i>		xx	x xxx
Gastropoda	Provannidae	<i>Provanna variabilis</i>		x	xx
Pycnogonida <sup>b</sup>	Ammotheidae	<i>Ammothea verenae</i>			xxxx
Crustacea	(Myodocopida)	<i>Euphilomedes climax</i>		x	x xxx
Crustacea	Dirivultidae	<i>Aphotopontius forcipatus</i>		xx	x
Crustacea <sup>b</sup>	Dirivultidae	<i>Benthoxynus spiculifer</i>		x	xxx
Crustacea	Dirivultidae	<i>Stylopontius quadrispinosus</i>			x
Crustacea	copepod	harpacticoid sp. 1			xx xx
Crustacea	copepod	calanoid sp. 2		x	
Crustacea <sup>b</sup>	Galatheidae	<i>Munidopsis alvisca</i>			xx
Nemertea <sup>a</sup>	Emplectonematidae	N. Gen. n. sp.	xx	xxx	
Nematoda	unknown	unknown			x xx
Protozoa <sup>b</sup>	Folliculinid	unknown			xx

Floc is the new vent area: 1995 collections are presented as those from healthy active areas (HDV, Marker 3A and Marker 18) and those from dying or unmeasurable emissions (Marker 11 and Marker 2). Source, the closest known vent active before the eruption, was well sampled. As quantitative collection was not possible, abundances are presented in orders of magnitude: x = 1-10, xx = tens, xxx = hundreds, xxxx = thousands. Clearly apparent differences are marked: <sup>a</sup>for those taxa at Floc not found at Source; <sup>b</sup>for those species abundant at Source and elsewhere on Juan de Fuca Ridge but with poor or no record from Floc. As these collection techniques are unlikely to return all species present, only clear anomalies are highlighted (*Paralvinella sulficola* is not anomalous as it is known to inhabit only active smokers).

in culture from 55°C anaerobic enrichments. There was a notable lack of diatomaceous debris, indicating a recent origin. Dried mat contained up to 32% sulphur whereas iron was relatively low (2-8% dry weight). In contrast, one location (Marker 3A) had broken orange mats composed of microbial filaments and cellular morphologies consistent with sulphur



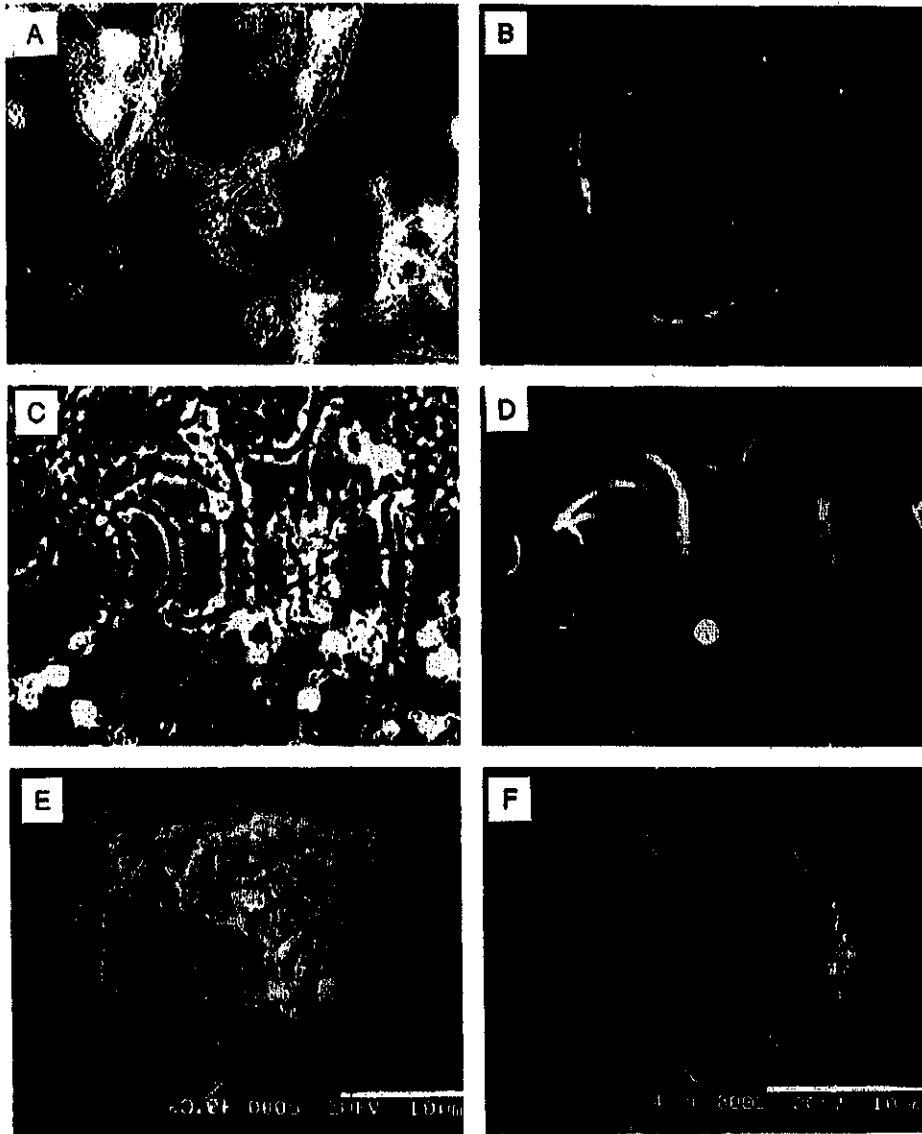


Fig. 4. Comparison of phase contrast illumination (A and C) and DAPI staining (B and D) in microbial mat material at the Flow site collected in July and October 1993. By October (A vs B) the proportion of "living" cells in mat material had decreased significantly from July (C vs D). (E and F) Electron micrographs of material collected from the Flow site in July 1994. White floc accumulations were generally devoid of recognizable cells but occasional aggregations (E) were found. Orange floc contained abundant filamentous forms (F) indicative of iron oxidizing bacteria.

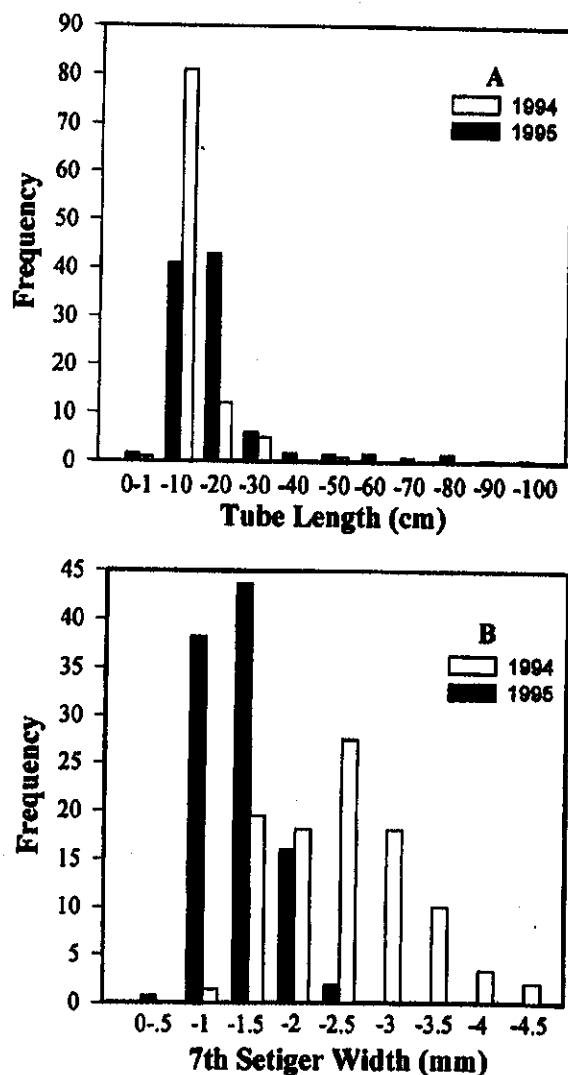


Fig. 5. Size-frequency plots of two species from HDV vent, Floc Site, from July 1994 and July 1995; samples taken about 1 m apart. (A) Vestimentiferan *Ridgeia piscesae* tube length. The 1994 profile suggests continuous recruitment from afar until self-recruitment begins. In 1995, the numerous post-settlement juveniles among the meiofauna were tubeless;  $n = 101$  (1994),  $n = 365$  (1995). (B) Polychaete *Paralvinella pandorae* body width at the seventh setiger: these subsamples represent all the animals taken from sheaths on the *Ridgeia* tubes measured in (A). Juveniles were not found in 1994; in 1995, washings contained many juveniles not attached to tubes;  $n = 85$  (1994),  $n = 276$  (1995).

and iron oxidizers (Fig. 4f); iron content (20–30% dry weight) was much higher than it was in the white mats.

Vestimentiferan tubeworms had colonized all active vents visited at Floc Site; their scattered distribution on pillow edges made collection difficult. Animal collections from two vents (HDV, Marker 2) yielded about 300 individuals in seven species. Only the vestimentiferan, an alvinellid polychaete and the nemertean occurred in abundance (Table 2). Tubeworms, *Ridgeia piscesae*, were up to 40 cm long (Fig. 5a) and, although two-thirds of the HDV specimens were immature, the gender of 22 of the 33 mature specimens could be distinguished. The five dissected mature specimens contained ripe gametes. Juveniles were plentiful and, although the size class under 1 cm length was not well represented, population size structure indicates continuous recruitment; many post-settlement juveniles (without tubes) were present in washings. "Shaved" branchial plumes on adults confirmed the predatory activity of polynoid polychaetes.

*Paralvinella pandorae*, deposit-feeding polychaetes attached to *Ridgeia* tubes, were anomalously large (maximum diameter 4.15 mm,  $x = 2.22$  mm) compared with collections from other Juan de Fuca sites, where the largest population mean width is 1.55 mm (McHugh, 1989, V. Tunnicliffe, unpublished data, 1995). The population size structure (Fig. 5b) indicates an ageing population in which most individuals appeared reproductively mature. Very few new recruits were found either on vestimentiferan tubes or among washings. On the white mats, near flowing hydrothermal fluid, a red nemertean was highly visible; this worm, of 2–3 cm length, is distinguished by unusually thick epidermal layers with embedded inorganic deposits (Rogers *et al.*, 1996).

#### July 1995

Flow Site had no active vents. The northern area at Floc Site had contracted to a swath 0.5 km along axis although maximum temperatures at the centre (HDV) had increased to 16°C. Floc release had ceased and the water column contained markedly less suspended matter. From 1994 to 1995, there was a significant drop in the average measured H<sub>2</sub>S/Fe ratio (from 180 to 66) at HDV, but there was no drastic change in the chemical character of the vented fluids (Fig. 3). Dives 2 km south located the extensive diffuse venting (to 6°C) that had been observed on towed instruments in 1994 (Marker 18; Fig. 1); initiation of venting at this site appears coincident with the eruption event affecting Floc and Flow sites judging by the extensive mats and the sparse animal recruitment.

Concentrations of microbes in Floc fluids did not change greatly from 1993 to 1995 at any of the sampled sites. However, where dense mat occurred (HDV and Marker 18) abundances were significantly higher (U-test;  $\alpha = 0.05$ ): counts from fluids over white mats averaged  $3.06 \times 10^6$  cells ml<sup>-1</sup> ( $n = 6$ ) compared with  $0.60 \times 10^6$  cells ml<sup>-1</sup> ( $n = 9$ ) in venting fluids with no mats. The 1995 faunal collections duplicated the two of 1994 within 1 m and added material from other vents. Biomass at HDV, along a crack of 30 m length, had increased. Alvinellid and polynoid polychaetes were abundant among the tubes, and the nemertean, a limpet and scale worms inhabited the mat. At HDV, *Ridgeia piscesae*, *Paralvinella pandorae* and the nemertean still dominated. Important additions were more polynoid predators, one copepod species and gastropods on tubes and rocks (Table 2). At least 16 species had colonized this site, most of which associate with *Ridgeia*. At three vents previously visited, mat and animals had all but disappeared. At the "dying" sites (Table 2), the suite of species was somewhat different. Marker 11 was dominated by limpets, a spionid

polychaete otherwise rare on Juan de Fuca, and an unknown harpacticoid copepod. At Markers 2 and 10, only the smallest tubeworms were still alive, and decaying sheaths marked the extinction of the alvinellid population. Majid crab and octopus predators were seen.

Twenty-four months post-eruption, *Ridgeia piscesae* tubes were up to 1.35 m long at HDV. The size represents a growth rate around 95 cm year<sup>-1</sup>, comparable with that of 9N EPR *Riftia pachyptila* (Lutz *et al.*, 1994). The abundance of post-settlement juveniles in the meiofauna and large numbers in small size classes (Fig. 5a) attest to active recruitment. The 1995 tubes were longer, but they were significantly smaller in width than those found in 1994. (Means tests with unequal variances: length  $t = 1.65$ , d.f. = 385,  $P = 0.015$ ; width  $t = 3.83$ , d.f. = 162,  $P < .01$ ,  $\alpha = 0.05$ .) Although trophosomes filled most of the tubes, space competition may have forced upward growth.

The population of polychaete *Paralvinella pandorae* differed markedly in 1995. Among thousands of individuals, fewer than 20 reached the mean size of the previous year; the 1994 year class was gone. Population structure had shifted to the smaller size classes (Fig. 5b) typical elsewhere on the ridge (McHugh, 1989). Mature egg sizes in both 1994 and 1995 specimens match sizes to 160  $\mu\text{m}$  reported by McHugh (1989). No released or brooded embryos could be found, although post-settlement juveniles (six-setiger stages) were present in the meiofauna in 1995. Alvinellid density was calculated by measuring the surface areas of vestimentiferan tubes from which the polychaetes were collected: 0.14 individuals cm<sup>-2</sup> in 1994 and 0.06 cm<sup>-2</sup> in 1995. Although packing density and individual biomass had diminished to about a half and third, respectively, of 1994 values, the greatly increased length and abundance of tubeworms sponsored a much greater overall abundance and biomass of polychaetes. A possible competitor, *Paralvinella palmiformis*, appeared in 1995—in low numbers but very large individual size. The mean 7.65 mm diameter ( $n = 14$ ) rivals the largest animals found among hundreds of individuals elsewhere on the ridge (McHugh, 1989; V. Tunnicliffe, unpublished data, 1995).

Chemical composition of high-temperature fluids at Source Site did not change significantly between 1993 and 1995. These vents appear unaffected by the volcanic event. The brine-like fluids (700 mmol kg<sup>-1</sup> Cl) have low H<sub>2</sub>S and Fe values for high-temperature vent fluids, indicative of a reaction zone temperature of approximately 300°C (Butterfield *et al.*, 1997). In 1995, a collection from one colonized chimney contained post-metamorphic larvae of many species in high abundances; the community was recently rejuvenated but many of these species had not colonized Floc Site. Notably absent at Source Site in all 3 years were the worms so abundant at Floc: *Paralvinella pandorae* and the nemertean (Table 2).

## DISCUSSION

The timing and sequence of events following the CoAxial eruption suggest causal links that may strongly influence the accumulation of vent biota. The connection is made through fluid and microbiotic properties. At the distal end of the dyke injection, hydrothermalism at Flow Site rapidly diminished, as confirmed by fluid observations. Although lava did not emerge at the shallower Floc Site, heat was diminishing more slowly and diffuse fluid chemistry is compatible with a persistent high-temperature reaction zone below the seafloor.

The evolution of hydrogen sulphide is of particular interest and may represent a distinctive post-eruption signature. The H<sub>2</sub>S/heat ratio peaked a year after the eruption:

from a maximum of  $1.2 \text{ nmol J}^{-1}$  in October 1993 to  $32 \text{ nmol J}^{-1}$  in 1994 to  $3.8 \text{ nmol J}^{-1}$  in 1995. This ratio showed the same behaviour with *in situ* SUAVE samples and the discrete water samples. Maximal values centre over HDV vent, suggesting the main vertical feeder dyke for the eruption lies below it. The  $\text{H}_2\text{S}/\text{heat}$  ratio was also high after the 9N EPR eruption, where it increased over the initial weeks measured (probably within a month or two of eruption) and remained high for a year: from the range  $8\text{--}23 \text{ nmol J}^{-1}$  in April 1991 to  $15.3 \pm 0.6 \text{ nmol J}^{-1}$  in March 1992 to  $5.8 \pm 0.4 \text{ nmol J}^{-1}$  in March 1994, as calculated from Von Damm *et al.* (1995).

The dyke injection induced a large blow-out of subterranean microbes, as deduced from "snowblowers" (Delaney *et al.*, 1994), hyperthermophile presence (Holden *et al.*, 1997) and sulphide oxidase activity levels in Flow mats (Juniper *et al.*, 1995). A subseafloor ecosystem could cause the post-eruption sulphide peak itself by microbial sulphate reduction, although direct evidence is lacking. Optimal conditions on the seafloor resulted in a large sulphide-oxidizer bloom at Floc Site. A similar phenomenon of dense mats was witnessed shortly after the 9N EPR event (Haymon *et al.*, 1993). However, at Flow Site, iron deposition swamped sulphide processes.

The role of microbes is probably the key to the rapid animal recruitment. The greatest animal recruitment occurred where microbial concentrations were the highest. Initial macrofaunal colonization took place as sulphide increased and this pulse of  $\text{H}_2\text{S}$  may be an important locator clue for nearby pelagic larvae. As early tubeworm larvae are feeding forms with no symbiotic microbes, it is suggested that vestimentiferans ingest the free-living form of their symbionts (Jones and Gardiner, 1988; Southward, 1988). Vestimentiferan larvae must have located and sequestered the requisite symbiont at Floc Site. Deposit-feeders had a ready food source; microbial filaments are observed in guts of several species (Tunnicliffe *et al.*, 1985; V. Tunnicliffe, personal observation). That hyperthermophiles have been cultured from guts of several vent species in low-temperature vent areas suggests an important role of these microbes, which probably come from a deeper source of higher temperature (Pledger and Baross, 1989).

CoAxial was colonized from a distal source as there was no local community apparent within the explored 15 km vicinity. The rapidity with which vent animals recruited to this site is extraordinary; a rough estimate of first colonization, assuming linear worm tube growth, is January 1994 or about 7 months after the eruption. *Ridgeia piscesae* occupies a wide range of vent habitats on northeast Pacific ridges, where it is found at every known vent site. High gene flow among sites indicates effective larval exchange (Southward *et al.*, 1995; Southward *et al.*, 1996). The 1994 size distribution suggests continual recruitment from afar. Its pelagic phase is unknown but the rapid recruitment at CoAxial adds to evidence that *Ridgeia piscesae* maintains a large pool of wide-ranging propagules over the ridge. Where rapid recruitment of vestimentiferans has been recorded elsewhere (Jollivet, 1993; Lutz *et al.*, 1994) potential parents were nearby: at 9N EPR the eruption did not kill all previous animals (Haymon *et al.*, 1993) and surviving adults may have contributed to the rapid recolonization.

The distribution of the polychaete *Paralvinella pandorae* is highly patchy on Juan de Fuca Ridge, the nearest known site being on Axial Seamount some 30 km south. This species has continual gamete production (McHugh, 1989), which should favour chance recruitment to new sites as seen here. Rapid colonization is seen on CoAxial in high abundance, but few juveniles were present in 1994 (Fig. 5b). The 1994 population profile suggests bulk transport of a single cohort with no sustained long-distance recruitment.

Concentrated patches of larvae could be transported in vortices shed from hydrothermal plumes (Mullineaux and France, 1995). The absence of the 1994 year class in 1995 gives the first indication of the life span of an alvinellid: less than 2 years. The second species, *Paralvinella palmiformis*, exhibits pulsed gametogenesis and recruitment (McHugh, 1989), characters consistent with its weak recruitment on CoAxial. The only other known occurrence of the nemertean and the stauromedusa is 150 km to the south on Cleft Segment, where they were collected shortly after a megaplume water signature suggested a recent eruptive event in 1986 (Baker *et al.*, 1987; Embley *et al.*, 1991); these species could be transient vent occupants.

Source Site, although close, is probably not the larval source. Many assemblage differences are evident in Table 2 such as the absence at Source of two abundant Floc species. Current data also do not support larval contributions from Source. The dominant bottom current field at Flow Site from August 1993 to April 1994 was south-south-east, at almost 90° to the ridge axis (Cannon *et al.*, 1995). Vector plots from another array near Floc Site (noted in Fig. 1) reveal only one period of current reversal, in November 1993, that could transport larvae even part way from Source to Floc (R. E. Thomson, unpublished data, 1996). These results suggest that another source site remains unlocated. Re-examination of SeaMarc images suggests that a parallel spreading valley exists to the northwest of Floc that remains to be explored for venting (Fig. 1).

The colonization rate at Coaxial rivals or exceeds that of other new habitats where distal colonization is required, such as new glacial streams (Milner, 1994), Mount St Helen's watershed (Steinman and Lamerti, 1988), or even nearshore marine fouling communities (Ardizzone *et al.*, 1989). High fecundity and dispersability must be a major adaptation in this group of vent animals, a subset of the entire ridge fauna. Several species are probably attracted by sulphide conditions that encourage associated microbes such as the microbes in the vestimentiferan in symbiosis, the commensals on limpet (*Lepetodrilus*) gills (De Burgh and Singla, 1984), and the mat microbes providing food for grazers such as the nemertean. Subsequently, *Ridgeia* is a key species for other species that seek the substratum (alvinellids and gastropods) or food (polynoids, hesionids) it provides. One-third of the 73 (Tunnicliffe and Fowler, 1996) species recorded on northeast Pacific vents had arrived by 1995. Among these species, several (nemertean, spionid, *Harmothoe*, harpacticoid and stauromedusa) are seen rarely elsewhere, suggesting adaptation to transient conditions or elimination in later stages of vent growth. Whereas *Benthoxynus* is by far the commonest copepod on Juan de Fuca, *Aphotopontius* shows greater abundance on CoAxial. The "termination" suite of species where vents ceased differed from the suite in active areas, suggesting a rapid succession. However, from this one event, we cannot distinguish a pioneer fauna from fortuitous recruitment of several species.

The CoAxial eruption is a relatively small event: megaplumes over southern Juan de Fuca were much larger (Baker *et al.*, 1987; Baker *et al.*, 1995a) and the 9N EPR heat output was sustained longer (Haymon *et al.*, 1993). If the present contraction continues, Coaxial will probably cool rapidly with hydrothermal output ceasing and no trace remaining of the emerging vent community in the next couple of years. At least one other small eruption occurred on CoAxial Segment in the past 15 years (Chadwick *et al.*, 1995), leaving no hydrothermal signature. Given that size and frequency of such events are probably negatively correlated (Embley *et al.*, 1995), ephemeral vent habitats probably play an important role in the adaptation and distribution of vent species. Because of the dynamics of faster-spreading ridge crests, most vent communities probably fail to reach stable or

equilibrium conditions (Juniper and Tunnicliffe, 1997). Such conditions would foster an opportunistic group of species with a ready larval supply that capitalizes on a blooming food source. "Sweepstakes" events, such as transient eddies containing larvae, may supply a different group of species. Many species will never colonize such ephemeral conditions. Examination of stable centres of hydrothermalism may determine if these areas sustain a larger pool of species whereas the "dynamic" ridges harbour few species with wider distributions and more general habitat requirements.

### CONCLUSION

This comprehensive record of ridge eruption, vent formation and colonization paints a remarkably dynamic picture of vent community succession initiated by a geological event. Microbial communities were established immediately, probably from a subsurface source; macrofauna arrived within a year despite no nearby source of recruits. The rapidity of exploitation of a newly available energy source by a complex community, including symbiotic associations, is extraordinary. Despite a habitat waning after only 2 years, growth and reproductive potential remained high. Such ephemeral habitats must be important in their contribution to a regional genetic reservoir. Further, as volcanic activity relates to spreading rate and habitat stability, eruptive frequency on a given ridge probably dictates the proportion of opportunistic species in the regional species pool.

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