A Novel Landscape Ecology Approach for Determining Microhabitat Correlations and Faunal Patchiness in Extreme Environments: Pilot Study for the Southern East Pacific Rise at 17-18˚S

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Introduction

Since their discovery in 1977, hydrothermal vent communities have offered scientists a unique glimpse into a world that is supported primarily by chemically derived energy rather than direct energy from the sun. Furthermore, studies of hydrothermal vent ecosystems have introduced scientists to amazing animals that have successfully adapted to living in extreme environments. Although much has been learned about the life histories of vent organisms, due to the difficulty and expense of performing large scale (spatial and temporal) studies at deep sea hydrothermal vent sites, our knowledge of vent faunal dynamics is largely based on observational studies that often lack the support of sound statistical analysis. Furthermore, data sets can be discordant in space and time, making it difficult to piece together the potentially complex life histories of vent animals. The main goal of this report is to study the applicability of point pattern analysis, a simple spatial statistical method based on principles of landscape ecology, for characterizing the distributions of organisms at hydrothermal vent sites.

The study began as a pilot project, and has focused on an existing high resolution, remotely sensed, data set from the superfast-spreading southern East Pacific Rise at 17-18° South (Figure 1). It was accomplished through an integration of remote sensing technology, landscape ecology principles, and geographic information science.

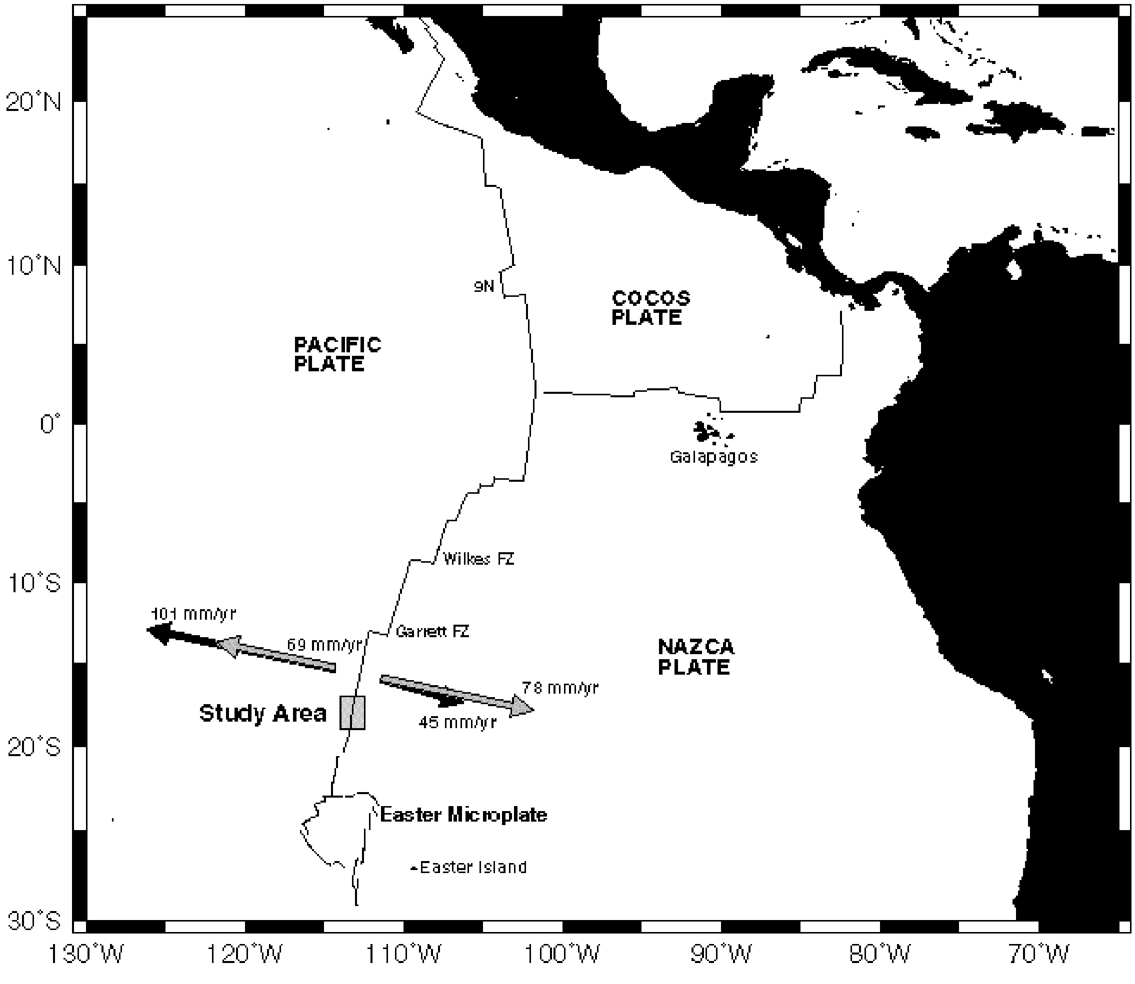

Figure 1. Regional location map of the study area on the southern East Pacific Rise, from Wright et al. (in press). Arrows near study area are Pacific-Nazca plate motion vectors from Cormier et al. (1996). Solid arrows represent absolute plate motion and gray arrows indicate relative plate motion.

This study was designed to identify: (1) patterns, if present in the arrangement of fauna at hydrothermal vent sites, and the scales at which the patterns are being expressed; and (2) the process or processes that may be influencing the patterns.

Background

Fifteen hundred to three thousand meters below the surface of the ocean, new oceanic crust is continuously being produced at mid-ocean spreading ridges. New crust is formed as molten rock deep within the earth's mantle that rises up to fill a rift in the ocean floor. Cracks in the ocean floor are formed by three processes: (1) magmatic intrusion (extensional cracking in the crust overlying dikes or magmatic diapers), (2) lithospheric stretching (amagmatic, tensile cracking as the ridge accelerates from zero velocity to its full spreading rate), or (3) thermal contraction of aging crust where tension cracks result from the shrinkage of cooling rock (Wright, 1998). These cracks allow seawater to trickle down towards the warm mantle where it is heated, then returns to the ocean floor as super hot (300-400˚C), chemically altered springs that are commonly known as hydrothermal vents.

The first hydrothermal vent systems were documented in 1977 by John Corliss of Oregon State University and John Edmond of Massachusetts Institute of Technology in an area known as the Galapagos spreading center (Corliss et. al, 1979). Hydrothermal vent discharge is often subdivided into low temperature (10-20˚C) flow, occurring diffusely along the cracks and fissures on a ridge and high temperature (300-400˚ C) flow, that spouts from isolated openings often only a few centimeters in diameter. A third type of flow is also recognized and referred to as episodic "event" discharge. Episodic discharge occurs less frequently and is usually associated with a tectonic or magmatic event that allows for the short-lived escape of vent fluid through cracks and fissures as the the ocean floor shifts (Helfrich and Speer, 1995; Mullineaux and France, 1995). The chemical nature of individual vents and “families” of vent effluent also vary from site to site depending on such factors as the temperature of the effluent, the age of the vent, the resident bacterial population, and the substrate underlying the vent opening (Jannasch, 1995). However, regardless of the exact composition of the effluent relative to ambient seawater, all vent fluids are characterized by the presence of high concentrations of ions such as S, Fe, Mn, and Mg. Another unique feature of vent effluent is that reduced ions are usually present at high enough concentrations to support chemosynthesis, and thus allow these light deprived hydrothermal systems to play host to a rich faunal community. Chemoautrophic bacteria are capable of harvesting a portion of the free energy that is released with the oxidation of electron donors such as H_2S, H_2, and CH_4 as vent fluid mixes with oxygen rich ambient seawater. The bacteria use this energy to drive the synthesis of organic matter from carbon dioxide and water. Studies to date indicate that quantitatively, hydrogen sulfide is the most significant reductant at deep sea hydrothermal vent sites (Jannasch, 1995).

Chemoautotrophic bacteria form the base of the food web as the vent primary producers (Fisher, 1995 ; Jannasch, 1995). These bacteria are present in vent effluent, in and on the walls surrounding the subsurface plumbing systems, on the substrate surrounding vents, and on the surfaces of other vent organisms. Chemoautotrophic symbiotic vent bacteria are hosted by animals such as vestimentiferon tube worms, vesicomyid clams, and mussels and provide these animals with organic carbon in exchange for essential nutrients such as sulfur and nitrate. This group of animals is considered as the vent primary consumers. Other hydrothermal vent primary consumers are the suspension feeders such as the serpulid worms, and the grazers such as the limpets and the Bresiliid shrimp. The presence of scavengers and carnivores such as crabs, fish, worms and shrimp is also a characteristic of vent ecosystems. A host of parasites and heterotrophic bacteria flourish in vent fields as well. Vent fields range in size from a few square meters to several hundred square meters and are composed of several combinations of the >300 species of vent animals that have been identified to date (Hessler and Kaharl, 1995). The area immediately adjacent to the site of discharging vent effluent is characterized by extreme shifts in temperature, metallic ion concentration, and oxygen saturation levels. As the current shifts, the vent animals are exposed alternately to vent effluent (high ion concentrations, high temperatures, low oxygen) and ambient seawater (low ion concentration, low temperature, high oxygen). Remarkably, some vent animals have adapted to and even taken advantage of the best of both environments. Animals that live near hydrothermal vent effluents have adapted to amazing variations in temperature. Tube worms have been observed in waters measuring 40˚C at their bases, while at the same time their gills are bathed in ambient bottom water at 2˚C. Vent animals such as the Pompeii worm have been observed swimming near temperature probes that have read 110˚C (Hessler and Kaharl, 1995), and vent bacteria are commonly observed at these temperatures (Jannasch, 1995). Furthermore, many vent animals have become tolerant of sulfide concentrations that would be toxic to most other animals on earth (Fisher, 1995).

To date, several hydrothermal vent systems have been documented, sampled, photographed and mapped with the aid of submersible vehicles such as *Alvin*, and various optical/acoustic towed systems. Vent communities have been identified and studied along the Reykjanes Ridge (North Atlantic; German et al., 1994), Mid-Atlantic Ridge (Klinkhammer et al., 1985; Nelson et al., 1986/1987; Charlou and Donval, 1993; Murton et al., 1994), Gulf of California (Lupton, 1979), northern and southern East Pacific Rise (Lupton and Craig, 1981; McConachy and Scott, 1987; Baker et al., 1987; Collier and Baker, 1990), and the North Fiji Basin (Auzende et al., 1994a). Knowledge of vent faunal dynamics however, is largely based on observational work and often life histories are inferred from vent related organisms that reside at more accessible and not so extreme environments such as seeps and whale falls. Furthermore, information is often discordant in space and time, leaving many holes to be filled in the life histories of vent ecosystems. For example, one of the most famous case studies of a hydrothermal vent system was performed at the Galapagos Rift in an area of venting called the Rose Garden at 00˚48.247'N, 86˚13.478'W. Faunal distributions were mapped from photographs taken by a near-bottom towed submersible camera initially in 1979, and again in 1985 (Hessler et. al, 1988). Results of the study showed that although the pattern of venting remained approximately the same over the interval, "virtually all" of the faunal groups had undergone dramatic changes of some sort. Faunal changes were observed in density and total number of organisms, species make-up of communities, and in the spatial arrangement of species. This discovery and others like it have provided evidence that vent-scapes are dynamic systems. We still lack, however, a detailed description of the complex interactions that occur among vent species and between these animal and their environment. It is these interactions that ultimately dictate the patterns that we observe in the ecosystem (Hessler et. al, 1988).

Observational studies have led to the commonly accepted hypothesis that vent biological communities are arranged in concentric layers around a source of effluent according to their mode for obtaining energy. *Hessler and Kaharl* (1995) describe vent fields as being composed of three zones starting from the vent source and radiating outward. The names of the zones are vent opening, near field, and periphery. The boundaries between each of the rings are delineated by the extent of the species groups that are found within each zone. Presumably, it is only the distance from the source of the effluent that is driving the distribution of vent fauna. This popular idea however, lacks significant statistical support and more recent discoveries about the physiology of vent related organisms at more accessible sites for study and studies that have looked at the feedback affects of vent fauna on their environments indicate that other factors may be involved in the arrangement of vent fauna as well.

For example, vesicomyid clams that have been studied at cold seep environments have the ability to plant their feet in cracks and crevices along ridges and take up sulfur via diffusion from pore water, and it is very likely that vesicomyid clams at deep sea vents have the same ability. In a similar manner, it has been hypothesized that close relatives of deep sea tubeworms that have also been studied at more accessible environments, such as cold seeps, have the ability to obtain sulfur by diffusion from pore water at their bases (Julian et al., 1999). If, in fact, vent animals are utilizing both the vent effluent and microenvironments as sources for obtaining sulfide, then spatio-temporal relationships with prominent vent openings may not be as simple as first presumed.

As mentioned in the introduction, the chemical composition of a given point source of discharge or family of discharge (as with diffuse flow) can vary from location to location as well as throughout the life cycle of a given vent. In general, “hot” (~350-360˚C) eruptive vents that exit the sea floor from a point source such as a chimney are high in FeS and Mn^{2+} while warm (~3-30˚C) diffuse flow vents tend to be high in S_2, CO_2, and CH_4 by comparison (Jannasch, 1995). Von Damm (1995) suggests that individual vents also experience chemical flux throughout their lifetime and describes three distinct stages with respect to this flux. The first stage is the early post-eruptive period and is characterized by large fluctuations in the chemical nature of the effluent. The second is a steady state period where the chemical makeup of the vent fluid appears to stabilize and remain constant. This steady state period may last up to several years. The third stage is described as a final “waning” phase whereby the fluid once again undergoes significant chemical flux until the vent is eventually exhausted. To date, a wide range of bacteria have been isolated from deep sea vent sites, many of which exhibit very special nutritional and environmental requirements. It is very likely that even subtle differences in the chemical makeup of individual vents will be important factors in determining the type of bacteria that are able to set up residence and eventually thrive at a particular vent site. In fact, scientists who study microbial interactions with hydrothermal fluid propose that sulfide content and oxygen saturation along with the temperature of the vent fluid are primarily responsible for driving the rate of microbial production. Jannasch (1995), notes that "effective production is ultimately a function of the geochemical setting."

There is also evidence suggesting that the chemical nature of vent fluid can be altered by the bacteria that colonize it. For example, the presence of certain chemosynthesizing bacteria can significantly influence the chemical nature of vent fluid through the production of methane during anaerobic chemosynthesis (Von Damm, 1995). It is also hypothesized that acidic microenvironments created by dense microbial mats at some deep sea vents may be supporting certain pH dependent hyperthermophiles. Physical characteristics of the venting environment may also influence colonization by vent organisms and vice versa. Juniper and Sarrazin (1995) describe a temperature selective process by which vent chimney surfaces are colonized by bacteria as they evolve from relatively unstable, porous structures with surface temperatures upwards of 100˚C to rigid non-porous structures with cool surface temperatures.

These same authors also cite several studies where faunal patterns and distributions at vent sites were observed to alter vent flow indirectly by influencing local deposit formation and destruction.

It is the author's hypothesis that the zonation around vents does not correlate strictly with distance from the effluent source but will be dependent on additional variables such as those described above. To date however, we do not have the tools in place to investigate these processes in a statistically sound manner. A landscape ecology-based study would begin to establish a foundation or framework for studying the multi-dimensional spatio-temperal dynamics of hydrothermal vent landscapes and establish a protocol for pursuing questions about pattern and process relationships. The intent of this report is to focus on hydrothermal vents as dynamic ecosystems and to develop a protocol for investigating the idiosyncrasies of vent fauna and the complex physical, chemical, and geological relationships that they have with their environments.

Landscape ecology is broadly defined as the study of pattern-process relationships as they occur over a spatially heterogeneous area or landscape (Turner, 1989). A landscape can be defined by its structural or functional characteristics and it can be studied over space and time. Landscape ecologists routinely classify space as patches (areas of homogeneity), or as networks (corridors for movement or connectivity beween patches), and they employ spatial statistical analysis to predict pattern-process interactions within an ecosystem.

Spatial statistical analysis is appropriate for studies in which one suspects that an underlying spatial phenomenon or process is driving the "structure" of the data in question (Legendre and Fortin, 1989). For example, many ecological models assume that sampling points that are close together in space have a greater influence on each other that those that are farther apart. When in fact this does occur, and an ecological phenomenon located at a given sampling point appears to exhibit influence on the value of its neighbors, the independence assumption of classical inferential statistics is breached. Sample values are said to be dependent on one another and as a consequence, the potential exists that classical statistical tests of correlation, regression, and analysis of variance will identify significant differences among groups where in reality none is present. Spatial statistical methods are not bound by such stringent assumptions and are used to actually identify pattern or "dependent variables" if present in the data. One goal of spatial statistical analysis might be to identify pattern so that it can be extracted from the data set in question. In this manner, methods of parametric statistical analysis can still be carried out on the residual data. The main goal of other studies however, is to highlight pattern if present in a data set and then use this information to gain insight into the processes that are driving the objects of the study.

Spatial statistical methods look for autocorrelation in a data set. "A variable is said to be autocorrelated when it is possible to predict the values of this variable at some points of space, from the known values at other sampling points, whose spatial (or temporal) positions are also known" (Legendre and Fortin, 1989). Autocorrelation can be "positive" or "negative" and can vary with the scale of a particular study. For example, a "patch" or tight group of organisms may exhibit positive autocorrelation at a landscape scale and negative autocorrelation at the scale of a few individuals. Gradients of distribution often exhibit positive correlation at small scales (short distances between sampling points), and negative correlation at large scales (long distances between sampling points; Legendre and Fortin, 1989).

Point pattern analysis (PPA) is a spatial statistical method that is used to study the distribution of objects that can be represented as points in geographic space. Specifically, PPA tests the hypothesis that the data in a particular study area are distributed randomly (Legendre and Fortin, 1989). A random distribution is specifically described as complete spatial randomness (CSR), and meets the assumptions of uniformity and independence. As described by Boots and Getis (1988), the uniformity assumption is met when each location in the study area has an equal chance of receiving a point. The independence assumption is met when the selection of a location for a point in no way influences the selection of locations for any other points (Boots and Getis, 1988). Patterns other than CSR in the data are described according to the way the points depart from CSR (Figure 2). For example, a "clustered" pattern describes a group of points that are significantly closer together than one would observe for the same number of points over the same area if the pattern was one of CSR. A "regular" pattern describes a group of points that are significantly further apart then one would observe for the same number of points over the same area if the pattern was one of CSR.

Examples of Pattern

Random Pattern (CSR)

Clustered Pattern

Regular Pattern

Figure 2. Examples of point patterns, after Boots and Getis (1988).

Methods

In this study, 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 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.

It is important to note however, that PPA cannot determine if this association is significant or coincidentally due to a common third variable (Legendre and Fortin, 1989).

The Data Set

The data set for this study includes high resolution, remotely sensed video imagery collected from the superfast-spreading southern East Pacific Rise (SEPR) from 17-18°S during the Sojourn II cruise aboard the *Research Vessel Melville* in 1996 (Haymon et al., 1997). The near-bottom imaging capability of *ARGO II*, a fiber-optical, acoustic towed camera system was used to obtain video footage of active and inactive hydrothermal vents, vent animals, lava flows of different ages and types, and fissures. Images were observed from *Argo II's* forward looking camera (swath width ~16m) as it was towed ~9m above the sea floor. Videographic images were observed in real time by two above-board scientists as they logged the information into a computer. Each observation was "stamped" with the time of observation as well as an x-y coordinate relative to a seafloor transponder navigational net, that was later transformed to longitude-latitude. This important step in data acquisition facilitated conversion to ArcInfo coverages or ArcView shapefiles for ease of mapping while still at sea, as well as for future statistical manipulation onshore (Wright et. al., in press).

The data for this project were originally collected to study the relationship between along-strike thermal gradients that are set up by the segmented supply of magma to fast-spreading mid ocean ridges, and the resulting distribution and types of hydrothermal vents and vent biota along the ridge (Haymon et al., 1997). Of particular interest at this site is a segment of the axial magma chamber from ~17˚25'-27'. The normally flat-topped profile of a magma chamber one would typically see underlying the seafloor at a mid-ocean ridge exhibits an unusual "spike" in this region. This "spike" allows for the intrusion of magma to a relatively shallow depth (within 0.8km of the seafloor), and sets up extremely steep along-strike thermal gradients (Detrick et al., 1993).

For the purposes of the current study, a subset of the original data set was obtained in order to achieve a more statistically manageable set of data points. This project focused specifically on the arrangement of vent animals along an 8km segment of the SEPR from 17˚26'-30'. This region is known as the Aldo Lake Segment (Haymon et al., 1997; White et al., 2000) and was chosen because it included examples of each of the response variables of interest (tube worms, serpullid worms, and brachyuran crabs), and because there was excellent videographic coverage (105-130%) in this area (Wright et. al, in press). Videography allowed for systematic sampling of the study area. Data were obtained for the entire width of the study area via multiple passes along a N-S transect. A systematic approach to sampling maximizes the potential for finding pattern (if it exists) in the data. 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 type, 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.

Response Variables:
a.) tube worms
b.) serpulid worms
c.) brachyuran crabs

Attribute Variables:
a.) fissures
b.) active venting
c.) black smoke
d.) white smoke
e.) cloudy water
f.) inactive chimneys
g.) sheet lava flow
h.) collapse lava flow
i.) pillow lava flow
j.) lobate lava flow
k.) .5 relative lava age
l.) 1.0 relative lava age
m.) 1.5 relative lava age
n.) 2.0 relative lava age

Relative lava ages for the *Argo II* survey areas are based on the apparent thickness of small interpillow sediment ponds. Relative age categories were based on Haymon et al. (1997): “youngest” or Age 1.0 lava flows (no sediment cover, highly vitreous luster on glassy flow surfaces); Age 1.2 lava flows (light “peach fuzz” of sediment cover, vitreous luster); Age 1.5 lava flows (light sediment cover within grooves and cracks in pillows, vitreous luster diminished, no sediment pockets); Age 1.7 (no vitreous luster, very small sediment pockets (~2cm across) on and between pillows;

“intermediate” or Age 2.0 flows (sediment pockets well-developed between pillows, and duller flow surfaces); and “oldest” or Age 3 flows (sediment pockets deep enough to connect between pillows, and dull, unreflective flow surfaces).

It was necessary to manipulate the Aldo Lake data further to fit the statistical package of choice. Observations were converted from their original lat./long. coordinates to decimal degrees and then to meters. Next, the Aldo Lake segment was broken down further into 1110m sections 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). The grid size was manipulated when ever possible to achieve more statistical significance at fine scales. Examples of study area extent ranged from 300,000m^2, to 42,400m^2, to 15m^2, to 65m^2.

Statistical Analyses

Ripley’s K(d) analysis was performed using a program that was developed by Melinda Moeur of the USDA Forest Service, Rocky Mountain Research Station (Moeur, 1999). The program runs in a DOS shell from Windows and is capable of computing both univariate and bivariate Ripley’s K analysis for random, clustered and uniform patterns.

Each response variable (serpullid worms, tube worms, and crabs) was analysed by 550m(NS) section for the presence of spatial pattern within the population (ie., univariate analysis). Next, each of the response variables were compared to each of the attribute variables by 550m (NS) section and analysed for the presence of spatial pattern between the two populations (ie., bivariate analyses). Comparisons were also made between the different response variables, for example between serpullid worms and brachyuran crabs. Analyses were run for all pairs of response and attribute variables where atleast one of the response variable observations was located within 300m of one of the attribute variable observations.

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*_*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 (_=.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. A negative value for *L(d)* might also be seen if the initial sampling interval was larger then the overall size of a cluster. 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 of the tube worm data set. This 55-m N-S section included 11 data points representing tube worm observations. Other sections containing tube worm observations were section 2b (2 observations), section 3a (1 observation), and section 4a (2 observations). The tube worm observations in section 2b were ~158m apart and the observations in section 4a were ~5m apart. Bivariate analyses indicated that there was a positive spatial association between tube worms and sheet flow and also between tube worms and brachyuran crabs. These associations were significant in each of the sections where tube worms were observed. In section 1a, the locations of tube worm point observations were also found to be associated with black and white smoke, collapse lava flow, fissures, and inactive hydrothermal chimneys. Tube worm point observations in sections 2b and 4a were also found to be significantly associated with inactive hydrothermal chimneys.

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

Univariate analyses of the arrangement of brachyuran crabs revealed clustered patterns in sections 1a, 1b, 2a, 2b, 3a, 4a, 5a, and 5b. Clustering was apparent at the scale of 1-2 meters for sections 1a, 1b, 2a, and 3a, 7-8 meters for sections 2b and 5b, 30 meters for section 4a, and 57 meters 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 tube worms as well as brachyuran crabs and serpulid worms for each section where tube worms and serpulid worms were observed. Bivariate analyses revealed a positive association between brachyuran crabs and collapse flow in eight of the eleven sections where brachyurans were observed. Bivariate analysis also revealed a positive spatial association between brachyuran crabs and sheet flow in nine of the eleven sections where brachyurans were observed. 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). See Tables 1a and 1b for a summary of the results described above.

Table 1a. Results of univariate and bivariate analyses involving lava flow distributions. + Indicates clustering (univariate analysis) + Indicates positive association in geographic space (bivariate analysis) Scale (m) of apparent aggregation/association in geographic space in parenthesis.

	a_combo	age 0.5	age 1.0	age 1.5	age 2.0	blk smk	coll	lob	pill
tube1a	+(1)					+(3)	+(4)		
tube2b									
tube3a	+(58)								
tube4a	+(2)								
serp1a	+(5)		+(19)			+(5)	+(1)		
serp1b	+(1)						+(3)		
brach1a	+(2)		+(24)				+(1)		
brach1b	+(2)						+(1)		
brach2a							+(1)	+(33)	
brach2b		+(1)					+(3)	+(8)	
brach3a	+(18)					+(28)	+(4)		
brach4a							+(19)		
brach4b							+(14)		
brach5a									
brach5b	+(4)					+(4)			
brach6a			+(14)	+(10)			+(24)		
brach6b				+(6)					+(11)

Table 1b. Results of univariate and bivariate analyses involving hydrothermal vent distributions. + Indicates clustering (univariate analysis) + Indicates positive association in geographic space (bivariate analysis) Scale (m) of apparent aggregation/association in geographic space in parenthesis.

	sheet	fissures	hya_chim	hyi_chim	wht_smk	serp	brac	tub
tube1a	+(6)	+(37)		+(16)	+(1)	+(1)	+(1)	+(1)
tube2b	+(36)			+(35)			+(8)	
tube3a	+(18)						+(8)	
tube4a	+(19)			+(57)			+(38)	
serp1a	+(8)	+(36)		+(7)	+(2)	+(1)	+(1)	+(1)
serp1b	+(14)	+(6)		+(2)	+(5)	+(1)	+(1)	
brach1a	+(1)	+(2)		+(4)	+(1)	+(1)	+(1)	+(1)
brach1b	+(3)	+(3)		+(1)	+(2)	+(1)	+(1)	
brach2a	+(5)	+(10)		+(9)			+(2)	
brach2b	+(2)	+(63)		+(35)			+(2)	+(8)
brach3a	+(4)		+(22)	+(16)	+(17)		+(1)	+(8)
brach4a	+(17)						+(19)	+(38)
brach4b								
brach5a	+(21)						+(58)	
brach5b	+(3)			+(4)	+(4)		+(2)	
brach6a								
brach6b								

Discussion

The combination of a systematic sampling method and the resolution of the camera used for videography ultimately determined the scale of analysis in this study, and as such limited the scope of this study to those relationships that were apparent at an intermediate scale (from ~5-10 m to a few hundred meters). Without sacrificing resolution, coarse scale analysis of this data set beyond the order of a few hundred meters of ridge segment would have involved more data points than the statistical package in this study could handle. Fine scale observations such as among individual animals, on the other hand, would have required a sampling method with greater resolution. Fine scale data would also have resulted in an even larger data set per area sampled, and entailed significantly higher costs for data aquisition.

One of the more interesting results that came out of this study was the lack of correlation between the arrangement of tube worm observations in sections 2b, 3a, and 4a and an active form of hydrothermal venting. Three obvious and very different conclusions might be drawn from these results: (1) tube worms are not dependent on vent fluid for their livelihood; (2) the tube worms observed in this study were associated with sources of active venting, however the vent sources were not observed or recorded by the Sojourn II scientists; and (3) Ripley's K analysis produced erroneous results with respect to this data set. As the first conclusion should be ruled out based on well-established knowledge of tube worm physiology (Childress et al., 1984,1987; Cavanaugh, 1985; Johnson et al., 1986; Childress, 1988), the second conclusion will be proposed in lieu of the third.

It is suggested 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) tube worms were utilizing sulfide from microenvironments in the sediment, (2) tube worms were utilizing sulfide from young point sources that were not obvious videographically. Support for microhabitat utilization comes from Julian et al., (1999). These scientists propose that vestimentiferan tube worms 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. This proposal comes from studies of vestimentiferans at cold seep environments on the Lousiana Slope in the Gulf of Mexico where chemical analysis of tubeworm habitat 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).

Support for the presence of "young," undeveloped point sources actually comes from earlier studies performed in the same vicinity as this data set by a team of French researchers. Scientists of the 1993 NAUDUR program concluded that the ridge segment in the vicinity of 17˚ 25' S was an area that had recently experienced significant volcanic activity (Auzende et al., 1994b). They based their conclusions 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., 1994b). Based on observations by the NAUDUR scientists, it is likely that the tube worms observed by the Sojourn II scientists were exploiting relatively young sources of vent fluid. In fact, tubeworms were found to be positively associated with young sheet flow lava in all of the sections and in three out of four of the sections containing tube worm observations, tube worms were found to be positively associated with inactive chimneys. The presence of inactive chimneys, new sheet flow, and young colonies of vent macrofauna along with results from the univariate and bivariate tubeworm analysis performed in this study, indicate that this segment of the SEPR continues to be a “hot spot” for volcanic as well as tectonic activity.

As expected, serpulid worms were positively associated with several types of active venting including fissures, and black & white smokers, although the scale of these associations differed dramatically. It would be useful to test these relationships further for causal significance and for possible preferences to a specific character of vent effluent. As with tube worms, serpulid worms were also found to be positively associated with sheet flow. Serpullids were also found to be associated positively with collapse flow. This association may indicate a connection between serpulid colonization and the relative age of a site of venting. As with serpulids and active venting however, further tests for causation are warranted.

Although brachyuran crabs were found in regions of the study area that did not show evidence of tubeworm or serpullid worm colonization, sections that reported the largest numbers of brachyurans were also those that contained tube worms and serpulid worms. Furthermore, brachyurans exhibited a positive spatial association with tube worms and serpulid worms in these same sections. This finding is in line with what is currently known about the brachyuran crab as an opportunistic feeder, and the author believes it to legitimatize the protocol that is outlined in this paper for studying relationships between volcanic, tectonic, and hydrothermal phenomena. Other relationships highlighted in this study, such as the relationship between serpullid worms and several forms of hydrothermal venting, serve to raise more questions about these relationships. Both positive and negative associations in the data set raise the question of a “causal linkage.” As described earlier, although PPA is an excellent tool for demonstrating spatial relationships between two variables, it is not capable of differentiating a “causal” relationship from an “incidental” relationship due to a third shared variable. Fortunately, there are additional spatial statistical methods available to which one can turn next to answer this question, although time did not allow for these to be performed during the author’s tenure at Oregon State University.

Conclusions

There is a great deal to be learned about the complex geologic, biologic, chemical and physical interactions that are inherent to our own unique and dynamic planetary ecosystem through the study of hydrothermal vent ecology. However, there is currently a need for the development of spatial and temporal analytical tools as well as protocols for their use in this field if we are to continue to make great strides in understanding these complex systems. These tools can be adapted from those of traditional landscape ecologists, whose main foci are to understand patter-process relationships. The techniques described in this paper should provide scientists with a powerful statistical protocol that will allow us to examine patterns in vent landscapes for spatial significance. Furthermore, these techniques will help us to answer the following questions:

- For a given species, are the numbers of animals observed correlated with microhabitat features?
- For a given species, what are the scales of aggregation (clumping)? 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?

Future Studies

Partial Mantel tests could be used to determine a “partial” correlation between a causal/attribute and response variable while controlling for the effects of spatial autocorrelation or a third variable that is partially influencing the expression of each. The author believes that this test would be appropriate for studying the arrangement of vent macrofauna in this data set to help answer the questions of causation and partial causation between the response and attribute variables that have been raised with PPA. This test will atleast rule out correlation where none exists between two variables that might have been “linked” by a common third variable such as venting or space. A combination of full and partial Mantel statistics (Legendre and Fortin, 1989) would begin to narrow the list of potential causal variables and possibly help to quantify these relationships. The following is a list of potentially useful Mantel comparisons that the author believes to have arisen from this study: (1) tube worms vs. sheet flow vs. space, (2) tube worms vs. brachyuran crabs vs. space, (3) serpulid worms vs. collapse flow vs. space, (4) serpulid worms vs. sheet flow vs. space, (5) serpulid worms vs. fissures vs. space, (6) serpulid worms vs. hydrothermally inactive chimneys vs. space, (7) serpulid worms vs. white smoke vs. space, (8) serpulid worms vs. brachyurans vs. space, (9) brachyurans vs. collapse flow vs. space, and (10) brachyurans vs. sheet flow vs. space.

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