

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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SEPR Faunal Patchiness

Introduction

In May 2002, scientists returned to the Rose Garden on the Galapagos Rift to commemorate the 25th anniversary of the historic discovery of deepsea hydrothermal vents (NOAA, 2002). Working from the coordinates that had been established during previous visits to the Rose Garden, several *Alvin* dives were dedicated to relocating this famous vent community. However, observational data from the cruise indicate that the Rose Garden vent community was likely buried under lava some time in the past ten years. Notably, while searching for Rose Garden, scientists documented a previously unknown and relatively young community of vent organisms in the vicinity of the search area. This new site was christened “Rosebud” and is said to be populated by the “nascent progenitors of a reborn Rose Garden” (NOAA, 2002). The dramatic obliteration of Rose Garden and the subsequent “birth” of Rosebud in its wake emphasize yet again that ventscapes are largely shaped by underlying magmatic and tectonic processes.

This paper provides further evidence, by way of spatial statistics, that dynamic seafloor processes influence the community structure of individual vent colonies. We employ 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. This study uses an existing high-resolution, remotely sensed, data set from the superfast-spreading southern East Pacific Rise (SEPR) at 17-18° S, and

was accomplished through an integration of that data with the principles of landscape ecology.

Data and Methods

In 1996 during the Sojourn II expedition, a very dense video survey of the superfast-spreading SEPR from 17-18°S (Figure 1) was conducted with the near-bottom imaging capability of *Argo II*, a fiber-optical, acoustic towed camera system as it was 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 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 widens 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's. 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. This facilitated conversion to geographic information system (GIS) formats (ArcInfo coverages or ArcView shapefiles) for ease of mapping while still at sea, as well as for future statistical manipulation onshore (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. A

combination of the camera resolution and the frequency with which the continuous environmental attribute variables were recorded makes this data set appropriate for interpretation at intermediate to coarse scales.

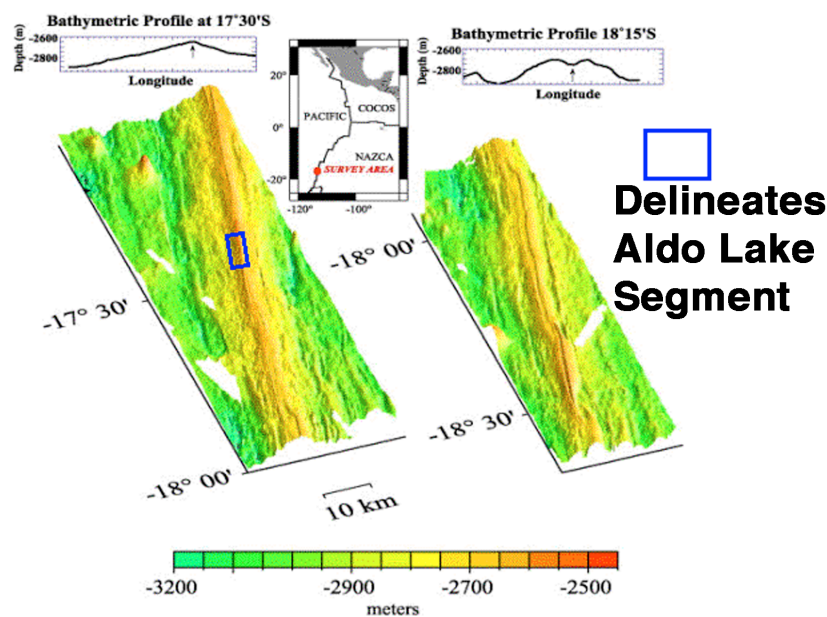


Figure 1. Sea Beam bathymetric maps and along-axis profiles of the sections along the southern East Pacific Rise (after White, 2001) that were surveyed on the Sojourn II expedition of 1996, from which the present study was derived (Sea Beam data from Scheirer et al., 1996). Aldo Lake section delineated by rectangle.

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). The hypothesis was tested at multiple scales, and could also be used to test whether or not the spatial arrangement between two different variables is that of CSR. An arrangement between two variables other than CSR infers that there may be a pattern-process relationship between them (Legendre and Fortin, 1989).

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 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). As such, the Ripley's K statistic is better suited to this analysis than other spatial statistics. For example, the Mantel test and partial Mantel tests are not suitable for point data, and moreover are restricted to detecting a single scale of pattern (Fortin and Gurevitch, 1993).

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 were observed, such as tubeworms, serpulid worms, and brachyuran crabs. A systematic approach to sampling in combination with >100% coverage of the study area produced a comprehensive data set for the spatial arrangement of the variables analyzed in this study at intermediate to coarse scales. Each species of vent animal 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 (after the relative age scale of Haymon et al., 1991), 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 (Table 1).

Observations were converted from their original lat./long. coordinates to decimal degrees and then to m. Then the geographic extent of the Aldo Lake segment was broken down further into 1110 m long sections from north to south. These segments were numbered 1-7 from North to South. 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). Ripley's K analysis was performed by 1110 m long section. Initial analysis indicated that clustering was common among and between variables at distances < 100 m for study areas $> 300,000 \text{ m}^2$. This prompted us to break the 1110m segments down further into 550 m long segments (1a,1b, 2a, 2b,etc ...), and re-calculate the Ripley's K statistics for each to obtain greater statistical significance. Each of the 550 m N-S segments was treated as a separate study area. Study areas ranged from $55,500 \text{ m}^2$ (narrowest) to $943,500 \text{ m}^2$ (widest). The results for the 550 m N-S segments are reported in tables 2 and 3 and will be the focus of discussion in this paper.

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. This program uses a toroidal-wrap edge correction method. Each response variable (serpulid worms, tubeworms, and brachyuran crabs) was analyzed 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 550 m (north-south) section, and analyzed 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 300 m of one of the attribute variable observations. The Ripley's K statistic was calculated for distance increments of 1m, from 1m to the distance of the shortest plot boundary. As described earlier however, inferences about clustering and spatial association between variables are only appropriate at distances greater than ~5-10 m's do to the resolution of the camera and the recording frequency of the continuous variables.

Ripley's K analysis was performed according to the protocol outlined by Moeur (1999). The following equation was utilized to calculate $K(d)$:

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

where

$$\Delta_{ij}(d) = \begin{cases} 1 & \text{if } d_{ij} \leq d \\ 0 & \text{if } d_{ij} > d \end{cases},$$

for n points on a plot of area A . $A / n \hat{K}(d)$ 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 $(100\% - 2\alpha \cdot 100\%)$ confidence envelope 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. One would expect the value of $L(d)$ to equal zero if the observed pattern were one of CSR or if there were no spatial relationship between the pattern of the response variable compared to that of a given attribute value. If $L(d)$ is positive (falls above the confidence envelope) as a result of a univariate analysis, the pattern observed in the data is considered to be aggregated or clustered. This means that in the observed data set, more points fall within a circle of radius d of a neighboring point than would be expected if the pattern were that of CSR. If $L(d)$ is negative (falls below the confidence envelope), as a result of a univariate analysis, the pattern observed in the data is considered to be uniform or regular. This means that in the observed data set, less points fall within a circle of radius d of a neighboring point than would be expected if the pattern were that of CSR. If $L(d)$ is positive as a result of a bivariate analysis then there are more response variable points observed to be within a circle of radius d of any given attribute variable point than one would expect to observe if both patterns had been generated independently by a Poisson process (Moeur, 1999). It is important to note

however that although a positive $L(d)$ suggests that there is a spatial relationship between two variables, PPA is limited in that it cannot make the distinction that this is a true “causal” relationship. A positive $L(d)$ in the case just described may represent an incidental relationship due to dependence on a shared third variable. The same holds true for a bivariate study that results in a negative $L(d)$ value relative the confidence envelope. Bivariate studies that result in a zero value for $L(d)$ however are sufficient to rule out a “causal” link between two variables.

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 2). 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 ~158m apart and the observations in section 4a were ~5 m apart. Bivariate analyses indicated that there was a positive spatial association between tubeworms and sheet flow and also between tubeworms and brachyuran crabs (Tables 2 and 3). 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 2 and 3). Tubeworm point observations in sections 2b and 4a were also found to be significantly associated with inactive hydrothermal chimneys (Table 3).

Univariate analysis revealed a clustered pattern (apparent at the scale of ~1m) for both of the 555 m north-south sections where serpulid worms were observed (Table 2). 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 flow (apparent at 1 and 3 m scales respectively), sheet flow (apparent at 8 and 14 m scales), fissures (apparent at the 45 and 6 m scales), hydrothermally inactive chimneys (apparent at the 7 and 2 m scales), white smoke (apparent at the 2 and 5 m scales), and brachyuran crabs (both apparent at the scale of 1m) (Tables 2 and 3). Positive associations between serpulid worms and tubeworms, age1 lava, and black smoke were also reported for section 1a (Tables 2 and 3).

Univariate analyses of the arrangement of brachyuran crabs revealed clustered patterns in sections 1a, 1b, 2a, 2b, 3a, 4a, 5a, and 5b (Table 2). 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, 19 m 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 2). Bivariate analyses revealed a positive association between brachyuran crabs and collapse flow in eight of the eleven sections where brachyurans were observed (Table 3). 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 3). 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 3).

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 m. 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 influenced by episodic eruptive processes. In 1993, scientists of the NAUDUR program characterized the ridge segment in the vicinity of 17° 25' S as an area that had recently experienced significant volcanic activity (Auzende et al., 1994). They based this conclusion on the gross appearance of the landscape. The lava flows of this particular ridge segment were characterized by the relative absence of sediment, the presence of several inactive hydrothermal chimneys, evidence of pre-existing vent macrofauna, and black smoke emerging directly from young lava (Auzende et al., 1994). The landscape described by the NAUDUR scientists is very similar to the landscape that was observed in 1996 by the Sojourn II scientists: active venting, inactive chimneys, and new sheet flow lava as well as mobile and sessile vent animals.

Our findings indicate 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 lava. However, while serpulid worms also showed a positive spatial association with collapse flow lava (thought to be relatively older than sheet flow) in both sections where they were observed, only the tubeworms in 1 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 indicate that tubeworms and serpulid worms may be temporally organized according to the “time since most recent eruption.”

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 3) 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 (e.g., Childress, 1988), so the absence of such features is puzzling. It is possible that the tubeworms observed in this study were associated with sources of active venting, but the vent sources were not observed or recorded by the Sojourner II scientists. If tubeworms are early colonizers of recently erupted areas, but are less well-adapted than e.g. serpulid worms to persist as active venting diminishes, then these tubeworm communities may be relictual from previous eruptions and would be expected to disappear or give way in favor of serpulid worms (or

other organisms) over time. An alternative hypothesis is that tubeworms are exploiting sub-seafloor sources connected to somewhat distant locations or sources indicative of a future eruption.

We suggest that vent fluid was available to the tubeworms in sections 2b, 3a, and 4a, however it was not detected by scientists aboard the Sojourn cruise for two possible reasons: (1) tubeworms were utilizing sulfide from microhabitats at their bases (2) tubeworms were utilizing sulfide from young point sources that were not obvious videographically. Support for microhabitat utilization comes from Julian et al. (1999) who propose that vestimentiferan tubeworms at certain cold seep sites and other low flow hydrothermal vent environments obtain sulfide exclusively via diffusion (at their bases) from pore water in the sediments. Their chemical analysis of tubeworm habitats on the Louisiana Slope in the Gulf of Mexico revealed high levels of sulfide in the sediments, and very little to zero levels in the vicinity of the tubeworm plumes (MacDonald et al., 1989; Simpkins, 1994). It is possible that tubeworms along the SEPR obtain sulfide at their bases as well, perhaps via a conduit to subsurface vent fluid.

The presence of “young,” undeveloped point sources is supported by the Auzende et al. (1994), who observed black smoke emerging directly from young lava in the vicinity of 17° 25' S. It is likely that the tubeworms in sections 2b, 3a, and 4a of the Aldo Lake segment were utilizing a similar form of venting although of a nature that was not obvious to Sojourn scientists remotely. As stated earlier, the Aldo Lake segment showed evidence of habitat turnover similar to that at 17° 25' S. 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 observation of Julian et al., (1999), MacDonald et al., (1989), and Simpkins, (1994) that we are still in the discovery phase with respect to our knowledge of the various idiosyncrasies and physiologic adaptations of vent animals. We have presented a statistical protocol that will aid in the examination of patterns in vent landscapes for spatial significance. Continued research is needed to develop statistically significant techniques for interpreting the costly and often complex data sets collected along mid ocean ridges. Spatial statistical tools can easily be adapted from those of traditional landscape ecologists, whose main foci are to understand pattern-process relationships. Furthermore, these techniques should be helpful in answering additional questions of causation such as:

- Are tubeworms and serpulid worms temporally organized according to “time since most recent eruption”?
- Are tubeworms at the SEPR capable of obtaining sulfide at their bases similar to tubeworms in the Gulf of Mexico?
- Are tubeworms less well adapted to persist than serpulid worms as active venting diminishes, or are the presence of small isolated tubeworm colonies somehow indicative of a future eruption?
- For a given species, 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 that are observed over the life of a given vent?

Armed with these questions, scientists should be able to optimize future data collection and design experiments more directly.

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Figure Caption

Figure 1. Sea Beam bathymetric maps and along-axis profiles of the sections along the southern East Pacific Rise (after White, 2001) that were surveyed on the Sojourn II expedition of 1996, from which the present study was derived (Sea Beam data from Scheirer et al., 1996). Aldo Lake section delineated by rectangle.

Table Captions

Table 1. Response and attribute variables used in the Ripley's K analysis of the study.

Table 2. 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.

Table 3. 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 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.

Table 1..

Response Variables (abbr.):	Attribute Variables (abbr.):
a) tubeworms (tube)	a) black smoke (blk. smk.)
b) serpulid worms (serp.)	b) white smoke (wht. smk.)
c) brachyuran crabs (brach.)	c) cloudy water
	d) fissures (fiss.)
	e) inactive chimneys
	f) sheet lava flow (sheet)
	g) collapse lava flow (collapse)
	h) pillow lava flow (pillow)
	i) lobate lava flow (lobate)
	j) 0.5 relative lava age (age 0.5)
	k) 1.0 relative lava age (age 1.0)
	l) 1.5 relative lava age (age 1.5)
	m) 2.0 relative lava age (age 2.0)

Table 3..

	blk.smk.	wht. smk.	cloudy water	fiss.	inactive chimneys	sheet	collapse	pillow	lobate	age 0.5
tube 1a (11)	+(3)	+(1)		+(37)	+(16)	+(6)	+(4)	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	
serp 1b (12)		+(5)		+(6)	+(2)	+(14)	+(3)	Ø	Ø	
brach 1a (103)		+(1)		+(2)	+(4)	+(1)	+(1)	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
brach 4a (8)					Ø	+(17)	+(19)	Ø	Ø	Ø
brach 4b (6)						Ø	+(14)		Ø	
brach 5a (7)						+(21)			Ø	
brach 5b (15)	+(4)	+(4)			+(4)	+(3)				
brach 6a (2)						Ø	+(24)	Ø		
brach 6b (1)							Ø	+(11)		