A novel landscape ecology approach for determining habitat correlations
and macrofaunal patchiness in extreme environments:
pilot study for the Southern East Pacific Rise at 17-18°S

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Introduction

In May 2002, researchers returned to the Rose Garden on the Galapagos Rift to commemorate the 25th anniversary of the historic discovery of deep-sea hydrothermal vents. Working from the coordinates established during previous visits to the Rose Garden, several *Alvin* dives were dedicated to relocating this famous vent community. However, observations indicated that the Rose Garden vent community had likely been buried under lava at some point during the previous ten years. Notably, divers documented a previously unknown and relatively young community of vent organisms in the vicinity of the search area. The dramatic obliteration of Rose Garden and the subsequent "birth" of a new community in its wake emphasize yet again that ventscapes are largely shaped by underlying magmatic and tectonic processes.

Haymon et al. (1993) and Tunnicliffe et al. (1997) describe other notable examples of how the interplay between disturbance and succession influences the biological structure of vent communities. Haymon et al. (1993) were the first researchers to record a recent seafloor volcanic event. The event occurred in 1991 along the East Pacific Rise crest between 9°45-52'N, and had a significant impact on the resident animal community. For example, in one particular colony of tubeworms, mussels and crabs aptly named "Tubeworm Barbeque", animals were described as being either charred, shattered or dismembered and part of the colony was buried by a fresh lava flow. Tunnicliffe et al. (1997) describe the first case of "de novo" hydrothermal vent community development in response to a 1993 eruptive event on CoAxial Segment, Juan de Fuca Ridge. Unlike the site near 9° N, there did not appear to have been any pre-existing vent communities in the CoAxial area prior to the eruption. Another notable study of vent community development is reported by Shank et al. (1998), who continued to focus on the 9°45-52' N site following the 1991 eruption. Their study provides additional evidence that vent community structure is continually shaped over time by the evolving physical and geochemical conditions characteristic of post-eruptive habitats.

Our paper uses spatial statistics to examine how seafloor processes influence the community structure of individual vent colonies. Working with an existing high-resolution, remotely sensed, data set from the superfast-spreading southern East Pacific Rise (SEPR) at 17-18° S, we integrated the data using the principles of landscape ecology. We employed point pattern analysis, a simple spatial statistical method for characterizing the distributions of macrofaunal organisms at hydrothermal vent sites, to identify: (1) patterns, if present in the arrangement of macrofauna at hydrothermal vent sites, the scales at which the patterns are being expressed; and (2) the process(es) that may be influencing the patterns.

Data and methods

During the 1996 Sojourn II expedition, a very dense video survey was conducted along the superfast-spreading SEPR from 17-18°S (Figure 1), using the near-bottom imaging capability of *Argo II*, a fiber-optical, acoustic towed camera system towed at ~6-10 m above the seafloor (see further details in Haymon et al., 1997 and Wright et al., 2002). Fifteen axis-parallel survey lines were made through the
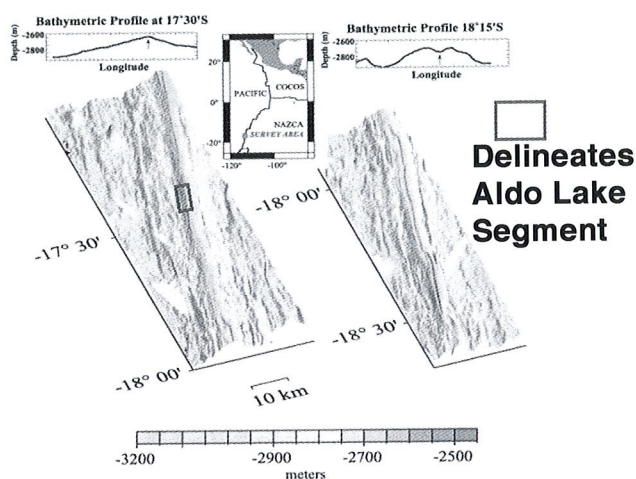
Figure 1. Sea Beam bathymetry map of the study area on the southern East Pacific Rise, from Cormier et al. (1996) & Scheirer et al. (1996). Figure after White, 2001. Cartography by Scott White, University of South Carolina. Aldo Lake section is delineated by a rectangle.

axial zone with line spacings of 10-30 m. This provided 80-100% visual coverage of the axial zone where it measured less than 100 m wide, down to a minimum coverage of ~45% where the axial zone widened to ~700 m. Data were obtained with *Argo II's* forward looking camera (swath width ~16 m); camera resolution ~100 cm². Locations of visible vent macrofauna, active and inactive hydrothermal vents and fissures were recorded in real time. Environmental variables such as lava flow type and age were also observed and recorded continuously at intervals of ~5-10 m. Each observation was "stamped" with time, as well as an x-y coordinate relative to a seafloor transponder navigational net, that was later transformed to longitude-latitude (Wright et al., 2002). The resulting data set was a collection of points representing the spatial locations of vent macrofauna, active and inactive sources of hydrothermal venting, and environmental attributes describing type of lava flow and relative age of lava.

Ripley's K analysis, a member of the point pattern analysis family of spatial statistics, was used to test the hypothesis that the arrangement of vent fauna within each species group exhibits a pattern of complete spatial randomness (CSR). We chose to use the Ripley's K statistic for several reasons. First, it is suitable for use with point data, such as were collected here in the form of digitized locations of organisms and corresponding physical habitat features. Second, it allows for analysis of patterns at multiple scales, as opposed to just a single scale of pattern. Third, the cross-Ripley's K allows for analysis of the spatial relationships between pairs of variables in cases where spatial relationships may be lagged at various (unknown) distances (Cressie, 1993). An arrangement between two variables other than CSR infers that there may be a pattern-process relationship between them. However it is important to note that PPA is limited in that it cannot make a distinction between a true "causal" relationship and an

"incidental" relationship due to shared dependence on a third variable. On the other hand, K(d) results that do not depart significantly from randomness are sufficient to rule out a "causal" link between two variables.

For the purpose of this study, we focus on a particular 8 km segment of the SEPR from 17°26'-30'S, the Aldo Lake segment (Haymon et al., 1997; White, 2001), chosen because the *Argo II* videographic coverage in this area is 105-130% of the axial zone (Wright et al., 2002) and a wide variety of vent macrofauna was present, including tubeworms, serpulid worms, and brachyuran crabs. Systematic sampling in combination with >100% coverage of the study area, produced a comprehensive data set for the spatial arrangement of the variables analysed in this study, at intermediate to coarse scales. Each vent animal species was treated as a binary response variable because we were interested in its presence or absence with respect to a specific environmental "attribute" variable. The attribute variables such as lava flow type, lava age, and type of venting were also treated as binary data because we were interested in their presence or absence within a pre-determined range of each response variable.

Observations were converted from their original lat./long. coordinates to decimal degrees and then to metres. The geographic extent of the Aldo Lake segment was then decomposed into 1110 m long sections from north to south. These segments were numbered 1-7 (N-S). The points in each section were standardized to fit a grid with boundaries of 0,0 (NE), -4400,0 (NW), -4440,-1110 (SW), and 0,-1110 (SE). Next, the 1110 m segments were broken down further into 550 m long segments (1a,1b, 2a, 2b, etc...), and separate Ripley's K analyses were performed for each section. Study areas ranged from 55,500 m² (narrowest) to 943,500 m² (widest). These results are reported in Tables 1 and 2.

Statistical Analyses

Ripley's K(d) analysis was performed using a program that was developed by Moeur (1999). The program is capable of computing both univariate and bivariate Ripley's K analysis for random, clustered and uniform patterns, and employs a toroidal-wrap edge correction method. The following equation was utilized to calculate K (d):

$$K(d) = A \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{\delta_{ij}(d)}{n^2}, \text{ for } i \neq j.$$

where

$$\delta_{ij}(d) = \begin{matrix} 1 & \text{if } d_{ij} \leq d \\ 0 & \text{if } d_{ij} > d' \end{matrix}$$

for *n* points on a plot of area A/n $\hat{K}(d)$ can be interpreted as the expected number of points within distance *d* of an arbitrary point. The $\hat{K}(d)$ distribution is computed for values of *d* from 0 to a maximum of 1/2 the length of the shortest plot boundary (Moeur, 1999). This particular statistics package reports and looks at comparisons between values of L(d) instead of K(d). L(d) is the linear transformation of the K (d) distribution that is computed from the observed data. L(d) is compared to the lower and upper boundaries of a two-sided point-wise (100%-2*α*100%) confidence en-

Table 1. Results of univariate and bivariate analyses involving macrofaunal distributions. + indicates clustering (univariate analysis) and positive association in geographic space (bivariate analysis). Ø indicates that the spatial arrangement between the two variables was not significantly different then CSR. A blank space indicates that Ripley's K analysis was not performed between the two variables due to too few points or a distance between the two closest points >300m. The distance of apparent aggregation/association in geographic space in parentheses. Variables listed by section with number of observations per section. Only sections with response variables of interest are reported. Tube= tube worm; serp= serpulid; brach= brachyuran crab.

	tube1a	tube2b	tube3a	tube4a	serp1a +(1)	serp1b	brach1a	brach1b	brach2a	brach2b	brach3a	brach4a	brach4b	brach5a	brach5b	brach6a	brach6b
tube1a (11)	+(1)																
tube2b (2)							+(1)										
tube3a (1)										+(8)							
tube4a (2)											+(7)						
serp1a (12)	+(1)				+(1)							+(38)					
serp1b (12)						+(1)	+(1)	+(1)									
brach1a (103)	+(1)					+(1)	+(1)										
brach1b (64)								+(1)									
brach2a (51)									+(2)								
brach2b (65)	+(8)																
brach3a (59)	+(7)									+(8)							
brach4a (8)	+(38)										+(1)						
brach4b (6)												+(19)	Ø				
brach5a (7)														+(58)			
brach5b (15)															+(7)		
brach6a (2)																	
brach6b (1)																	

Table 2. Results of univariate and bivariate analyses involving macrofaunal associations with environmental attribute variables. + indicates clustering (univariate analysis) and positive association in geographic space (bivariate analysis). Ø indicates that the spatial arrangement between the two variables was not significantly different than CSR. A blank space indicates that Ripley's K analysis was not performed between the two variables due to too few points or a distance between the two closest points >300m. The distance of apparent aggregation/association in geographic space in parentheses. Variables listed by section with number of observations per section. Only sections with response variables of interest are reported.

	black smoke	white smoke	cloudy water	fissures	inactive chimneys	sheet lava flow	collapse lava flow	pillow lava flow	lobate lava flow	0.5 relative lava age	1.0 relative lava age	1.5 relative lava age	2.0 relative lava age
tube1a (11)	+(3)	+(1)		+(37)	+(16)	+(6)	+(4)	Ø	Ø			Ø	
tube 2b (2)					+(35)	+(36)	Ø						
tube 3a (1)		Ø			Ø	+(18)	Ø						
tube 4a (2)					+(57)	+(62)	Ø						
serp 1a (12)	+(5)	+(2)		+(45)	+(7)	+(8)	+(1)	Ø	Ø		+(19)		Ø
serp 1b (12)		+(5)		+(6)	+(2)	+(14)	+(3)	Ø	Ø				
brach 1a (103)		+(1)		+(2)	+(4)	+(1)	+(1)	Ø	Ø			Ø	
brach 1b (64)		+(2)		+(7)	+(1)	+(3)	+(1)	Ø	Ø				
brach 2a (51)				+(10)	+(9)	+(5)	+(7)		+(55)				
brach 2b (65)				+(63)	+(35)	+(2)	+(3)		+(8)	+(10)			
brach 3a (59)	+(28)	+(17)			+(16)	+(4)	+(4)	Ø	Ø	Ø			
brach 4a (8)					Ø	+(17)	+(19)	Ø	Ø	Ø		Ø	
brach 4b (6)						Ø	+(14)		Ø				
brach 5a (7)						+(21)			Ø			Ø	
brach 5b (15)	+(4)	+(4)			+(4)	+(3)							Ø
brach 6a (2)						Ø	+(24)	Ø			+(14)	+(10)	
brach 6b (1)						Ø	+(11)				Ø	+(6)	

velope to determine whether or not the pattern in the observed data departs significantly from CSR. Confidence envelopes are calculated via Monte Carlo simulation and are unique to each of the comparisons that were tested by study area and number of positive observations. For this project, the author selected a 95% confidence envelope ($\alpha=.025$) to determine statistical significance.

Each response variable (serpulid worms, tubeworms, and brachyuran crabs) was analysed within a 550 m (north-south) section for the presence of spatial pattern within the population (i.e., univariate analysis). Next, each of the response variables was compared to each of the attribute variables within a 550m (north-south) section, and analysed for the presence of spatial pattern between the two

populations (i.e., bivariate analyses). Comparisons were also made between the different response variables, for example between serpulid worms and brachyuran crabs. Analyses were run for all pairs of response and attribute variables where at least one of the response variable observations was located within 300m of one of the attribute variable observations.

Results

Univariate analyses revealed a clustered pattern, apparent at the scale of 1m in section 1a, a 55-m north-south region that included 11 data points representing tubeworm observations (Table 1). Other sections containing tubeworm observations were section 2b (2 observations), section 3a (1 observation), and section 4a (2 observations). The tubeworm observations in section 2b were ~158 m apart and the observations in section 4a were ~5m apart. Bivariate analyses indicated that there was a positive spatial association between tubeworms and sheet flow and also between tubeworms and brachyuran crabs (Tables 1 and 2). These associations were significant in each of the sections where tubeworms were observed. In section 1a, the locations of tubeworm point observations were also found to be associated with serpulid worms, black and white smoke, collapse lava flow, fissures, and inactive hydrothermal chimneys (Tables 1 and 2). Tubeworm point observations in sections 2b and 4a were also found to be significantly associated with inactive hydrothermal chimneys (Table 2).

Univariate analysis revealed a clustered pattern (apparent at the scale of ~1 m) for both of the 555 m north-south sections where serpulid worms were observed (Table 1). Section 1a and section 1b contained twelve serpulid worm observations each. Bivariate analysis indicated that there was a positive spatial association between serpulid worms and collapse flows (apparent at 1 m and 3 m scales, respectively), sheet flows (apparent at 8 and 14 m scales), fissures (apparent at 45 and 6 m scales), hydrothermally inactive chimneys (apparent at 7 and 2 m scales), white smoke (apparent at 2 and 5 m scales), and brachyuran crabs (both apparent at the scale of 1m) (Tables 1 and 2). Positive associations between serpulid worms and tubeworms, age1 lava, and black smoke were also reported for section 1a (Tables 1 and 2).

Univariate analyses of the arrangement of brachyuran crabs revealed clustered patterns in sections 1a, 1b, 2a, 2b, 3a, 4a, 5a, and 5b (Table 1). Clustering was apparent at the scale of 1-2 m for sections 1a, 1b, 2a, and 3a, 7-8 m for sections 2b and 5b, 19m for section 4a, and 58 m for section 5a. Brachyurans were also observed in sections 4b (seven observations), 6a (two observations >100m apart), and 6b (one observation).

Bivariate analysis revealed a positive association between the arrangement of brachyuran crabs and tubeworms as well as brachyuran crabs and serpulid worms for each section where tubeworms and serpulid worms were observed (Table 1). Bivariate analyses revealed a positive association between brachyuran crabs and collapse flow in eight of the eleven sections where brachyurans were observed (Table 2). Bivariate analysis also revealed a positive spatial association between brachyuran crabs and sheet flow in eight of the eleven sections where brachyurans were observed (Table 2). In general, the sections with relatively high numbers of crab observations also showed a positive association with some form of active venting (e.g., white or black smoke, or fissures; Table 2).

Discussion

As in any statistical analysis, inferences about causation are limited, so we derive our conclusions from spatial associations, limited to spatial scales with a minimum grain of 5-10 m, and maximum extent of a few hundred metres. Nevertheless, the findings are consistent with the notion that, like terrestrial and aquatic communities, seafloor communities are shaped by the interplay between disturbance and succession.

Observations from the Sojourn II cruise in 1996 as well as those from a previous expedition to the SEPR in 1993 indicate that the vent communities from 17-18° S are under the influence of episodic eruptive processes (Auzende et al., 1994; Wright et al., 2002). This study provides statistical evidence that seafloor communities are characterized by a dynamic patchwork of areas in various stages of succession following seafloor eruptions. The most striking evidence of patch dynamics and community structure is provided by the arrangement of tubeworms and serpulid worms relative to lava flow type. In all sections where tubeworms and or serpulid worms were present, they were positively associated with sheet flow lavas. However, while serpulid worms also showed a positive spatial association with collapse flows (thought to be relatively older than sheet flow) in both sections where they were observed, only the tubeworms in one of the four sections where tubeworms were observed (section 1a) were positively associated with collapse flow. Incidentally, this was also the section with the most tubeworm observations. These results provide evidence that tubeworms and serpulid worms may be temporally organized according to the "time since most recent eruption", and are consistent with the model of vent community succession proposed in Shank et al. (1998). Based on post-eruptive biological and geochemical observations near 9° North over a four and a half year period, Shank et al. (1998) propose that post-eruptive diffuse flow is initially settled by tubeworms, with serpulid worms arriving and increasing in abundance as emissions become more focused and the concentration of H_2S in the vent fluid declines.

The lack of correlation between tubeworm locations and an active form of hydrothermal venting such as an active chimney, black or white smoke, or fissures in three of the four sections where tubeworms were observed (Table 2) may also be evidence of the dynamic patchwork of seafloor vent communities. Tubeworms are generally considered to be dependent on vent fluid for their livelihood, so the absence of such features is puzzling. We suggest that vent fluid was available to the tubeworms observed, however it was not detected by scientists aboard the Sojourn cruise because tubeworms were utilizing sulfide from "young", undeveloped point sources that were not obvious

videographically. The presence of "young", undeveloped point sources in post-eruptive areas is supported by both Haymon et al. (1993) and Auzende et al. (1994) who observed diffuse venting directly from lava flows and rubble at 9°45-52'N and 17°25'S respectively. If tubeworms are early colonizers of recently erupted areas, but are less well-adapted than e.g. serpulid worms to persist as the biological, geo-chemical and physical properties of a particular vent evolves, then these tubeworm communities may be relictual from previous eruptions and would be expected to disappear or give way to serpulid worms (or other organisms) over time. As expected, serpulid worms were positively associated with at least one type of active venting. In both sections where serpulid worms were observed, they were found to be associated with fissures, and black and or white smokers, although the scale of these associations differed dramatically.

The spatial distributions of brachyuran crabs are consistent with the behavior of grazers. Brachyuran crabs occurred throughout the study area, but their densities were highest in sections that contained tubeworms and serpulid worms. Brachyurans were positively spatially associated with tubeworms and serpulid worms in these sections. Interestingly, brachyuran crabs were also found to be positively associated with active forms of venting in sections where no tubeworms or serpulid worms were observed. These findings raise the possibility that brachyuran crabs use environmental cues to locate potential prey.

Conclusion

Our findings underscore the observations and conclusions of Haymon et al. (1993), Tunnicliffe et al. (1997), and Shank et al. (1998), who emphasize that vent community structure is largely influenced by underlying tectonic and magmatic processes. There is still a great deal to be learned however with respect to these complex geologic, biologic, chemical and physical interactions, and continued research is needed to develop statistically significant techniques for analyzing the costly and often complex data sets collected along deep ocean spreading ridges. We offer one such technique, based on the principles of landscape ecology for examining the spatial arrangement of organisms in hydrothermal vent environments. Studies such as ours can raise important questions of causation. For example, are tubeworms and serpulid worms temporally organized according to "time since most recent eruption"? Are tubeworms less well adapted to persist than serpulid worms as the biological, physical, and geo-chemical nature of vent fluid evolves over time, and is the presence of small isolated tubeworm colonies somehow indicative of future eruptive activity? Armed with these questions, researchers will be able to optimize future data collection and experimental design. Furthermore, these techniques should be helpful in answering broader scientific questions such as:

For a given species, are the numbers of animals observed correlated with habitat features? What are its scale-specific spatial patterns of distribution? What are the physical, or physiological constraints operating on a given population?

Are the pattern-process relationships between vent animals and their environment different at fast versus slow spreading centers, or at spreading centers in the Atlantic versus the Pacific?

What is the significance of changes in species composition and arrangement observed over the lifetime of a given vent?

References

Auzende J.M., Sinton J., & Scientific Party 1994. NAUDUR explorers discover recent volcanic activity along the East Pacific Rise. *Eos, Transactions of the American Geophysical Union*, 75: 601, 604-605.

Cressie N. 1993. *Statistics for Spatial Data*. Wiley and Sons: New York. 900 pp.

Haymon R.M., Fornari D.J., Von Damm K.L., Lilley M.D., Perfit M.R., Edmond J.M., Shanks III W.C., Lutz R.A., Grebmeier J.M., Carbotte S., Wright D., McLaughlin E., Smith M., Beedle N. & Olson E. 1993. Volcanic eruption of the mid-ocean ridge along the East Pacific Rise crest at 9°45-52'N: Direct submersible observations of seafloor phenomena associated with an eruption event in April, 1991. *Earth and Planetary Science Letters*, 119: 85-101.

Haymon R.M., Macdonald K.C., Baron S., Crowder L., Hobson J., Sharfstein P., White S., Bezy B., Birk E., Terra F., Scheirer D., Wright D.J., Magde L., Van Dover C., Sudarikov S. & Levai G. 1997. Distribution of fine-scale hydrothermal, volcanic, and tectonic features along the EPR crest, 17°15'-18°30'S: Results of near- bottom acoustic and optical surveys (abstract). *Eos, Transactions of the American Geophysical Union*, 78: F705.

Moeur M. 1999. *User's Manual for Ripley's K Analysis*. USDA Forest Service, Rocky Mountain Research Station: Fort Collins, Colorado. 15 pp.

Scheirer D.S., Macdonald K.C., Forsyth D.W, Miller S.P., Wright D.J., Cormier M.-H. & Weiland C.M. 1996. A map series of the southern East Pacific Rise and its flanks, 15°S to 19°S. *Marine Geophysical Researches*, 18: 1-12.

Shank T.M., Fornari D.J., Von Damm K.L., Lilley M.D., Haymon R.M. & Lutz R.A. 1998. Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents (9°50'N, East Pacific Rise). *Deep-Sea Research II*, 45: 465-515.

Tunnicliffe V., Embley R.W., Holden J.F., Butterfield D.A., Massoth G.J. & Juniper S.K. 1997. Biological colonization of new hydrothermal vents following an eruption on Juan de Fuca Ridge. *Deep-Sea Research I*, 44 (9-10): 1627-1644.

White S.M. 2001. *The Linkage of Volcanic and Tectonic Processes at Fast Spreading Mid-Ocean Ridges: Constraints on the Spatial and Temporal Evolution of Volcanic Systems from the Distribution of Volcanic Edifices and Lava Flow Morphology on the East Pacific Rise*, Ph.D. Dissertation. University of California: Santa Barbara, California.

Wright D.J., Haymon R.M., White S.M. & Macdonald K.C. 2002. Crustal fissuring on the crest of the southern East Pacific Rise, 17° 15'-40'S. *Journal of Geophysical Research*, 107(B5): 10.1029/2001JB000544.