Spatial and temporal patterns of colonization by deep-sea hydrothermal vent invertebrates on the Juan de Fuca Ridge, NE Pacific

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ABSTRACT: This study quantifies patterns in settlement and colonization of hydrothermal vent invertebrates and explores relationships with the biotic and abiotic factors that may influence these patterns. Colonization was measured between 2001 and 2003 in 2 segments of the Juan de Fuca Ridge, by deploying sets of basalt blocks at vents with different flow characteristics, over different spatial (cm to 100 km) and temporal (1 to 2 yr) scales. Spatial variation in colonization was greater between vents within a segment (m to km scale) than between segments, which we suggest reflects a species-specific response to varying environmental conditions at a particular vent. For gastropods, gregarious settlement enhanced colonization, while post-settlement mortality influenced colonization patterns of polychaetes. In 2003, we characterized the spatial variability in environmental conditions among 3 vent sites, through discrete *in situ* measures of the temperature and chemical properties of venting fluid near basalt blocks. Most colonist and settler abundances were positively correlated with vent fluid properties, notably dissolved H_2S and temperature. Our results suggest that the variation in settlement and colonization of hydrothermal vent species is mainly influenced by the properties of the vent fluid, but biological interactions can also have a significant influence on colonization processes. Our study is the first to experimentally quantify colonization by invertebrates at Juan de Fuca Ridge vent sites, and extends the understanding of the role of physical and biological factors in the regulation of early life-history stages.

KEY WORDS: Colonization · Settlement · Hydrothermal vent · Post-settlement mortality · Gregarious settlement · Temperature · Dissolved sulphide · Juan de Fuca Ridge

INTRODUCTION

Hydrothermal vents are model systems to study processes that regulate population dynamics, as they are amongst the most geologically dynamic regions on earth, and community extinctions and rebirths are common. Additionally, these regions are fragmented, as individual areas of active venting are often separated by hundreds of kilometres along the mid-ocean ridges. Dense invertebrate populations are maintained through the dispersal of larvae that must be able to cover great distances, find suitable substrates for settlement and recruit successfully. Thus, colonization is thought to be the consequence of a combination of the life-history strategies of

different species, the physical oceanographic processes affecting dispersal, biological interactions, and species responses to the dynamic hydrothermal environment (Lutz et al. 1980, Shank et al. 1998).

Invertebrate populations inhabiting hydrothermal vent habitats ultimately depend on the properties of the vent fluid for survival and growth, since reactions between vent fluids and oxygenated seawater provide the energy for chemosynthetic microbes (symbiotic and free-living) that are the primary producers of the ecosystem (Karl et al. 1980, Jannasch 1995, Tunnicliffe et al. 1997). Vent faunal species frequently experience large gradients in the physico-chemical conditions of the vent fluid that can vary over short time scales (hours

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to days) (Johnson et al. 1986, 1988a, Chevaldonne et al. 1991, Sarrazin et al. 1997), as well as frequent disturbance, chimney collapse or volcanic eruption (Tunnicliffe & Juniper 1990, Sarrazin et al. 1999). Consequently, environmental conditions have been considered the main factor regulating community structure at hydrothermal vents, and biological interactions can only influence this structure within the constraints imposed by environmental factors (Sarrazin et al. 1999, Luther et al. 2001). For example, changes in community structure coincide with disturbance events (local perturbations or eruptions), and consequent modifications in hydrothermal fluid flow (cessation or local reactivation) over sub-annual and/or sub-decadal time scales (Tunnicliffe & Juniper 1990, Sarrazin et al. 1997, Shank et al. 1998). However, several studies have suggested that biological interactions, such as competition, facilitation, predation and grazing, also contribute to the regulation of macrofaunal invertebrate populations (Van Dover et al. 1988, Tunnicliffe & Juniper 1990, Sarrazin et al. 1997, Tunnicliffe et al. 1997, Mullineaux et al. 2000, Micheli et al. 2002, Hunt et al. 2004).

Few studies to date have examined the importance of variation in settlement and recruitment at hydrothermal vents, due to the relative inaccessibility and current technological and logistical constraints of conducting manipulative experiments in these locations. Further, relationships between faunal distributions and the chemistry and temperature of hydrothermal vents has been explored in less than a handful of sites. Thus, it is unknown whether the same factors influence community structure of adults and earlier life-history stages. Van Dover et al. (1988) found that total recruitment was higher in active regions of vents, suggesting these conditions were most conducive to settlement and/or early survival of vent fauna. Mullineaux et al. (2003) showed that negative biological interactions were most prominent at vents where the fluid flux and faunal densities were highest, while positive interactions occurred at the low end of the fluid flux gradient where faunal densities were lower. However, measures of recruitment taken with coincident measures of temperature or chemical vent fluid composition are currently lacking.

In this study, we quantified settlement and colonization of invertebrates in hydrothermal vent habitats and identified biotic and abiotic factors in these habitats that may influence the patterns of settlement and colonization on the Juan de Fuca Ridge. Specifically, we used basalt blocks deployed at hydrothermal vents, at different spatial (cm to 100 km) and temporal (1 to 2 yr) scales, to quantify patterns and the sources of variation in settlement and colonization. We measured the temperature and chemical properties of venting fluid at these sites to examine the influence of fluid properties on colonization and settlement. Also, we used sequential and overlapping deployment periods of basalt blocks to identify potential intra-specific interactions that may regulate colonist abundances. This is the first study to experimentally quantify invertebrate colonization at Juan de Fuca Ridge hydrothermal vents.

MATERIALS AND METHODS

Study sites. The Juan de Fuca Ridge (JdFR) in the Northeast Pacific is located 400 to 500 km off the northwest coast of North America, at the junction of the Pacific and Juan de Fuca tectonic plates (from 44.5 to 48° N) (Lavelle & Cannon 2001). This study was conducted at 2 ridge segments separated by ~200 km: Axial Volcano off the Oregon Coast (46° N, 130° W; depth ca. 1400 m), and the Endeavour segment off the west coast of Vancouver Island (48° N, 129° W; depth ca. 2200 m). Colonization experiments were conducted at 2 vent sites within each ridge segment: (1) at Axial Volcano, the ROPOS vent site within the ASHES vent field (45° 55′ 59″ N, 130° 0′ 51″ W), and Cloud vent site ('Cloud$_{near}$': directly at the venting orifice; 'Cloud$_{far}$' 8 m away) located in the South Rift Zone (SRZ; 46° 56′ 00″ N, 129° 58′ 53″ W); and (2) at the Endeavour Segment, the Clam Bed vent site (47° 57′ 47″ N, 129° 5′ 19″ W), and the Smoke and Mirrors (SM) vent site, in the Main Endeavour field (47° 56′ 54″ N, 129° 05′ 54″ W) (Table 1, Fig. 1). Within each segment, pairs of vent sites are separated by ~2 km.

The terminology defined by Zal et al. (1995) is used to describe the hierarchical levels of hydrothermal vent distribution throughout the JdFR. 'Vent' refers to a single, localized emission of hydrothermal fluid; 'vent site' refers to a spatially continuous venting area containing several vent emissions (m scale) that are linked by subterranean ducts; a 'vent field' is a cluster of vent sites (100 m scale) undergoing the same temporal variations; and 'vent sectors' are the largest spatial units, corresponding to oceanic ridge segments (10 – 100s km scale).

Chemical characteristics of the vent sites. In 2003, discrete *in situ* measures of the temperature and chemical properties of venting fluid, were taken at Cloud, Clam Bed, and SM vent sites. Vent water samples were collected with titanium major samplers and with the Hydrothermal Fluid and Particle Sampler (HFPS) (Butterfield et al. 2004), and processed and analyzed as described in Lilley et al. (1993) and Butterfield et al. (1994, 2004). Total hydrogen sulphide (5% 2-sigma precision) and dissolved silicate (1%) were measured colorimetrically on board ship. Magnesium (0.5%), total dissolved iron (5%) and manganese (5%) were measured on shore.

Concentrations of chemical species in hydrothermal fluids are highly correlated with fluid temperature.

Table 1. Location, position, depth, year of deployment, and length of deployment of basalt blocks. Temperature (T) was measured at the level of the basalt blocks at time of recovery (maximum above ambient: Axial = 2.2°C; Endeavour = 1.9°C). nd: no data (not measured). SRZ: South Rift Zone; MEF: Main Endeavour Field; ASHES: Axial Seamount Hydrothermal Emissions Study vent field

Ridge/ Segment	Vent field	Vent site	Lat./long.	Depth (m)	Deployment period	Length of deployment (d)	T (°C)
Axial Volcano	ASHES	ROPOS	45° 55′ 59″ N /130° 00′ 50″ W	1550	2001–2002	362	nd
					2002–2003	409	8.5
					2001–2003	762	3.5
	SRZ	Cloud$_{near}$	45° 56′ 00″ N /129° 58′ 53″ W	1525	2001–2002	354	5.8
					2002–2003	410	5
					2001–2003	764	1
		Cloud$_{far}$		1525	2001–2002	354	0
					2001–2003	764	0
Endeavour segment	500 m S of High Rise	Clam Bed	47° 57′ 47″ N /129° 05′ 19″ W	2190	2002–2003	357	nd
					2001–2003	822	6
	MEF	Smoke and Mirrors	47° 56′ 54″ N /129° 05′ 19″ W	2200	2002–2003	350	nd
					2001–2003	815	3

Because we compare vents with a wide range in temperature, we measured vent fluid properties that reflected both the intensity of venting (e.g. maximum temperature) and those largely independent of mixing or intensity (e.g. ratio of dissolved Si or Mn to heat content). Additionally, H_2S and Fe are affected by high-temperature processes and by precipitation and redox reactions in the shallow mixing zone supplying low-temperature vents, producing strong water column signals proximal to vent sites, and are biologically important as the substrates for chemosynthesis for free-living or symbiotic micro-organisms.

Excess chemical properties (measured concentration – background concentration) were normalized to heat content [heat capacity × (vent temperature – background seawater temperature)] of vent fluid (μmol kJ^{-1}). Using heat-normalized chemical properties provides a better measure of the underlying chemical character of the venting fluid, rather than the amount of mixing taking place during sampling. This method is also more
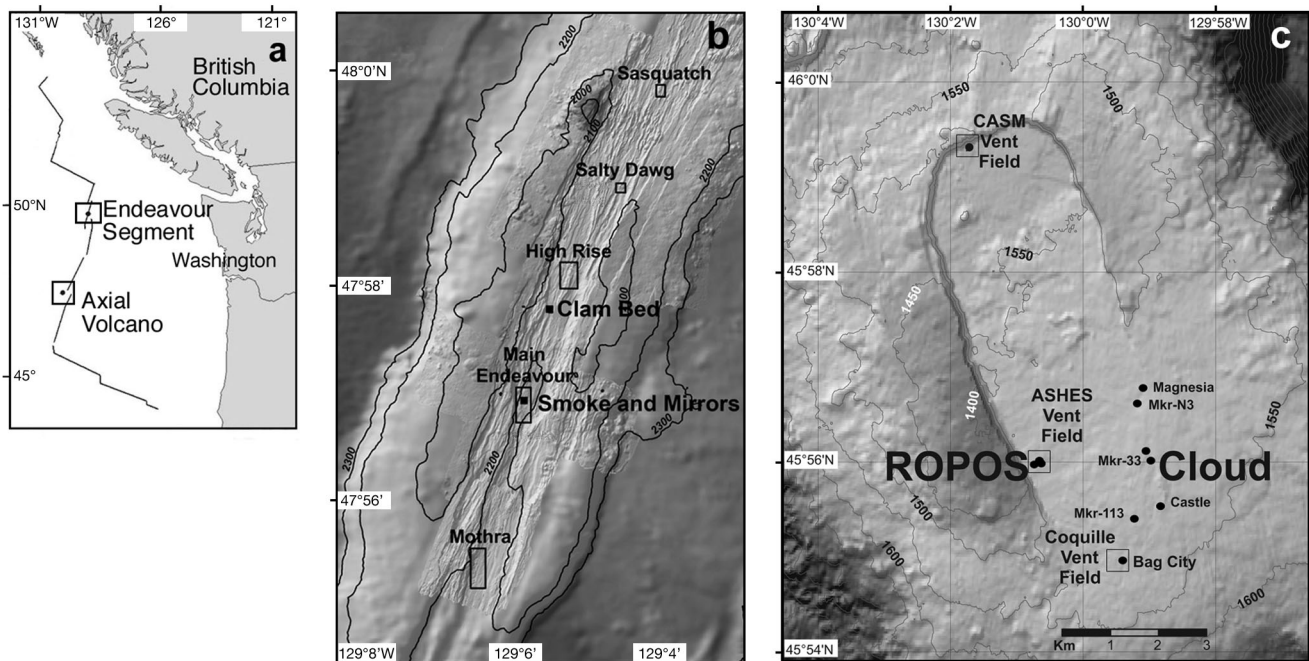

Fig. 1. (a) Location of Juan de Fuca Ridge, showing positions of Axial Volcano and Endeavour Segment. (b) Endeavour Segment, showing locations of Clam Bed and Smoke and Mirrors vent sites. Adapted from Glickson et al. (2007). (c) Axial Volcano, showing positions of ROPOS and Cloud vent sites

directly tied to the effective chemical/heat anomalies produced in the hydrothermal plume. Maximum vent temperature (°C) was measured directly at exit point. For SM, which was sampled with a titanium major sampler, the highest temperature in the vent orifice measured near the time of sampling was combined with the end-member concentration (measured value extrapolated to zero Mg concentration to remove the entrained seawater component). For all other vents, the average chemical concentration measured and the corresponding average in-line fluid temperature anomaly recorded by HFPS during sampling were used to calculate the property-to-heat ratio directly.

Experimental design and sample collection. Colonization was measured between 2001 and 2003, on blocks made of solid basalt collected from a talus pile in Nova Scotia, Canada (45° 11′ 15″ N, 64° 27′ 04″ W). Basalts were selected to maintain a similarity in surface roughness and cut to a standard size (~7 × 10 × 2 cm). For ease of deployment and recovery with the remotely operated vehicle (ROV) 'ROPOS', blocks within a vent site were attached to a single galvanized steel frame with a 20 cm galvanized steel threaded rod and held in plastic containers with holes pierced on the underside allowing for the diffusion of fluid through (or around) the substrate. Blocks within each frame were not in contact, and thus provide independent replicates (Fig. 2). We attempted to manipulate access by grazers and immigrants. Smooth polyethylene tubes covering the rod allowed grazer access, whereas an inverted funnel filled with Tanglefoot™ (tree resin) in combination with the uncovered threaded rod prevented immigrants from accessing the substrate. The position of each block was assigned randomly within a frame. We did not detect a significant difference in the number of colonists

between 'grazer access' treatments for any species. Thus, replicate blocks on a frame were pooled across these treatments for all other analyses.

Sets of basalt blocks were deployed in pairs in 2001 at each vent site (Table 1). For each vent site, one set was collected after 1 yr (in 2002) and replaced with a set of clean, uncolonized blocks. All remaining blocks were collected after 2 yr (in 2003). While we were restricted to deployment periods of 1 yr intervals, we argue that a year is a sufficient period to allow for multiple episodic settlement and colonization events to occur. A preliminary deployment of a set of blocks for 1 wk in 2001 at Axial Volcano yielded no settlers (A. Metaxas pers. obs.). Van Dover et al. (1988) found few recruits on hard blocks after 26 d, but observed 'significant recruitment' after 260 d. Thus, the temporal scale in our study maximizes the probability of colonization, although it does not allow for high temporal resolution of post-settlement interactions.

Due to inclement weather conditions at Endeavour during the 2002 cruise, the blocks were not recovered, but uncolonized blocks were deployed. Consequently, we do not have colonization data for 2001–2002 at Clam Bed and SM. Also, the loss of 3 basalt blocks at SM (2002–2003) and one block from ROPOS (2001–2002) reduced the number of replicates at these vent sites.

For recovery, each set of blocks was gently placed in a LEXAN lidded box (~80 × 60 × 35 cm), previously positioned within 0.5 to 1 m of the frame on the ocean floor. On the underside of the box lid, a glued 5 cm layer of open cell foam ensured a snug fit, preventing the dislodgment of organisms from the blocks during transport. Upon recovery, individual blocks (and the corresponding section of foam overlying the block) were removed from the frame, frozen at −80°C aboard

Fig. 2. *In situ* photographs of colonization substrates deployed on the Juan de Fuca Ridge from 2001–2003. Left panel: Clam Bed, Endeavour Segment; Right panel: Cloud vent (Cloud$_{near}$), Axial Volcano

ship and then transferred into 95% ethyl alcohol for long-term storage. Since knowledge of vent species biology is poor, and a conventional recruitment stage could not be identified for most species, we defined as colonists the accumulated number of post-larval staged individuals at the end of the recovery period of the blocks. All individuals on a block were enumerated and identified to the highest possible taxonomic resolution. Colonization was quantified for the 5 most abundant species (species containing >10% of total numbers for >50% of substrates) as abundance per unit surface area of basalt. Point measurements of fluid temperature (°C above ambient) were taken with the ROV 'ROPOS' temperature probe (± 1°C) at the level of the blocks during recovery (Table 1).

Statistical analyses. To quantify the sources of both spatial and temporal variation, for the 5 most abundant species of colonists, we used the 1 yr deployments (2001–2002 and 2002–2003) from Axial Volcano. Using MANOVA with factors Vent (fixed) and Year (random), spatial comparisons were made over 2 scales: (1) within each vent site at ROPOS, and Cloud$_{near}$ (cm to m scale); and (2) among these vent sites within Axial Volcano (km scale). Spatial comparisons were done over 3 scales, using a nested MANOVA design with Vent (random) nested within Segment (fixed) and the 2002–2003 and 2001–2003 deployments: (1) within ROPOS, Cloud$_{near}$, Clam Bed, and SM vent sites (cm to m scale); (2) between these vent sites within segments (ROPOS and Cloud$_{near}$ at Axial; Clam Bed and SM at Endeavour) (km scale); and (3) between segments (100 km scale). Prior to all analyses, colonization data were square-root transformed to remove heterogeneity of variances, as detected by Levene's test.

The effect of distance from venting on colonization was examined at Cloud vent site by comparing basalt blocks from Cloud$_{near}$ (<1 m) and Cloud$_{far}$ (10 m) using 1-way MANOVA, with Distance as a fixed factor. Separate MANOVAs were done for the 2002–2003 (5 species) and 2001–2003 (6 species) deployment periods. Prior to analysis, colonization data were ln(x+1)-transformed to reduce heterogeneity of variances.

Settlement was quantified for 2 gastropod species, *Lepetodrilus fucensis* and *Depressigyra globulus*, by enumeration of individuals in the protoconch stage, defined as those that did not possess a post-larval shell. As for colonists, settlers were enumerated and quantified as abundance per unit surface area of basalt. Spatial and temporal patterns of gastropod settlers were analysed similarly to colonists, except using a nested ANOVA for each gastropod species instead of MANOVA. Prior to analysis, settler abundance was ln(x+1)-transformed to remove heterogeneity of variances. We did not observe larval stages of any other species on the basalt block surfaces.

For all MANOVAs, ANOVAs for each species were conducted if MANOVA indicated significant differences within species. Tukey's Honestly Significantly Difference (HSD) post-hoc tests were used to examine differences as detected by ANOVA. Where sample sizes were unbalanced, geometric instead of arithmetic means were used in post-hoc testing.

To explore the influence of intraspecific biological factors on colonization patterns, the sum of the colonists from the two 1 yr basalt blocks (consecutive) was compared to the single 2 yr colonization blocks (continuous) placed at the same vent site (as in Mullineaux et al. 2003). If the sum of the mean abundance of colonists on blocks in the 2 consecutive 1 yr deployments (2001–2002 plus 2002–2003) is not different than the abundance in the continuous 2 yr deployment (2001–2003), then colonization variability is mainly determined by processes affecting larvae in the plankton or at settlement, but not after settlement. This hypothesis serves as our null model. If the sum of the abundance of colonists in the consecutive deployments is significantly greater than the abundance in the continuous deployment, negative interactions such as post-settlement mortality are considered to be regulating colonization patterns. However, if the sum of the abundance of colonists in the consecutive deployments is lower than in the 2 yr continuous deployment, then colonization variability is considered to be mainly regulated by positive interactions, such as gregarious settlement (i.e. larvae settle close to juveniles or adults). For each of the 5 most abundant species, one-sample *t*-tests were used to compare abundance of colonists on the blocks from the continuous 2 yr deployment to the sum of mean abundance in the two 1 yr deployments, for ROPOS and Cloud vent sites. To make these comparisons, we assumed there was no variation in initial settlement between paired block deployments at the same vent.

For 2 gastropod species, *Lepetodrilus fucensis* and *Depressigyra globulus*, the influence of neutral, positive and negative intraspecific effects were further explored by linear regression of number of settlers against number of colonists, for Cloud, ROPOS, and Clam Bed vent sites. SM vent site was not included, because of the low numbers of settlers collected. Prior to regression, abundances of settlers and colonists were ln(x+1)-transformed to remove heterogeneity of variances. If there is no relationship between colonization and settlement, larvae settle randomly relative to conspecifics.

RESULTS

A total of 27 taxa colonized the basalt blocks, but only 7 were present at all vents. The gastropod *Lepetodrilus fucensis* was the most abundant, while the gastropods

Table 2. Mean abundance (per 100 cm^2) ± (SE) of taxa found on basalt blocks deployed from 2001–2002, 2002–2003, and 2001–2003 at ROPOS and Cloud vent sites (Axial Volcano), and Clam Bed and Smoke and Mirrors vent sites (Endeavour), along the Juan de Fuca Ridge, NE Pacific. n: no. of replicate basalt blocks in each vent site and deployment year

| Taxonomy | Axial | | | | | | | | Endeavour | | | |
| | ROPOS | | | Cloud$_{near}$ | | | Cloud$_{far}$ | | Clam Bed | | Smoke and Mirrors | |
	2001–2002 (n = 7)	2002–2003 (n = 8)	2001–2003 (n = 8)	2001–2002 (n = 8)	2002–2003 (n = 8)	2001–2003 (n = 8)	2001–2002 (n = 8)	2001–2003 (n = 8)	2002–2003 (n = 8)	2001–2003 (n = 8)	2002–2003 (n = 5)	2001–2003 (n = 8)
Gastropoda												
Lepetodrilus fucensis (protoconchs)	29.8 ±10.8	344.5 ±55.7	457.7 ±95.3	58.9 ±31.4	468.3 ±82.6	557.7 ±150.9	0	0.4 ±0.4	105.4 ±32.4	2037.8 ±507.7	1.1 ±1.1	1.0 ±0.6
Lepetodrilus fucensis (colonists)	93.1 ±26.6	96.3 ±12.5	493.7 ±123.0	98.6 ±22.7	317.8 ±28.3	478.0 ±133.6	0.2 ±0.2	1.0 ±0.5	87.8 ±14.2	702.9 ±157.1	15.8 ±7.6	14.9 ±4.1
Depressigyra globulus (protoconchs)	6.9 ±6.9	11.8 ±10.3	4.8 ±1.9	2.7 ±0.5	8.1 ±2.0	6.9 ±1.5	0	0	54.7 ±15.11	184.2 ±51.2	1.0 ±0.5	1.4 ±0.6
Depressigyra globulus (colonists)	20.2 ±9.9	31.9 ±5.9	39.4 ±8.2	8.5 ±2.2	32.3 ±8.5	31.2 ±5.4	0	0	16.2 ±2.6	425.0 ±49.0	2.7 ±0.6	2.7 ±0.9
Provanna variabilis	4.4 ±0.9	13.0 ±1.4	39.43 ±4.8	0.8 ±0.3	2.3 ±0.7	2.7 ±0.8	0.2 ±0.2	0.1 ±0.1	4.6 ±1.3	10.1 ±1.4	3.7 ±3.1	2.9 ±0.5
Hyalogyrina globularis	0.4 ±0.4	0	0	0	0	0	0	0	1.1 ±0.6	28.7 ±6.8	0	0
Clypeosectus curvus	0	0	0	0.4 ±0.2	0.2 ±0.1	0.1 ±0.1	0	0	0.2 ±0.1	0.3 ±0.2	0	0.1 ±0.1
Pyropelta musaica	0.1 ±0.1	0	0.4 ±0.2	0	0	1.1 ±0.7	0	0.5 ±0.5	0	0	0	0
Buccinum sp.	0	0	0	0	0	0	0	0	0	0	0	0.1 ±0.1
Melanodrymia brightae	0	0	0	0	0	0	0	0	0	0.1 ±0.1	0	0
Bivalvia												
Unidentified bivalve spp.	1.3 ±0.7	1.1 ±0.2	0.7 ±0.4	0.4 ±0.2	0.2 ±0.1	0.5 ±0.2	0	0	0.3 ±0.2	0.7 ±0.4	0	0
Aplacophora												
Helicoradomenia juani	0	0	0	0	0	0	0	0	1.4 ±0.5	43.5 ±12.6	0	0.7 ±0.4
Polychaeta												
Amphisamytha galapagensis	58.2 ±8.6	25.5 ±3.5	33.4 ±4.3	17.6 ±3.6	14.2 ±2.1	22.8 ±4.9	0.2 ±0.1	0.8 ±0.4	37.1 ±3.2	145.7 ±26.2	7.8 ±2.8	29.4 ±4.0
Parougia wolfi	3.1 ±1.0	1.4 ±0.4	1.2 ±0.5	0.3 ±0.2	1.0 ±0.4	0.5 ±0.2	0.2 ±0.1	0	0	0.1 ±0.1	0	0
Ophryotrocha globopalpata	1.0 ±0.5	0.3 ±0.2	0.1 ±0.1	0	0	0	0	0	0.2 ±0.1	1.2 ±0.7	0	0
Protomystides verenae	0	0.1 ±0.1	0.2 ±0.2	0	0	0	0	0	0	0	0	0
Nereis piscesae	0	0.1 ±0.1	0	0	0	0	0	0	0	0	0	0
Hesiospina vestimentifera	0	0.1 ±0.1	0	0.1 ±0.1	0	0	0	0	0	0	0	0
Branchinotogluma sp.	0.4 ±0.3	0.1 ±0.1	0.3 ±0.2	0	0.1 ±0.1	0.1 ±0.1	0	0	0.1 ±0.1	0.4 ±0.2	0.2 ±0.2	0.1 ±0.1
Lepidonotopodium piscesae	0	0	0.1 ±0.1	0	0	0.1 ±0.1	0	0	0.5 ±0.3	0.4 ±0.3	0	0
Levensteiniella kincaidi	0	0	0.1 ±0.1	0	0	0	0	0	0	0	0	0
Branchinotogluma tunnicliffeae	0	0.1 ±0.1	0	0	0	0	0	0	0	0	0	0
Vestimentifera												
Ridgeia piscesae	0	0	0	0	0	0	0	0	0	0.3 ±0.3	0	0
Pycnogonida												
Ammothea verenae	0	0.2 ±0.2	0.3 ±0.2	0	0.1 ±0.1	0	0	0	0	0	0	0
Sericosura venticola	0	0	0	0	0	0	0	0	0.5 ±0.2	4.0 ±1.6	0	0

Table 2. (continued)

Taxonomy	Axial								Endeavour			
	ROPOS			Cloud$_{near}$			Cloud$_{far}$		Clam Bed		Smoke and Mirrors	
	2001–2002 (n = 7)	2002–2003 (n = 8)	2001–2003 (n = 8)	2001–2002 (n = 8)	2002–2003 (n = 8)	2001–2003 (n = 8)	2001–2002 (n = 8)	2001–2003 (n = 8)	2002–2003 (n = 8)	2001–2003 (n = 8)	2002–2003 (n = 5)	2001–2003 (n = 8)
Acarina												
Copidognathus papillatus	0	0	0	0	0	0	0	0	0.1 ±0.1	0.4 ±0.2	0.9 ±0.7	5.0 ±1.4
Ostracoda												
Unidentified ostracod spp.	2.8 ±0.9	1.0 ±0.3	7.2 ±3.8	0.2 ±0.1	2.3 ±0.6	3.2 ±0.5	0	0.4 ±0.2	16.3 ±3.8	106.8 ±38.9	0	3.5 ±1.1
Copepoda												
Unidentified copepod spp.	5.5 ±1.7	5.2 ±1.1	21.8 ±6.2	4.6 ±1.3	7.7 ±1.5	4.4 ±1.3	0.1 ±0.1	0.1 ±0.1	13.2 ±3.9	412.3 ±125.2	0.9 ±0.7	2.2 ±1.1
Ophiuroidea												
Unidentified ophiuroid spp.	0.1 ±0.1	0	0	0	0	0	0	0	0	0	0	0

Depressigyra globulus and *Provanna variabilis*, and the polychaetes *Amphisamytha galapagensis* and *Parougia wolfi*, were also abundant, although usually one to two orders of magnitude less so than *L. fucensis*. Nine taxa were present at only 1 vent (Table 2). It is possible that a few individuals of mobile species may have migrated onto or away from the blocks during deployment. However, most mobile colonists recovered from the blocks were small, juvenile stages, implying their origin as settlement to the blocks rather than immigration. Species >1.5 mm were easily viewed in digital images of block surfaces taken immediately prior to recovery. Of the species visible in digital images, counts of all individuals on blocks after recovery were higher than counts of all individuals *in situ* prior to recovery leading to the conclusion that few to no individuals were lost from the surfaces of the blocks, from all vents and deployment periods, during recovery.

Patterns in settlement

Gastropod settlement varied spatially and temporally for both *Lepetodrilus fucensis* and *Depressigyra globulus* (Fig. 3). At Axial Volcano, settlement of *L. fucensis* varied between years but not between vents, while settlement of *D. globulus* varied between vents and years (Fig. 3, Table 3). For both the 2002–2003 and 2001–2003 deployment periods at Axial and Endeavour, settlement of *L. fucensis* and *D. globulus* varied among vents within segments, but not among segments (Fig. 4, Table 4).

Patterns in colonization

At Axial Volcano, colonization varied spatially and temporally for 4 of the 5 most abundant species examined (Table 5). There were significant Vent × Year interactions for *Lepetodrilus fucensis*, *Provanna variabilis*, and *Amphisamytha galapagensis* (Fig. 5a). However, the pattern of variation between vents and years was not consistent among these 3 species (Fig. 5a, Table 5). *L. fucensis* colonist abundance was greatest at Cloud in 2002–2003, but was not different
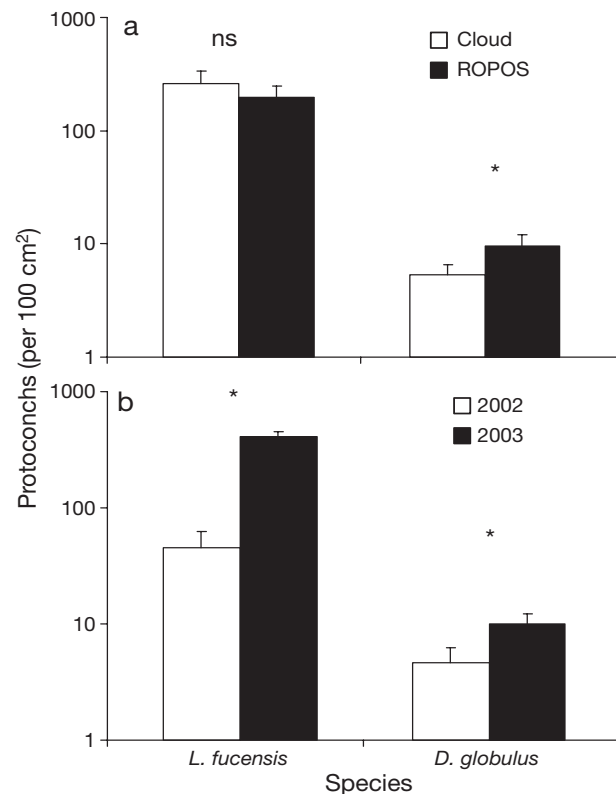

Fig. 3. *Lepetodrilus fucensis* and *Depressigyra globulus*. Abundance of settlers (mean + SE) on basalt blocks collected (a) from ROPOS and Cloud vent sites, Axial Volcano and (b) in 2002 and 2003. ns: no significant differences; (∗) significant differences in settlement. n given in Table 2

Table 3. *Lepetodrilus fucensis* and *Depressigyra globulus*. F-values of univariate analyses of variance (ANOVA) examining the spatial and temporal variation within a segment in settlement (no. of protoconchs) of *L. fucensis* and *D. globulus* between ROPOS and Cloud vent sites for the 2001–2002 and 2002–2003 deployment periods. df: degrees of freedom, *p < 0.05, **p < 0.01, ***p < 0.001

Species	Factor					
	Vent		Year		Vent × Year	
	F	df	F	df	F	df
L. fucensis	3.01	1,1	55.97***	1,27	0.06	1,27
D. globulus	196.0*	1,1	9.580**	1,27	0.01	1,27

Table 4. *Lepetodrilus fucensis* and *Depressigyra globulus*. F-values of univariate analyses of variance (ANOVA) examining the sources for spatial variation between segments in settlement (no. of protoconchs) among ROPOS, Cloud, Clam Bed and Smoke and Mirrors vent sites within Axial and Endeavour segments for the 2002–2003 and 2001–2003 deployment periods. df: degrees of freedom; *p < 0.05, **p < 0.01, ***p < 0.001

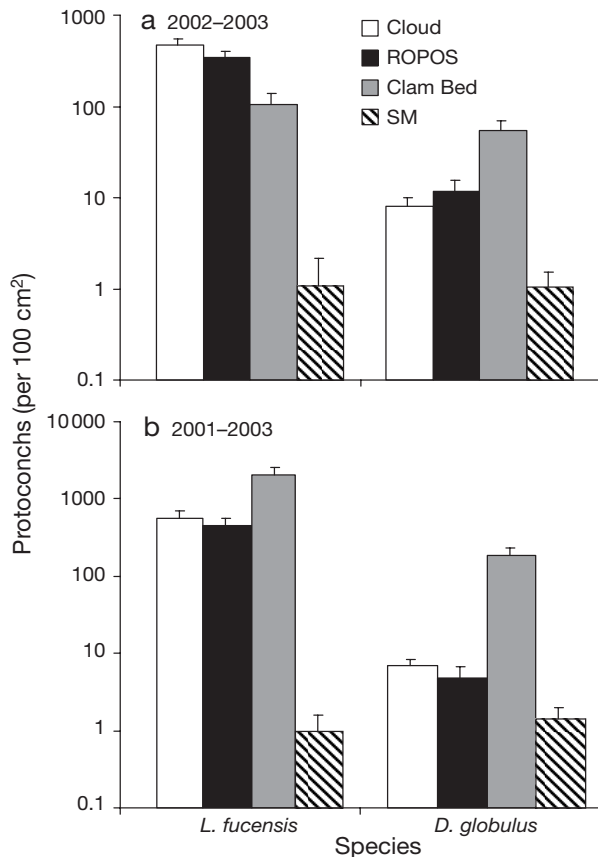| Species	Deployment year	Factor			
		Segment		Vent (Segment)	
		F	df	F	df
L. fucensis	2002–2003	2.753	1,2	41.21***	2,25
	2001–2003	0.459	1,2	88.95***	2,28
D. globulus	2002–2003	0.048	1,2	33.51***	2,25
	2001–2003	0.245	1,2	31.55***	2,28

Fig. 4. *Lepetodrilus fucensis* and *Depressigyra globulus*. Abundance of settlers (mean + SE) on basalt blocks deployed at vents sites at Axial Volcano: ROPOS, Cloud; and Endeavour segment: Clam Bed, Smoke and Mirrors (SM), collected in 2003 after (a) 1 yr (2002–2003) and (b) 2 yr deployment (2001–2003). n given in Table 2

at ROPOS between years, nor between ROPOS and Cloud in 2001–2002. For *P. variabilis*, colonist abundance did not vary between years at Cloud, but was greater in 2002–2003 than 2001–2002 at ROPOS, and was greater at ROPOS than at Cloud in both years. *A. galapagensis* colonist abundance was significantly greater at ROPOS than Cloud in both years, did not

vary between years at Cloud, but was greater in 2001–2002 than 2002–2003 at ROPOS. For *Depressigyra globulus* and *Parougia wolfi* there were no significant interactions between Vent and Year. The abundance of *D. globulus* or *P. wolfi* colonists did not vary between ROPOS and Cloud in either year (Fig. 5b). Number of colonists of *D. globulus* was significantly greater in 2002–2003 than in 2001–2002, but there was no difference in the number of colonists of *P. wolfi* between years (Fig. 5b,c).

Abundance of the numerically dominant colonists varied spatially between vents within segments, but not between segments. For the 2002–2003 deployment period, there were significant effects both of Vent within Segment and between Segments (Table 6). For *Lepetodrilus fucensis*, *Depressigyra globulus*, *Provanna variabilis*, and *Amphisamytha galapagensis*, the numbers of colonists varied among vents within segments but not between segments, whereas the opposite was observed for *Parougia wolfi* (Fig. 6a, Table 6). Over the 2001–2003 deployment year, colonization also varied significantly between Segments, and among Vents within Segments (Fig 6b). However, nested ANOVA did not reveal a significant effect of segment for any species, and number of colonists varied with Vent within Segment for all species, except *P. wolfi* (Fig. 6b, Table 6).

Proximity to hydrothermal vent fluid at Cloud vent site had a significant effect on the number of colonists during both the 2001–2002 and 2001–2003 deployment periods (Table 7). Numbers of colonists was significantly greater at Cloud$_{near}$ than Cloud$_{far}$ locations for *Lepetodrilus fucensis* and *Amphisamytha galapagensis* in both 2001–2002 and 2001– 2003 (Fig. 7, Table 7). Neither *Provanna variabilis* nor *Parougia wolfi* showed differences in number of colonists with increasing distance from the vent source after 1 yr (2001–2002), but there was a significant dif-
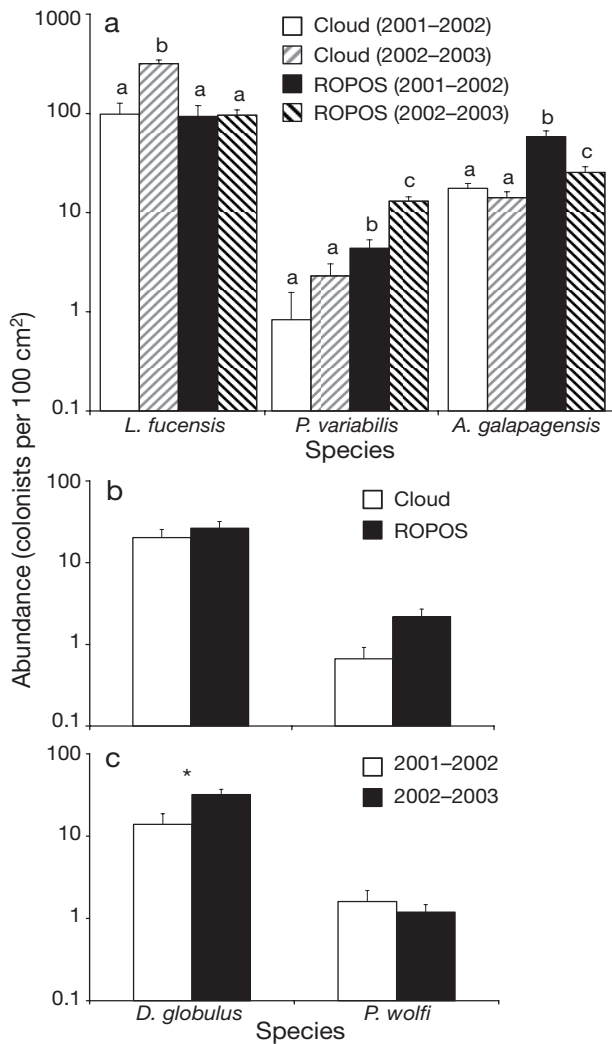
Fig. 5. (a) *Lepetodrilus fucensis*, *Provanna variabilis* and *Amphisamytha galapagensis*, (b) and (c) *Depressigyra globulus and Parougia wolfi*. Spatial and temporal variation in colonization abundance (mean + SE) for the 5 most abundant species found on basalt blocks deployed at ROPOS and Cloud vent, Axial Volcano, between 2001–2002 and 2002–2003 deployment periods. (a) Significant interactions between vent sites (ROPOS, Cloud) and deployment years (2001–2002 and 2002–2003). Different letters over bars indicate significant difference in colonization within a species (Tukey's HSD, p < 0.05). Abundance is pooled across (b) deployment years (2001–2002 and 2002–2003) and (c) vent sites (ROPOS, Cloud) because of the lack of a significant interaction. *significant difference. n given in Table 2

Table 5. *Lepetodrilus fucensis, Provanna variabilis, Amphisamytha galapagensis, Depressigyra globulus* and *Parougia wolfi*. F-values of MANOVA (Wilk's λ) and ANOVA examining the spatial and temporal variation in colonization of the 5 most abundant species among ROPOS and Cloud vent sites for the 2001–2002 and 2002–2003 deployment periods. All: MANOVA results; individual species: ANOVA results; df: degrees of freedom; *p < 0.05, **p < 0.01, ***p < 0.001

| Species | Factor | | | | | |
| | Vent | | Year | | Vent × Year | |
	F	df	F	df	F	df
All	19.52***	5, 23	12.56***	5, 23	5.18**	5, 23
L. fucensis	1.221	1, 1	18.47***	1, 27	13.30**	1, 27
D. globulus	1.702	1, 1	10.48**	1, 27	0.372	1, 27
P. variabilis	8.739	1, 1	23.98***	1, 27	6.928*	1, 27
A. galapagensis	4.579	1, 1	11.78**	1, 27	6.974*	1, 27
P. wolfi	2.145	1, 1	0.231	1, 1	4.150	1, 27

Table 6. *Lepetodrilus fucensis, Provanna variabilis, Amphisamytha galapagensis, Depressigyra globulus* and *Parougia wolfi*. F-values of significant MANOVA (Wilk's λ) and ANOVA examining the sources for spatial variation in colonization of the 5 most abundant species among ROPOS, Cloud, Clam Bed and Smoke and Mirrors vent sites within Axial and Endeavour segments for the 2002–2003 and 2001–2003 deployment periods. All: MANOVA results; individual species: ANOVA results; df: degrees of freedom; *p < 0.05, **p < 0.01, ***p < 0.001

| Species | Factor | | | |
| | Segment | | Vent (Segment) | |
	F	df	F	df
2002–2003				
All	19.92***	5, 21	15.27***	10, 42
L. fucensis	1.72	1, 2	43.72***	2, 25
D. globulus	4.87	1, 2	4.13*	2, 25
P. variabilis	0.31	1, 2	12.38***	2, 25
A. galapagensis	0.05	1, 2	26.21***	2, 25
P. wolfi	46.54*	1, 2	0.47	2, 25
2001–2003				
All	22.63***	5, 24	39.23***	10, 48
L. fucensis	0.34	1, 2	18.69***	2, 28
D. globulus	0.32	1, 2	139.93***	2, 28
P. variabilis	0.39	1, 2	85.91***	2, 28
A. galapagensis	1.08	1, 2	22.95***	2, 28
P. wolfi	6.84	1, 2	1.29	2, 28

ference after 2 yr (2001–2003). There was no significant difference in number of colonists of *Pyropelta musaica* between Cloud$_{near}$ and Cloud$_{far}$ in 2001–2003. *Depressigyra globulus* was only found at Cloud$_{near}$ distances in both deployment periods (Fig. 7).

Variation in the composition of hydrothermal vent fluids was evident among 3 vent sites (Cloud, Clam Bed and SM) in 2003 (Table 8). For these vent sites, the abundances of *Depressigyra globulus*, *Provanna variabilis*, and *Amphisamytha galapagensis* colonists, and *Lepetodrilus fucensis* and *D. globulus* settlers, were positively correlated, while abundance of *Parougia wolfi* was negatively correlated, with most vent fluid properties (Table 9).
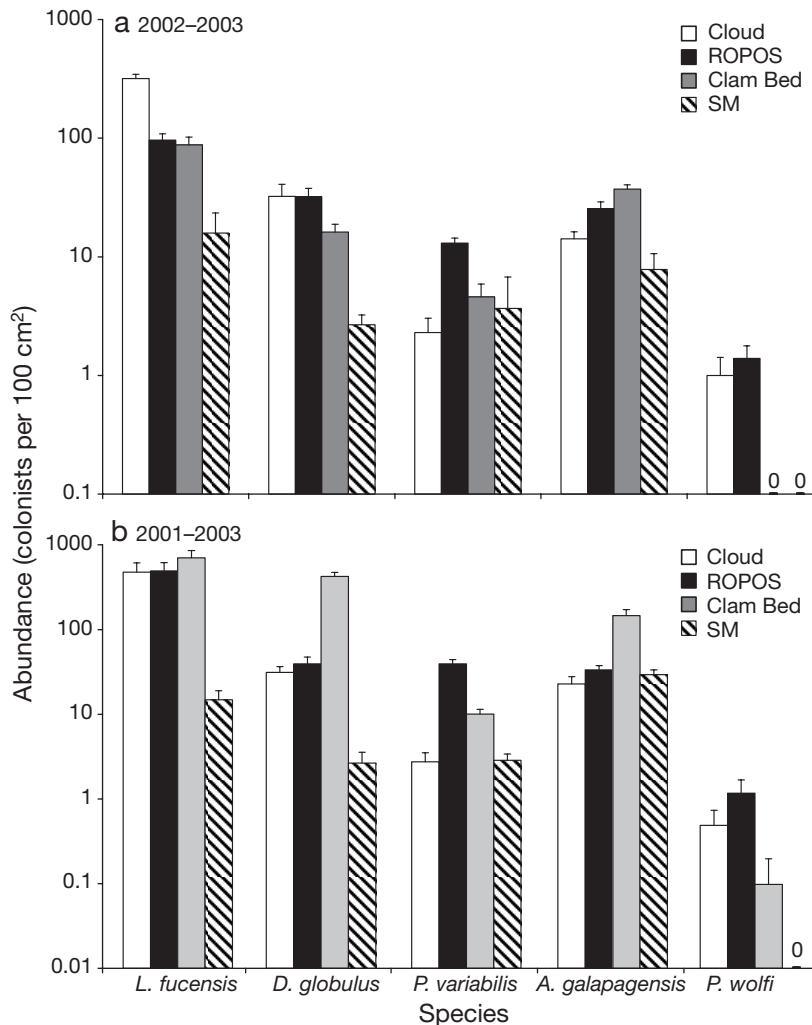
Fig. 6. *Lepetodrilus fucensis, Provanna variabilis, Amphisamytha galapagensis, Depressigyra globulus* and *Parougia wolfi.* Abundance of colonists (mean + SE) for the 5 most abundant species found on basalt blocks deployed at vents sites at Axial Volcano: ROPOS, Cloud; and Endeavour Segment: Clam Bed, Smoke and Mirrors (SM), for (a) the 2002–2003 deployment period and (b) for the 2001–2003 deployment period. n given in Table 2

Intraspecific influences on colonization

According to our hypotheses, positive intraspecific interactions were indicated if the sum of the mean abundance of colonists from the consecutive 1 yr deployments was significantly lower than the mean abundance of colonists from the continuous 2 yr deployment. In contrast, if the summed abundance from the consecutive deployments was significantly greater than the continuous deployment, negative interactions were indicated in regulating colonization patterns. Neutral interactions, such that there was no significant different in the summed abundance from the consecutive deployments compared to the continuous deployment, served as our null model. Intraspecific interactions influenced the pattern of colo-

nization of 4 of the 5 most abundant species at ROPOS, but not at Cloud vent site at Axial Volcano (Fig. 8, Table 10). At Cloud vent site, neutral interactions were indicated to be regulating the abundance of *Lepetodrilus fucensis*, *Depressigyra globulus*, *Provanna variabilis*, or *Amphisamytha galapagensis* colonists (Fig. 8a). In contrast, at ROPOS vent site, positive interactions were indicated for both *L. fucensis* and *P. variabilis*, a neutral interaction was indicated for *D. globulus*, and negative interactions indicated for *A. galapagensis* (Fig. 8b). Negative interactions were indicated for *Parougia wolfi*, at both Cloud and ROPOS vent sites.

For *Lepetodrilus fucensis*, there was a significant positive linear relationship between abundance of settlers and abundance of colonists for all vent sites tested (Fig. 9). For *Depressigyra globulus*, there was a significant positive linear relationship between settlers and colonists for Cloud, but not for ROPOS or Clam Bed (Fig. 9).

DISCUSSION

Faunal composition

Gastropods and polychaetes were the numerically dominant faunal groups that colonized basalt blocks at all vent sites over all deployment periods. These same taxa have also been documented in large abundances at Axial Volcano (Tsurumi & Tunnicliffe 2003) and Endeavour (Sarrazin et al. 1999). In contrast to previous studies (Sarrazin & Juniper 1999, Tsurumi & Tunnicliffe 2001), we recorded more species recruiting to basalt blocks at Endeavour than at Axial Volcano, although there was much overlap in diversity (i.e. both segments had the same dominant species recruiting). Few to no individuals of *Ridgeia piscesae* or *Paralvinella* recruited, which are species typically abundant in diffuse flow habitats at Juan de Fuca vents (Tunnicliffe et al. 1993, Sarrazin & Juniper 1999). While Van Dover et al. (1988) and Mullineaux et al. (1998) found very few vestimentiferan recruits on their basalt blocks, Mullineaux et al. (2000, 2003) and Hunt et al. (2004) observed large numbers of recruits after several months. However, Mullineaux et al. (1998) noticed that vestimentiferans only recruited to cracks

Table 7. *Lepetodrilus fucensis, Provanna variabilis, Amphisamytha galapagensis* and *Parougia wolfi. F*-values of significant MANOVA (Wilk's λ) and ANOVA exploring differences in colonization between Cloud$_{near}$ and Cloud$_{far}$ locations at Cloud vent site, Axial Volcano, for 2 deployment periods, 2001–2002 and 2001–2003. Analyses were only conducted for species present at both locations. All: MANOVA results; individual species: ANOVA results; df: Degrees of freedom. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

Species	F	df
2001–2002		
All	139.8***	5, 10
Lepetodrilus fucensis	155.14***	1, 14
Provanna variabilis	3.04	1, 14
Amphisamytha galapagensis	108.17***	1, 14
Parougia wolfi	0.15	1, 14
2001–2003		
All	87.97***	4, 9
Lepetodrilus fucensis	298.46***	1, 14
Amphisamytha galapagensis	98.09***	1, 14
Pyropelta musaica	0.96	1, 14

Table 8. Chemical variables (H_2S, Fe, Mn, Si) and maximum temperature (Temp) measured in venting fluid at Cloud, Clam Bed, and Smoke and Mirrors (SM) vent sites in 2003 (Butterfield et al. 2004). Chemical variables are standardized per unit of heat of vent fluid (µmol kJ^{-1}); temperature in °C

Vent site	H_2S	Fe	Mn	Si	Temp
Cloud	0.41	0.18	0.20	10.76	8.1
Clam Bed	12.83	2.19	1.82	48.01	41.6
SM	3.45	1.14	0.32	10.35	352.0

and other cryptic habitats, or the underside of plates with direct access to fluids. These species may require specific conditions for successful colonization that were not met in our settling substrate environments.

Spatial variation in settlement and colonization

The differences in settler and colonist abundances were greater over small spatial scales (m to km: within and among vents), than larger ones (100 km: among segments) for most species examined. Since the pattern of colonization differed among species, we suggest that this small-scale variation reflects a species-specific response to the varying environmental conditions at a particular vent. In a comparison of the faunal distributions in different vent segments across the Juan de Fuca Ridge, Tsurumi & Tunnicliffe (2001) observed that it was the level of hydrothermalism rather than the geographic affinities of the vent sites that defined the faunal assemblages.

Settlement of the 2 most abundant gastropods, *Lepetodrilus fucensis*, and *Depressigyra globulus*, occurred at all vent sites at both segments in all deployment years. Settlement at all vents at the same time suggests that synchrony in gastropod settlement occurred on km scales within Axial Volcano and Endeavour. On the East Pacific Rise, Mullineaux et al. (1998) observed a settlement event of protoconch-staged *L. elevatus* on basalt plates separated as far as 1 km. At Axial and Endeavour, a spatially homogeneous larval pool within the axial valleys (Metaxas 2004) would facilitate synchrony in settlement among spatially separated vent sites.

Temperature and dissolved H_2S were the vent fluid properties most consistently correlated with settler and colonist abundance across all species. Block temperature was positively correlated to abundance of all colonists except the predator *Parougia wolfi*, which may be influenced more by prey distribution than habitat characteristics. Temperature may act as a cue for colonists to locate preferred vent flows, or to minimize exposure to a combination of environmental stressors (Bates et al. 2005). H_2S has also been proposed as a chemical habitat cue, because sulphide oxidation is the dominant chemical energy source for microbial metabolism (Karl et al. 1980, Jannasch 1995). In our study, the majority of species colonizing basalt blocks were primary consumers of bacterial production, and the availability of H_2S in vent flows could reflect the availability of nutritional resources. At Endeavour vents, Rittschof et al. (1998) found vent polychaete post-larvae burrowed into filters containing 0.3 M sulphide, whereas none colonized filters without sulphide. On sulphide edifices along the Juan de Fuca Ridge, H_2S, but not temperature, was among the principal factors influencing adult distributions (Sarrazin et al. 1999). Environmental factors important in influencing faunal distributions may vary over the life history of a species.

Temperature could promote a major cue for settling larvae, indicating suitable habitats for settlement within a vent site. Larvae dispersing in currents or plumes (Mullineaux & France 1995) would experience cold ambient temperatures, which are hypothesized to reduce their metabolic rates (Berg 1985). Temperature as a habitat cue is also the most parsimonious explanation, as encountering higher temperature buoyant hydrothermal fluids could invoke an instantaneous physiological response triggering settlement in dispersing larvae (Lutz et al. 1980). However, it is possible that hydrothermal species use multiple cues, such as temperature or chemical anomalies, to locate suitable vent habitats.

Our environmental measurements provide information on the physical and chemical characteristics of
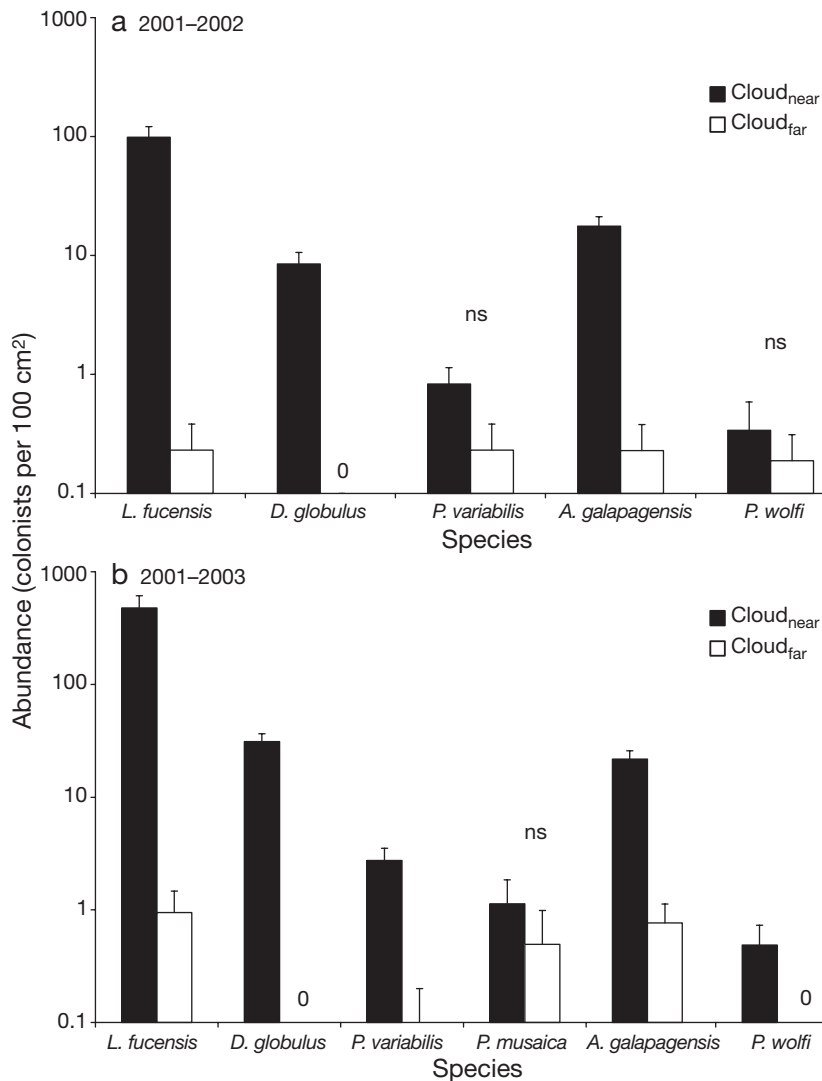
Fig. 7. *Lepetodrilus fucensis, Depressigyra globulus, Provanna variabilis, Amphisamytha galapagensis, Parougia wolfi* and *Pyropelta musaica.* Abundance of colonists (mean + SE) found on basalt blocks deployed at Cloud$_{near}$ (<1 m) and Cloud$_{far}$ (<10 m) locations from Cloud vent for (a) the 2001–2002, and (b) the 2001–2003 deployment period. ns: no significant differences; all other comparisons were significant (p < 0.05). n given in Table 2

only 3 vent sites at one point in time. Hydrothermal vent species experience fluctuations in the physico-chemical characteristics of hydrothermal fluid over spatial and temporal scales (Tunnicliffe et al. 1985, Johnson et al. 1988a, 1988b, Little et al. 1988, Chevaldonne et al. 1991, Sarrazin et al. 1997, 1999), which need to be considered when comparing faunal distributions over different sites and times. Additionally, many vent fluid characters are highly correlated (Johnson et al. 1988b, 1994, Sarrazin et al. 1999, Butterfield et al. 2004; but see Luther et al. 2001). Other environmental factors may also have a significant effect on the survival of settlers and colonists of vent species, such as food and O$_2$ availability, flow intensity, or variation in habitat complexity (Sarrazin et al. 1999). It is most likely that suites of environmental variables regulate the distributions of hydrothermal vent invertebrates, depending on the specific physiological tolerances and nutritional requirements of each species.

Colonization was always higher near than far from the vent opening, although for *Provanna variabilis* and *Pyropelta musaica*, the difference was not significant, possibly because of the low incidence of these species. Thus, close proximity to venting fluid appears critical for the successful colonization of some species (e.g. *Depressigyra globulus*), but not others. The presence of *Amphisamytha galapagensis* at both distances is not surprising, as it has been found on basaltic crusts up to 50 m away from a venting source (McHugh & Tunnicliffe

Table 9. *Lepetodrilus fucensis, Provanna variabilis, Amphisamytha galapagensis, Depressigyra globulus* and *Parougia wolfi.* Pearson's correlation coefficients between environmental variables given in Table 8 (including block temperature given in Table 1) and abundances of the 5 most abundant species on basalt blocks (n = 45, except for block temperature, where n = 32). *p < 0.05, **p < 0.01, ***p < 0.001

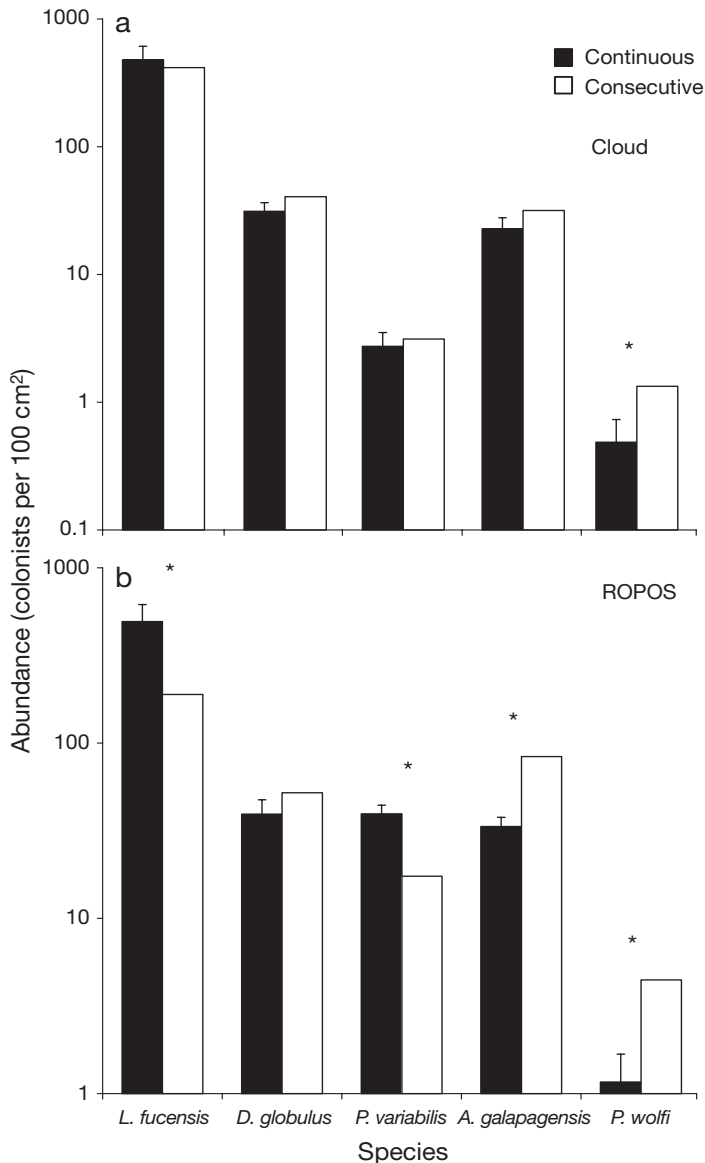| Species		H$_2$S	Fe	Mn	Si	Vent temp	Block temp
L. fucensis	(protoconchs)	0.344*	0.261	0.388**	0.405**	−0.358*	0.499**
	(colonists)	0.129	0.009	0.205	0.238	−0.497**	0.452**
D. globulus	(protoconchs)	0.589***	0.533***	0.608***	0.611***	−0.263	0.505**
	(colonists)	0.533***	0.489**	0.578***	0.584***	−0.291	0.630***
P. variabilis		0.521***	0.484**	0.514***	0.511***	−0.142	0.571**
A. galapagensis		0.600***	0.544***	0.610***	0.610***	−0.216	0.592***
P. wolfi		−0.348*	−0.428**	−0.284	−0.252	−0.306*	−0.323

Fig. 8. *Lepetodrilus fucensis*, *Provanna variabilis*, *Amphisamytha galapagensis*, *Depressigyra globulus* and *Parougia wolfi*. Abundance of colonists (mean + SE) of the 5 most abundant species summed from basalt blocks deployed for two 1 yr intervals (sum of mean number of colonists from 2001–2002 plus 2002–2003; 'consecutive') and compared to abundance of colonists on basalt blocks deployed for a 2 yr interval in 2001–2003 ('continuous') at (a) Cloud and (b) ROPOS vent sites at Axial Volcano. *Significant difference within a species

may prefer peripheral areas as an optimal zone for foraging, since non-vent food resources may also be available. The presence of vent species on $Cloud_{far}$ blocks in our study suggests that vent influence may be exported out to ~10 m distances, potentially increasing the amount of habitat available for colonization. However, we found few to no recent settlers on $Cloud_{far}$ blocks, implying either settlement to far vent locations is low, post-settlement survival is low, or, more likely, at this distance vent fluid concentrations are too low to support large faunal abundances.

Temporal variation in settlement and colonization

Colonization was variable between years for most species, possibly reflecting variability in settlement. At Axial vent sites, settlement of both gastropod species was higher in 2003 than in 2002. Metaxas (2004) found that near bottom (< 50 cm) larval supply at the same sites at Axial Volcano also varied, by an order of magnitude, between 2000 and 2001. Larval supply could vary temporally due to variations in adult population abundance, especially as a result of ecological succession after an eruption (Tunnicliffe et al. 1997, Shank et al. 1998). The colonization patterns observed in this study likely reflected this variation in larval supply. For example, at Cloud vent, the increase in *Lepetodrilus fucensis* settler abundance observed in this study between 2002 and 2003 likely reflected the increase in the relative abundance of adult *L. fucensis* since 2000 (Marcus 2003, N. Kelly pers. obs.). Temporal variations in larval supply may also be attributed to oscillations of oceanic currents within, along, or above axial valleys or ridge crests (Thompson et al. 2003, Marsh et al. 2001).

At Axial Volcano, spatial variability in colonization among vent sites was lower after 2 yr than after 1 yr. On the Juan de Fuca Ridge, Tsurumi & Tunnicliffe (2003) documented that 3 yr after an eruption the composition of new vent assemblages was not distinct from that of older vents, while those 1 or 2 yr after were. In newly opened habitats (in our case, uncolonized basalt blocks), pulses of larvae may regulate vent communities over short time scales (Sarrazin et al. 1997, Tsurumi & Tunnicliffe 2001), particularly if a homogeneous larval pool exists over km scales (Metaxas 2004). Processes operating over periods of years may obscure early patterns of colonization (Mullineaux et al. 2003). In contrast, at Endeavour, spatial patterns in the abundance of colonists remain consistent over time. The timescale of assemblage development may be different at Endeavour than at Axial vent sites, possibly due to the greater temporal stability in venting conditions at Endeavour vent sites.

1994). Recruitment to hard substrates outside of direct vent influence has also been recorded for species on the East Pacific Rise (Van Dover et al. 1988, Mullineaux et al. 1998, Van Dover 2002). Marcus & Tunnicliffe (2002) documented a distinct faunal signature in peripheral habitats 5 to 6 m away from the venting source at Cloud, and suggested that some vent species

Table 10. *Lepetodrilus fucensis, Provanna variabilis, Amphi-samytha galapagensis, Depressigyra globulus* and *Parougia wolfi*. One-sample Student's *t*-tests examining differences between the summed mean abundance of colonists from the consecutive 1 yr deployments (2001–2002 plus 2002–2003) and the continuous 2 yr deployment (2001–2003) for the 5 most abundant species at ROPOS and Cloud vent sites. df for all tests = 7. (+) positive interactions: summed consecutive < continuous; (–) negative interactions: summed consecutive > continuous; (0) neutral interactions: summed consecutive = continuous

Species	ROPOS			Cloud		
	t	p	Effect	*t*	p	Effect
L. fucensis	2.47	0.043	+	0.46	0.659	0
D. globulus	–1.55	0.164	0	–1.76	0.121	0
P. variabilis	4.62	0.002	+	–0.50	0.633	0
A. galapagensis	–11.76	<0.001	–	–1.82	0.112	0
P. wolfi	–6.43	<0.001	–	–3.48	0.010	–
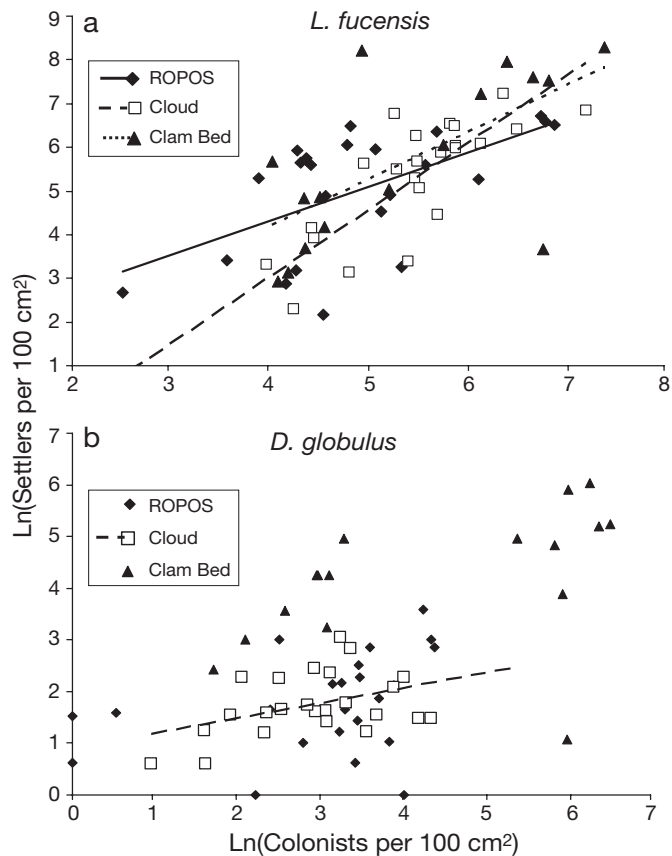
Fig. 9. *Lepetodrilus fucensis* and *Depressigyra globulus.* Relationship between settlers (S) and colonists (C) on basalt blocks deployed at ROPOS and Cloud vent sites at Axial Volcano and Clam Bed at Endeavour Segment, for (a) *L. fucensis* [ROPOS: $\ln(S+1) = 0.79 \times \ln(C+1) + 1.13$, $r^2 = 0.35$, p = 0.002; Cloud: $\ln(S+1) = 1.56 \times \ln(C+1) – 3.19$, $r^2 = 0.76$, p < 0.001; Clam Bed: $\ln(S+1) = 1.09 \times \ln(C+1) – 0.16$, $r^2 = 0.43$, p = 0.006] and (b) *D. globulus* [ROPOS: $\ln(S+1) = 0.27 \times \ln(C+1) + 0.94$, $r^2 = 0.13$, p > 0.05; Cloud: $\ln(S+1) = 0.3 \times \ln(C+1) + 0.89$, $r^2 = 0.18$, p < 0.05; Clam Bed: $\ln(S+1) = 0.33 \times \ln(C+1) + 2.73$, $r^2 = 0.20$, p > 0.05]. Note different scales on *x*-axes

Biological influences on settlement and colonization

Intraspecific influences on colonization of hydrothermal vent species were evident for 4 of the 5 species examined. Positive interactions, which we interpreted as gregarious settlement, were inferred for *Lepetodrilus fucensis* and *Provanna variabilis*. Gregarious settlement may in part explain the large abundance of *L. fucensis* at Juan de Fuca Ridge vent sites (Bates et al. 2005). Settlement cues produced by conspecifics or related species have been suggested for promoting vestimentiferan colonization on the East Pacific Rise (Shank et al. 1998, Mullineaux et al. 2000, Hunt et al. 2004). The use of biogenic cues by larvae, rather than the instantaneous physico-chemical conditions, would provide an integrated measure of habitat suitability, implying that favourable environmental conditions have persisted at least as long as the age of the species producing it (Mullineaux et al. 2000). *P. variabilis* develops directly within egg cases laid by the parent on basalt surfaces, although there may be a short planktonic stage before the onset of benthic life (A. Warén, pers. comm.). These egg cases may be laid in aggregations, and juveniles would emerge in a gregarious pattern. While a significant, although weak, relationship between settlers and colonists existed for *Depressigyra globulus* at Cloud vent site, there were no other indications of intraspecific biological interactions influencing colonization for this species. Thus, we suggest pre-settlement factors, such as mortality of larvae in the water column during dispersal, larval behaviour when encountering a settlement cue, or variations in larval supply, are influencing subsequent settlement and colonization for *D. globulus*.

Negative, inhibitory interactions, which we interpreted as post-settlement mortality, appear to be regulating colonization patterns of the polychaetes *Amphisamytha galapagensis* and *Parougia wolfi*. *A. galapagensis* is a sessile deposit feeder (McHugh & Tunnicliffe 1994) and competition for substratum space and/or food resources could result in post-settlement mortality. At Juan de Fuca vents, interspecific competition for food resources has been demonstrated in regulating the distributions of another polychaete, *Paralvinella* sp. (Levesque et al. 2003). Colonists of *A. galapagensis* were often found on or within the mucus tubes of larger individuals (McHugh & Tunnicliffe 1994, N. Kelly pers. obs.), suggesting there may be some positive effect conferred by adults on colonist survival. However, large abundances of mobile gastropods could accidentally bulldoze small *A. galapagensis* colonists that settle randomly, and this high post-settlement mortality would result in juveniles being more frequently observed in close association with adult conspecifics. Bulldozing of sessile recruits

by gastropods has been documented at low temperature vents on the East Pacific Rise (Micheli et al. 2002, Mullineaux et al. 2003). *P. wolfi* is a small predator, and its biology is mostly unknown (Blake & Hilbig 1990), but competition for prey causing starvation or forced migration from blocks, or vulnerability to other predators, could explain the lower abundances on continuously deployed blocks. Van Dover et al. (1988) suggested predation by fish, crabs and other organisms was responsible for the immaturity of colonists on slate panels after 3 yr of deployment. Large predatory polychaetes (*Nereis piscesae* and polynoid polychaetes) and large mobile crustaceans (*Munidopsis alvisca*, *Macroregonia macrochira*) were also found on or near our basalt blocks.

Mean abundance of *Lepetodrilus fucensis*, *Provanna variabilis*, *Amphisamytha galapagensis*, and *Parougia wolfi* were all slightly higher at ROPOS than at Cloud, and intraspecific interactions occurred more frequently at ROPOS than at Cloud. These results suggest that an 'abundance threshold' may be required for intraspecific interactions that regulate vent faunal abundances at Juan de Fuca vent sites to take effect. For example, there may need to be enough individuals present at a vent to produce a cue to facilitate gregarious settlement, or enough individuals present to reduce the abundance of subsequent colonists.

CONCLUSIONS

This is the first study to quantify the scales of spatial and temporal variability in settlement and colonization of hydrothermal vent species on the Juan de Fuca Ridge. Through the deployment of basalt blocks, we demonstrated that for most species, variation in settlement and colonization is greater among vent sites (over km scales) than between ridge segments (over 100 km scales), and within a vent site. Environmental properties of the hydrothermal vent fluid, most notably temperature and dissolved H_2S, appear to be important factors influencing this variation among spatially separated vent sites. However, for some species, the initial patterns of variation in colonization can be obscured over longer periods, in part due to intraspecific biological interactions, such as gregarious settlement and post-settlement mortality, particularly when faunal abundances are high. In combination, our results suggest that the variability in settlement and colonization of hydrothermal vent species is regulated primarily by a species-specific response to the varying environmental conditions at a particular vent, and secondarily by biological interactions that further alter subsequent colonization patterns. Our findings indicate that the hypotheses previously erected on the factors that reg-

ulate adult populations on the Juan de Fuca Ridge (Sarrazin et al. 1997, 1999), also hold for settlers and colonizers. Increased temporal resolution and simultaneous measures of vent fluid properties with invertebrate colonization would identify the specific inductive and causative factors influencing early-life history stages of species in these habitats.

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