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Crustal accretion and the hot vent ecosystem

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We examine evidence for links between seafloor spreading rate and properties of vent habitat most likely to influence species diversity and other ecosystem properties. Abundance of vent habitat along spreading centres appears positively related to spreading rate while habitat stability shows an opposite relationship. Habitat heterogeneity is lowest at faster spreading ridges. Limited data indicate an increasing species diversity with spreading rate, complicated by historical factors. Ecosystem productivity and efficiency of resource utilisation may also reflect diversity differences.

1. Introduction

In explaining organism distribution or in quantifying flows of energy and materials, ecologists are confronted with changing communities whose component populations shift as do interactions with the environment. Fitting patterns to observed changes and formulating predictive models are important elements of contemporary ecology. How we examine a novel system, like that of deep-sea hydrothermal vents, depends partly on our *a priori* beliefs on what the important controls will be. Explanations of community composition and structure include three fundamental view-points: (1) control through biological interactions such as competition and predation; (2) control through environmental limitations such as energy supply or growing conditions; and (3) influence of historical events (see Real & Brown 1991). Their relative importance seems to vary depending upon the system under study, as well as the spatial and temporal scales being examined.

The hydrothermal vent ecosystem requires the chemical energy present in discharging fluids. Distribution of vent communities is thus controlled by the mantle and crustal processes that determine the nature and distribution of hydrothermalism. Even vent community composition is subject to geological and geophysical controls, at all levels: from locally through hydrology (Grehan & Juniper 1996), to globally, through the historic relations of tectonic plates (Tunnicliffe & Fowler 1996). While every ecosystem is shaped by the environment in which it is found, physical (environemental) controls are often complicated, if not obscured, by interaction with biotic processes. Vent ecosystems appear to provide a prime example of accommodation to the physical environment, where geological and geophysical controls are clearly evident across a broad spectrum of space and time scales. Hot vent faunas are influenced

TEX Paper

460   S. K. Juniper and V. Tunnicliffe

ecosystem properties

Composition	Structure
species present habitat conditions	spatial distribution biomass/abundance population data trophic relationships

Dynamics

    succession
    growth & productivity
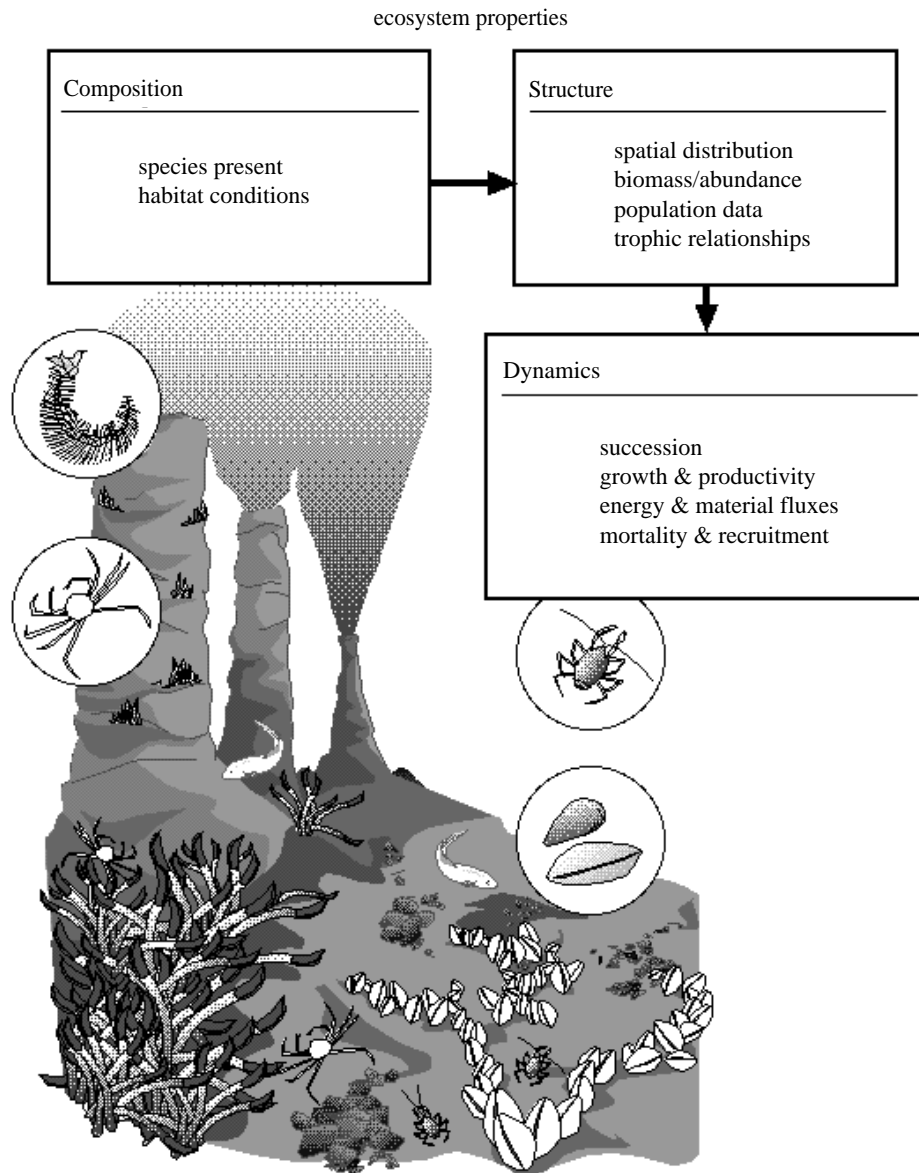   energy & material fluxes
    mortality & recruitment

Figure 1. Major ecosystem properties in relation to information required to understand them.

by the tectonic and volcanic processes of crustal accretion because hydrothermalism dictates the habitat. Numerous papers discuss the link between tectonism and volcanism and venting; a most complete recent review is that of Fornari & Embley (1995). It is a small step to make a further link to the biological system. The present challenge is to identify those processes with the greatest control on ecosystem development and functioning and to evaluate whether or not these relationships are amenable to predictive models.

Ecosystem properties can be seen to exist at three conceptual levels that require different levels of knowledge of organisms and environment (figure 1). A first level of

understanding is essentially an inventory of the species present and a description of their habitat derived from collections and simple field observations. At the next level, to understand ecosystem structure and identify functional links, quantitative information on species abundance and biomass and knowledge of trophic relationships is required. Finally, measurement of biological rate processes (metabolism, growth, reproduction, etc.), time series observations (colonization, succession) and experimentation enable ecologists to develop models of ecosystem dynamics. Dynamic models require equivalent environmental information for consideration of the physical forces that can drive ecosystem processes.

While the hierarchical representation in figure 1 implies a progressive path of information sophistication and depth of understanding, present knowledge of vent ecosystems tends to reflect the logistic realities of working in the deep sea more than it does any model of how ecological research is conducted. Until recently, vent ecologists were primarily limited to data describing ecosystem elements. Quantitative sampling at vents with submersibles has proved technically difficult and the few estimates that exist do not allow any consideration of environmental influences on biomass or abundance. Knowledge of feeding relationships and trophic structure is incomplete, and the contribution of chemosynthetically produced organic matter remains unquantified (Karl 1995). We know that chemosynthetic microbes provide at least some food for the macrofauna either in symbiosis or through ingestion of free living cells (see conceptual model in Tunnicliffe (1991)). Vent fluids provide the compounds that microorganisms oxidize to generate energy for organic carbon synthesis. Dissolved O_2 for oxidation processes at vents originates from photosynthetic sources. Hydrogen sulphide abundance and the energetics of the oxidation reaction result in a predominance of sulphide-oxidizing microbes at vents (Jannasch 1985, and this volume). Beyond this, we have only a rudimentary grasp of vent ecosystem structure and its accommodation to physical controls.

Vent ecosystem properties are thus understood in an unequal and incomplete manner, imposing definite constraints on the questions that can be addressed in this paper. One of the few comparative pieces of information available on global vent communities is the type and number of species present. Naming and classifying species has represented a major effort partly because of the unusual nature of many of these animals and the fact that more than 90% are species new to science (Tunnicliffe 1991). Numbers of species vary dramatically across the ecosystems of our planet and among similar ecosystems. The major explanations for this variation include habitat stability, level of productivity, habitat heterogeneity (Brown 1988) and geological age (Sanders 1968). We will consider different spatial and temporal properties of the Mid-Ocean Ridge (MOR) vent environment and examine evidence for influences across the three levels of ecosystem properties outlined in figure 1. Reliance on species distribution information limits the scope of our evaluation, since occurrence data are not powerful indicators of community structure or dynamics. Precise locations of all sites mentioned can be found in Fornari & Embley (1995) and Hannington *et al.* (1995).

2. Distribution of vent habitat

Vent habitat has a highly irregular distribution in an approximately linear trend. Communication between vents becomes erratic or intermittent beyond the turbu-
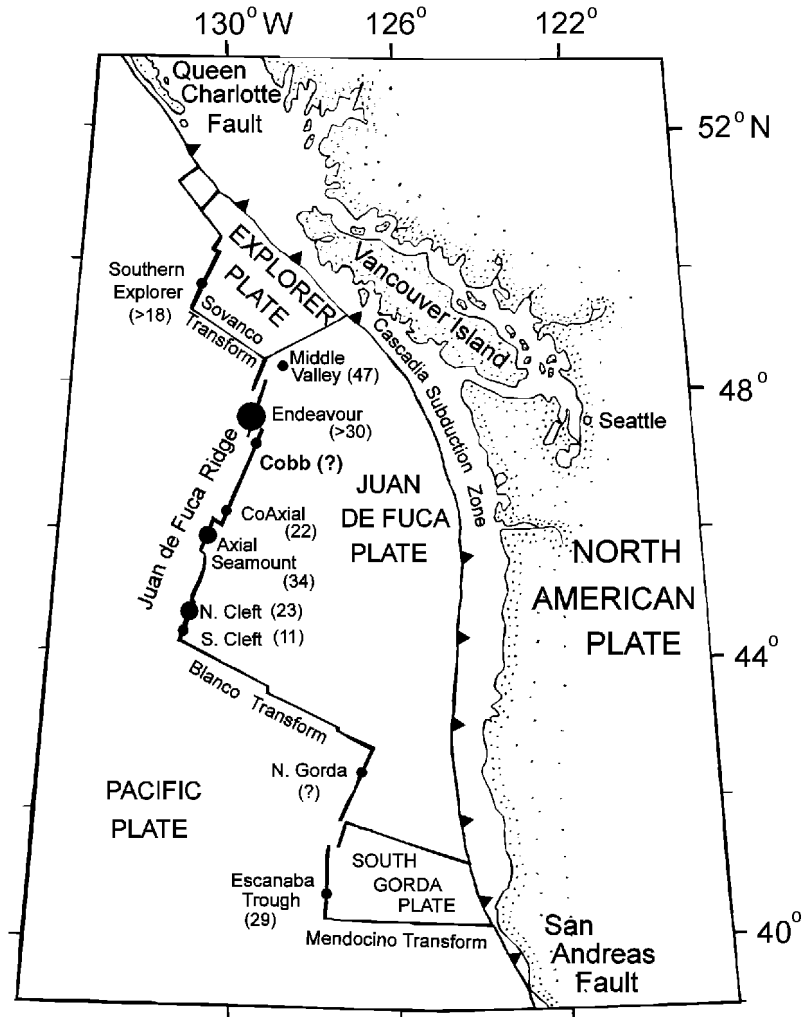
Figure 2. Sites of known vent fields in the northeast Pacific. Size of dot indicates the relative size of the vent field. Numbers in brackets indicate numbers of species sorted from site collections.

lence and fluid dispersion of a single field. The next vent field may be located on the next ridge segment or further. The concept of island stepping stones and the application of island biogeography theory have been suggested several times for use in vent distributions and diversity analysis. However, the theory was developed using a 'source' or continental mass from which species would migrate to offshore islands (MacArthur & Wilson 1967). For vents, the total 'island' fauna is the source and the more the islands the higher the diversity. Abundant small islands will hold more diversity among them than a few larger ones (Rey & Strong 1983). We sampled 16 vents on a 2.2 km length of north Cleft Segment, Juan de Fuca. These young vents held 23 species among them but a maximum of only 75% of them were found at any one vent (Milligan 1993).

With the linear distribution of vents, one can expect to see either a clinal distribution in community and population characters or a complete interchange over the entire region. Such a comparative analysis has not been completed for total faunal di-
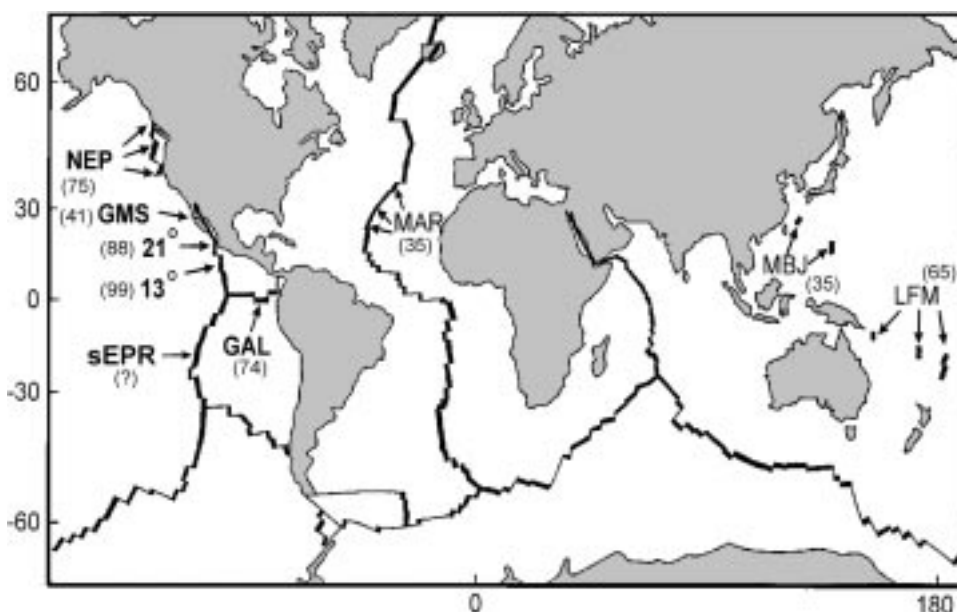
Figure 3. Locations of global sites from which faunal collections have been analysed. Numbers indicate the species presently known from these sites. After Tunnicliffe *et al.* (1997). See figure 4 for relative spreading rates of ridges.

versity along ridge segments. However, the genetic structure of populations of several species has been examined. Two species, a polychaete on EPR (Jollivet *et al.* 1994) and a tubeworm on Juan de Fuca Ridge (Southward *et al.* 1996) both show extensive communication and mixing: there is no clinal variation over 600–1000 km. The EPR tubeworm (Riftia) does show some genetic differences along 5000 km (Black *et al.* 1994) but major differentiation across transform faults was not present to the extent reported by France (1992) for amphipods. There is a tendency for extensive mixing of larvae in a common pool over mid-ocean ridges. Models addressing larval entrainment in hydrothermal plumes (Kim *et al.* 1994; Mullineaux & France 1995) describe the mixing and transport of larvae in distinct water masses above the ridge crest.

Figure 2 illustrates the occurrence of vent sites along the Northeast Pacific Ridges. Within each site indicated, the number of vent openings is highly variable (numbering from hundreds at Endeavour to just a few on Cobb Segment and CoAxial) so that the within-site pool of species should vary just as the within-regional pool will vary. For the present, the larger vent fields remain undersampled and the influence of vent field size on species abundance cannot be critically evaluated. Van Dover (1995) compares spacing of vents on the Mid Atlantic Ridge (100s of kilometres) with those on northern East Pacific Rise (as low as 5 km) (figure 3). She notes that local endemism should be much higher in the first case where exchange among sites will be limited.

Generally, if there is more habitat, more species can fit even if the system is in a state of flux; pioneer species may live at one site while succeeding species dominate another. The distribution of hydrothermal plumes over active ridges approximates vent distribution (Baker *et al.* 1995). Plume occurrence increases with spreading rate (figure 4) to the extreme that 60% of surveyed segments of the southern EPR have

Figure 4. Proposed relationship of vent habitat abundance in relation to the plume incidence, convective heat flow and seafloor spreading rate. Horizontal and left vertical axes adapted from Baker *et al.* (1995, fig. 22*b*).

hydrothermal activity (Urabe *et al.* 1995). Size of regional species pools should relate to abundance of the habitat along a ridge – and thus the spreading rate (figure 3). Diversity data from the Mid-Atlantic Ridge, the northern EPR and the Juan de Fuca regions appear to support the predicted trend (figure 3), although sampling effort is uneven. The relationship of segment scale plume incidence to area and spacing of vent habitat needs to be better defined.

3. Habitat stability

In this section, we propose that annual to decadal scale stability of vent habitat relates to ridge spreading rate through magmatic activity. Thus the stability and predictability of the vent habitat varies among ridges and we could see this variability reflected in community diversity – and possibly structure and dynamics. For example, habitat stability will interact with reproductive strategy, which is highly variable among vent taxa (Mullineaux & France 1995), in determining species presence within a vent field or region.

Ecologists have long asserted that the type, frequency and/or intensity of disruption of a community influences diversity (see Connell 1978). Disturbance that occurs at frequencies on the order of organism generation times can interfere with biological patterns and the gradual adjustment of community components to each other. The relative importance of habitat stability compared to other factors is debatable (see Huston 1979; Ricklefs 1987), as is the relevance of discussions of equilibrium states in natural communities. Many ecosystems may be out of equilibrium much of the time (Wiens 1984; Sousa 1979). In the non-equilibrium state, species tend to respond to environmental variations independently of one another and exploit resources oppor-
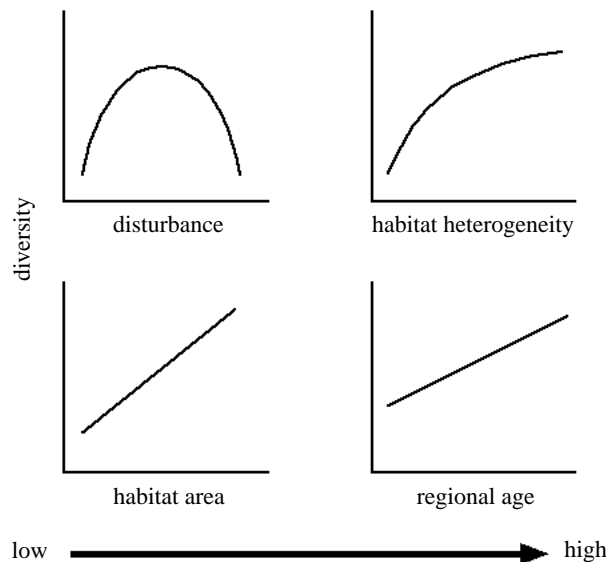
Figure 5. Summary representation of influence of major physical controls on diversity of natural communities. See text for explanation.

tunistically, and habitats can be undersaturated with species and individuals (Wiens 1984).

Vent community stability relates most strongly to constancy of fluid supply. Evidence for the longevity of vent sites indicates a range from as short as two years (CoAxial; Tunnicliffe *et al.* 1997) to at least 80 years (TAG; Lalou *et al.* 1993). Controls on fluid supply are complex but can be related to surface deposit characters, subsurface conduits and heat source behaviour (Alt 1995).

To consider surface controls first: Venting through sedimentary deposits is likely to be stable in the medium-term. However, sites like Middle Valley and Escanaba Trough are overlain by turbidite sequences deposited over hundreds of years (Davis *et al.* 1987), thus catastrophic deposition and community annihilation must occur at intervals. Habitat stability on active sulphide chimneys and mounds varies with the space and time scales under consideration. While sulphide accretion can result in rapid habitat alteration at decimeter to metre scales, chimneys represent an expanding substratum in a space-limited system. The long-lived hydrothermal mounds such as those on the Mid-Atlantic Ridge or Explorer Ridge contain a large area of habitat within which small scale changes are frequent (Tunnicliffe *et al.* 1986; Karson & Brown 1988; Segonzac 1992). Tunnicliffe & Juniper (1990) document the effects of chimney collapse including mortality of proximal animals. Fustec (1987) has mapped faunal changes on a growing chimney over two years. Modern sulphides frequently contain engulfed vent animals (Koski *et al.* 1984; Hannington & Scott 1988; Cook & Stakes 1995). The rapid adjustments of flow, sulphide deposition and fauna represent a fertile area of investigation.

Secondly, stability of habitat is influenced by subsurface crustal features (figure 5). Deposition of sulphide within the stockwork (Fouquet *et al.* 1993; Hannington *et al.* 1995) may be a common mechanism of influencing quality and constancy of the overlying habitat. Intrusive magma emplacement or diking is another mechanism. The former will be more common in slower spreading situations that foster sulphide ac-

cumulation and the latter in ridges with high magmatic activity (Embley & Fornari 1995). Individual tectonic faulting events can disturb vent habitat while longer term faulting processes can be critical to maintaining hydrothermal circulation. Fujioka (1995) reports a seismic event at TAG that caused slumps and animal deaths. Yet, at sites with a less robust magma supply, sustained hydrothermal activity may depend on deep faulting to provide access to a diminishing heat source, as has been proposed for TAG and other Mid-Atlantic Ridge sites (Fouquet *et al.* 1993; Rona *et al.* 1993) and Endeavour Segment, Juan de Fuca (Delaney *et al.* 1992). Even on fast and superfast spreading segments of the East Pacific Rise, long-lived and high temperature vents are typically located along major faults (Fustec *et al.* 1987; Haymon *et al.* 1993; Auzende *et al.* 1996).

Thirdly, heat source can have a wide influence on venting in terms of both vent distribution and stability. Eruptive activity appears to correlate with spreading rate (Fornari & Embley 1995). Creation of vent habitat occurs after an eruption; high frequency of magmatic activity also must alter the pattern of subsurface hydrothermal circulation to cause frequent vent closure. Recent observations of eruptions at ridges are expanding our view of crustal dynamics and faunal responses.

We have followed post-eruption development of communities on Cleft and CoAxial Segments (Juan de Fuca Ridge) and work proceeds on the eruptive site at 9° N East Pacific Rise (Lutz *et al.* 1994). In terms of stability, the most prominent features are: the immediacy of the food supply, the swift colonization response by vent animals and the high rate of change in these new communities. Magma movement stimulates and/or flushes subsurface microbial production (Holden 1996; Juniper *et al.* 1995) providing an instant food source and probably 'seeds' initial seafloor production. Dense white mats of (presumably) sulphide-oxidizing bacteria appeared within weeks/months of eruption (Haymon *et al.* 1993, Delaney *et al.* 1994; Tunnicliffe *et al.* 1997). On CoAxial, we know the date of the eruption (Embley *et al.* 1995) and that no vent fauna existed previously in the area. After one year, five vent species were observed; by two years, 22 species were present (Tunnicliffe *et al.* 1997). After two years, these vent communities were still changing, with some having disappeared with short-lived venting. After three years, known vents were inactive and their communities were essentially dead.

Biological observations commenced on Cleft Segment in 1988, two years after a large megaplume was observed over the site (Baker *et al.* 1987). While the exact nature of previous venting remains obscure, it was evident the biological communities were in a state of change. The biomass was high but diversity was low (Milligan & Tunnicliffe 1994). Over the subsequent years, we observed the contraction of venting and diminution of biota. By 1993, 15 km of venting had contracted to under 5 km; large numbers of deep-sea predators were observed. These observations fit the evolution of H_2S/heat ratios that peaked shortly after eruption (Butterfield *et al.*, this volume). Both events show rapid cooling. Between the short time-frame and changing fluid conditions, neither habitat nor community will come to equilibrium.

4. Spatial heterogeneity

Within any given habitat, competition for resources, predation and disease can limit the number of species that coexist and thus restrict diversity and food web complexity. A more heterogeneous physical environment can enhance diversity by

offering more opportunities for specialized primary producers and dependent consumers, and a broader resource base for mobile predators and omnivores. Habitat heterogeneity can thus interact with input of immigrants from a regional species pool in determining local diversity (Ricklefs 1987). In this section we will consider how crustal accretion might influence the composition of vent communities by controlling spatial heterogeneity of habitat at local and regional scales.

Within a vent field, habitat heterogeneity is augmented by variations in flow rate, fluid chemistry and substratum type. Although habitat requirements of most vent species remain poorly defined, several descriptive models relate the fine scale distribution of larger organisms to temperature and sulphide concentrations (reviewed by Juniper & Sarrazin 1995). While the complete range of conditions from smokers to weak diffuse flows can be observed at most sites, high temperature chimneys and associated organisms can be locally and even regionally absent, such as on the present day Galapagos Ridge.

Venting through sediments and sulphide deposits creates heterogeneity of flow and fluid chemical characteristics. The large number of species found at Middle Valley (Juan de Fuca Ridge) vents has been attributed to the greater diversity of habitat created by the presence of a sediment cover (Juniper *et al.* 1992). Variability in faunal assemblages colonizing actively-forming sulphide deposits has been described by Fustec *et al.* (1987), Tunnicliffe & Juniper (1990) and Segonzac *et al.* (1993). Venting through large sulphide deposits at sites such as Endeavour Segment (Juan de Fuca Ridge) and TAG (MAR) can produce broad patterns of habitat zonation as hydrothermal activity waxes and wanes in different areas of the deposit. At a finer scale, spatial heterogeneity can result from processes such as infilling and local reductions in porosity that alter fluid supply to different areas of chimney surfaces. New opportunities for colonization are created by chimney structural failure and abrupt fluid flow variations (Tunnicliffe 1991; Gaill & Hunt 1991; Hannington *et al.* 1995). Large sulphide deposits can represent long lived habitats that feature a great deal of heterogeneity in both the spatial and time domains. Opportunities for increased species diversity are extensive.

The importance of regional heterogeneity of habitat is understood in a theoretical sense, in that it should permit a province to hold a larger pool of species. On the Juan de Fuca/Explorer Ridge system, venting through sulphides and sediments in the north gives way in the south to a more robust magma supply and venting through small sulphide edifices and basaltic substrata. This contrasts with the northern EPR where more homogeneous substratum and fluid conditions are encountered. Yet the northern EPR pool of vent species is larger than that of the northeast Pacific (figure 3). Other influences, such as habitat abundance and spreading history probably interact with large scale habitat diversity. As more of the global ridge system is systematically surveyed it may be possible to separately evaluate the influence of regional habitat diversity on species pool size.

5. Historical factors

The diversity and distribution of marsupial mammals in Asia, the Americas and Australia were difficult to understand before reference to historical processes and plate tectonics (Marshall *et al.* 1982). In the same manner, given their position on spreading ridges, vent communities are likely to carry a strong imprint of tectonic

history. Comparison of the faunas of different regions of the world (figure 3) can be deceptive using only modern proximity. The ridges themselves have been the major pathways for distribution of the global fauna and past positions and juxtapositions of the ridges are important to understanding relative diversity and composition (Tunnicliffe & Fowler 1996). Factors that influence the accumulation of species in a region include: age of the region, history of connectedness to another region and proximity to a diverse region. Figure 3 demonstrates considerable differences in diversity (= species richness). Caution must be used in interpreting differences as sampling methods and intensity varies dramatically. In particular, the western Pacific and Atlantic have seen much less biological sampling. Nonetheless, it is likely the pattern presented will remain. The following examples illustrate the different ages of global vent provinces.

The East Pacific Rise is a traceable ridge from the early Mesozoic. Northern EPR presently holds the greatest species diversity. Since it is of similar age, the poorly sampled southern EPR could provide equal diversity. The Galapagos Rift began propagating about 25 Ma BP and was probably populated from the EPR although many endemic species are now found at Galapagos (see Tunnicliffe *et al.* (1996) for details). The Gorda/Juan de Fuca/Explorer region at the northern end of the original ridgeway was isolated when North America overran the ridge some 30 Ma BP, thus separating part of the ancestral fauna. That separation may have taken only part of the original fauna (Tunnicliffe 1988) leaving a lower diversity community that embarked on a diverging evolutionary path from EPR. In contrast, the Lau/Fiji/Manus area and the Atlantic are spreading ridges of younger age that formed conjoining the East Pacific Rise. They did not form independent faunas but show great similarity to the eastern Pacific in higher taxonomic structure. Van Dover (1995) presents the spreading history of the Atlantic suggesting the earlier opening northern Atlantic (175 Ma BP) may have been colonized via a shallow link through the Caribbean region. At present, faunal similarities suggest the Indian Ocean as the most likely conduit (Tunnicliffe & Fowler 1996). Perhaps successive extinctions and recolonizations occurred in the Atlantic. The greatly different character of the Atlantic vent fauna is not well explained by biogeography. Better information from the Indian and south Atlantic ridges is required.

6. Discussion

We have identified several physical factors that influence vent faunas. It is much more difficult to identify biological controls on these communities. Competition for nutrients may explain the compositional shift seen at Rose Garden, Galapagos (Hessler *et al.* 1988) or the size shift in worms one to two years after the CoAxial eruption (Tunnicliffe *et al.* 1997); Jollivet (1993) suggests that crab predation can be important especially as crabs often select dominant organisms. Much more work is needed. The energy supply at vents has a variable and often unpredictable behaviour, a phenomenon fundamentally different from solar-powered systems. Relative stability of the vent site or region is a potentially important factor affecting species accumulation, succession and the trophic structure and energy flow that ensue. Habitat abundance may counter instability at regional scales and we suspect that the history of spreading in a region is important to faunal accumulation through both immigra-

tion and speciation. Faunal origins will also dictate the initiating fauna in a region and the pattern of subsequent species interactions.

Figure 5 illustrates the expected response of species diversity to the various phenomena discussed in this paper. The peak of diversity at moderate levels of disturbance follows the intermediate disturbance hypothesis of Connell (1978). Increasing diversity with habitat heterogeneity on both local and regional scales has been verified in many ecosystems (Ricklefs 1987). Diversity increase with habitat area is adapted from island biogeography theory (MacArthur & Wilson 1967) while the influence of regional age is presented by Valentine (1971) among others. The net result of all these factors will vary depending on their relative importance. In the following section we consider these influences in relation to species occurrence data known from the major spreading centres.

(a) Slow spreading: the Mid-Atlantic Ridge

The MAR appears to be a region of low frequency of major disturbance, moderate/high local habitat heterogeneity with low regional heterogeneity, small habitat area, and high age. The relatively low species diversity seems consistent but remains a puzzle to explain in relation to the Pacific. Endosymbioses are generally rare, many taxa are absent, yet consumer biomass appears high. Stochastic extinction processes may be very important here. Dating by Lalou *et al.* (1993) indicates episodicity of venting at TAG and Snake Pit. At widely spaced vents, if one should shut down, local extinction has a high probability (Van Dover 1995). If several adjacent areas cease for several thousand years then the probability of regional species extinction becomes much higher. The modern MAR community may a product of widespread extinctions in quiescent periods. A possible test may be to examine local to regional diversity ratios: the value should be higher in areas where venting persistence has supported species diversification. However, further work on phylogenetic relations of separate groups is necessary to track the probably origins of the individual components of the MAR fauna. The utilization of alternative food supplies may be crucial to the persistence of species between episodes of venting. Phytoplankton derived lipids are abundant in postlarval MAR vent shrimp, and present even in adult animals (Dixon & Dixon 1996; Dixon *et al.* 1995). As well, MAR shrimp have been observed on inactive, weathering sulphides where films of mineral degrading bacteria (Wirsen *et al.* 1993) may provide sustenance for deposit feeders. Abundant methane emissions resulting from reaction of seawater with outcropping ultramafic rock (Bougault *et al.* 1993) could provide a stable refuge for MAR mussels, the only endosymbiosis known from vents in the region. These mussels harbour both sulphide oxidizing and methanotrophic bacteria in their gill tissues (Cavanaugh *et al.* 1992; A. Fiala-Médioni, personal communication).

(b) Intermediate spreading: Juan de Fuca area

In this region major disturbances should be moderately frequent and perhaps more varied than on the MAR. Local habitat heterogeneity varies depending on substratum and there is a high regional heterogeneity. Total habitat area is moderate (low on Explorer and Gorda), regional age high but there may be a mixed spreading history (slow spreading on Gorda). Observed lower diversity (versus EPR) may have some element of stochastic events in that extinctions over the last 20 million years could not be easily reseeded from EPR. We see less development in trophic structure in this

region compared to the EPR (large endemic predators missing, planktonic grazers missing, peripheral suspension-feeders poorly developed).

(c) *Lau/Fiji back-arc basins*

There has been little collection here but the diversity appears high. Descriptions by Desbruyères *et al.* (1994) and Galkin (1992) suggest that species diversity may be favoured by a diverse habitat, augmented by spatial separation (i.e. many separated small sites) and a long history of spreading activity in the southwestern Pacific. Like the Juan de Fuca, there are discrete areas of venting through sediments, through sulphide deposits and through bare basalts. Site speciation may be occurring, judging from the numbers of new taxa of known genera that are reported.

(d) *Fast spreading, the northern EPR*

The high species diversity observed on the northern EPR corresponds to a moderate/high disturbance rate, moderate habitat heterogeneity, moderate/high habitat area, high regional age and diversity ($9°$ *vs* $13°$ *vs* stable $21°$ *vs* sedimented Guaymas). Niche diversity and many aspects of trophic structure appear to be the most developed here: three tube worm and two bivalve symbioses, endemic predators both small and large, abundant peripheral suspension feeders and detrivores in addition to the large biomass in symbiont hosts. The latter observation raises the issue of relative productivity of different hydrothermal systems. Is the development of a peripheral fauna resource limited in other areas? Or have the combined physical and historic features of northern EPR provided a unique setting for the development of a vent dependent suspension feeding fauna? Why is the giant tube worm *Riftia pachyptila* so massive compared to its northeast Pacific counterpart *Ridgeia piscesae*?

(e) *Ultra-fast spreading, the southern EPR*

Very high disturbance, low heterogeneity, high habitat area and high regional age combine at this little explored end of the spreading rate spectrum. Our discussion above suggests that the net effect is likely to be a moderate diversity, perhaps lower than northern EPR. The proliferation of venting provides tremendous opportunities for fast growing, rapidly reproducing animals that directly exploit chemosynthesis. At the same time, the high frequency of eruption must continually destabilize incipient communities. Dives in 1984 indicated a mostly mobile vent fauna (Renard *et al.* 1985; Juniper *et al.* 1990) and low diversity, as would be predicted for such ephemeral conditions. However, more extensive surveys in 1993 between $17°$ S and $19°$ S documented a wide range of venting conditions (Fouquet *et al.* 1994; Auzende *et al.* 1996), with most major EPR macrofaunal species being present (Geistdoerfer *et al.* 1995), although communities appeared to be evolving rapidly. Extensive biological work is required in this area to better understand the opposing influences of habitat abundance and instability.

7. Conclusion

Vent habitat is inherently unstable at many scales. Magmatic activity – reflecting spreading rate – is probably the ultimate determinant of both vent distribution and stability. The clearest biological expression of spreading rate is likely to be found in the composition of regional species pools. Since diversity can be linked to ecosystem productivity and efficiency (Darwin 1859; May 1973; Tilman *et al.* 1996) these

ecosystem properties merit comparative study at regional scales. Fornari & Embley (1995) caution against simplistic, global correlations of spreading rate and vent behaviour. Biologists must await the time when the relations among spreading rate, magmatic activity, tectonism, sulphide accumulation and venting are clearer to the geologists. The inaccessibility of vents leaves us with limited data to formulate ecological theories. It remains important in these early stages to adopt a 'fluid' approach and continue to test different theories. However, no matter how sophisticated the ecological model undertaken, we still require a fundamental understanding of what the creatures are that inhabit the system. 'The value of model-making is that it provides us with a series of possibilities... however, a wide and deep understanding of organisms, past and present, is a basic requirement...' (Hutchinson 1975, p. 515).

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