



Temporal variations in the vent communities on the East Pacific Rise and Galápagos Spreading Centre: a review of present knowledge

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Introduction

Since the early days of the discovery of vent communities, observations of graveyards of partially dissolved clam shells on the East Pacific Rise (EPR), and of mineralized extinct smokers have given clear indications of the temporal discontinuity of vent environments. Repeated visits to several locations on the EPR and the Galápagos Spreading Centre (GSC) have revealed conspicuous temporal variability in communities. To date, all the published research has focused on the part of the vent communities located within the turbulent zone of mixing between the hydrothermal fluid and seawater where positive temperature anomalies are detected. No information is available on temporal variations within other habitats comprising the same ecosystem such as in hydrothermal plumes, cold polymetallic deposits, hypothesized sub-surface environments, or diffuse methane venting. This paper describes the observed responses of hydrothermal vent communities to venting instability.

Methods

Surveys have focused on four hydrothermal sectors during the last two decades: 21°N/EPR (Hessler et al., 1985), 13°N/EPR (Fustec et al., 1987; Jollivet, 1993; Desbruyères, 1995), 9°50'N/EPR (Haymon et al., 1993; Lutz & Haymon, 1994), and the GSC (Hessler et al., 1988). All these temporal studies were based on discrete time series of observations made by manned submersibles with a frequency ranging from three visits per decade (21°N/EPR) to several visits per year (9°50'N/EPR). These temporal studies were based on careful mapping of the communities using acoustic navigation, and mosaics of photographs or of

digitized video frames. In some cases, the studied areas are considered "sanctuaries" and are protected against the sampling bias, but most of them are frequently affected by both small-scale sampling of the animal populations and by more extensive sampling for physiology and genetic studies. Passive markers of different designs have been deployed on the bottom for the precise location of observations during successive visits.

Results and discussion

The different EPR and GSC vent fields display contrasting temporal patterns. The 21°N site, "Clam Acres", was visited in 1979, 1982 and 1990. Beds of dead clams indicate that the segment has been active for at least 300 years according to the dissolution rates of the shells (Kennish et al., 1997). A short shift in activity, due to the partial clogging or flow instability, probably occurred within the last century. Continuous activity of the vent site for at least 30 years is evidenced by the growth rates and trophic behaviour of the giant clam *Calymene magnifica* Boss & Turner, 1980. The comparison of venting patterns and community distribution between 1979 and 1990 demonstrates temporal stability at the decade scale. *Riftia* thickets, destroyed by over-sampling during the "Oasis" cruise in 1982, had recovered by 1990.

At 13°N, a complex vent field composed of five active sites (Pogosud, Parigo, Genesis, Actinoir and Totem) was visited in 1982, 1984, 1987, 1991, 1992 and 1996. Between 1982 and 1984, only a few changes affecting sub-populations were noted such as the growth or regression of *Riftia pachyptila* Jones, 1981, the growth of active sulphide edifices, and the migration of populations of "Pompei worms" along the wall of a smoker.

Between 1984 and 1987 activity at some of these vent fields had either died (Parigo, Pogodus, Actinoir) or greatly increased (Totem, Genesis). Conversely, some sites situated 100 m north of this field were not affected. Genesis was visited in 1984 and showed no measurable temperature anomaly; the fauna was composed of only a few inconspicuous clumps of small-sized mussels (45 mm < l < 65 mm), and some groups of a few rusty tubes, likely empty, belonging to the vestimentiferan worm *Tevnia jerichonana* Jones, 1985. By 1987, this zone had been reactivated. Warm water venting (<23° C) covered an extensive area and whitish deposits were observed around the vent openings. The fauna was made up of a large number of *Bythograea thermydron* Williams, 1980, crabs gathered in piles, large populations of the vestimentiferan *Tevnia jerichonana*, and juveniles of *Riftia pachyptila* (<25 cm). A nearby site, containing mineralized polymetallic sulphide dated to be over 75 years old (Lalou, pers. comm.), had become active again and had produced small sulphide edifices (< 2 m).

In 1990, diffuse emission from Genesis was concentrated at several points in the site. The extensive *Tevnia jerichonana* population had collapsed and had been replaced by some dense patches of *Riftia pachyptila*. Mytilids had resumed rapid growth (100 mm < l < 120 mm). Active high temperature sulphide chimneys, 1 to 5 m high, had developed and were colonized by large alvinellid communities dominated by *Alvinella pompejana* Desbruyères & Laubier, 1980. In 1991 and 1992, these characteristics had not fundamentally changed – stabilization of venting conditions was observed. *Calyptogena magnifica*, which had only been observed as partially dissolved shells near Pogonord, had resettled, and several individuals, ranging from 12.3 to 14.6 cm at their widest point, were sampled. According to growth estimates made in the Galápagos (Lutz et al., 1988) this size corresponds to about 7 years of age, i.e. colonization took place during the site's revitalization in 1985 (Roux et al., 1989). Assuming that the habitat requirements for *Calyptogena magnifica* are stringent compared to those of *Bathymodiolus thermophilus* Kenk & Wilson, 1985, it can be hypothesized that the 13°N vent field underwent a stable period about two centuries ago based on recent dissolution measurements (Kennish et al., 1997), followed by an unstable period which prevented the former species from colonizing. In 1996, the focusing of venting activity was accentuated by the collapse of several smokers in the Genesis vent field. The life span of smokers has been observed to be rather short in this area: less than five years, and around ten years in other sites in the same segment. Sulphide edifices remained very fragile and frequently collapsed under natural conditions.

There have been a large number of cruises at 9°50'N since the eruption which was observed there in April 1991. These numerous observations have allowed the documentation of the very first steps of temporal variations in vent communities (Shank et al., 1998). In April 1991, a large lava flow, which partially covered the axial summit caldera, destroyed part of an established biological community which had previously been surveyed using deep-tow. Black and glassy lava pillows passed through some mussel beds, killing the individuals at the frontal part of the lava flow. At the "Tubeworm Barbecue" vent, a cluster of *Riftia pachyptila* were destroyed by either the eruption or a shift in venting. Nevertheless, in some places, clumps of worms and mussels survived the eruption and lava flow. Extensive but patchy white bacterial floc covered the bottom, and the water was cloudy with apparent floc of bacteria. These bacterial floc had a low organic content, a high chemoautotrophic activity, and a high sulphur content. Taylor & Wirsén (1997) have since hypothesized that the floc was produced by bacterial oxidation of sulphide. The venting was characterized by a large, disorganized flux of hydrothermal effluent emitted directly from the basaltic seabed, producing unfocused flow temperatures of milky water less than 100°C. There were a few plumes of grey to black hot fluid which were exiting from the rubble with temperatures exceeding 360°C. Large populations of *Bythograea thermydron* were observed, which were probably feeding on bacterial mats.

In September 1991, the bacterial coverage had decreased and was restricted to vent openings and some active lava pillars. The venting was more focused and restricted to a few areas. Chimney growth was noticeable, with some reaching over 1 m in height. In early 1992, numerous venting fissures were occupied by extensive populations of *Tevnia jerichonana*, with tubes measuring up to 30 cm long.

Less than two years later, in December 1993, dramatic changes in the vent community were observed at the same location. Large clumps of *Riftia pachyptila* had settled and reached lengths in excess of 1.5 m. Growth rates of the species were estimated to be more than 85 cm per year (Lutz et al., 1994). The smokers had grown rapidly and their walls had become colonized by Alvinellid populations within the first two years. These hot vent communities are likely distributed under rubble, where hot venting occurs extensively early in the vent's evolution.

At the Galápagos Spreading Centre, the Rose Garden vent site was visited in 1979, 1985, 1988 and 1990. During these visits, no major venting fluctuations were observed. In 1979, the *Riftia pachyptila* population was luxuriant and even the large mussel clumps were dominated by tubeworms. However, between 1979 and 1985, most of the vestimentiferan worms had disappeared and the remaining *Riftia pachyptila* were grouped together, emerging from the

top of a large mussel bed (Hessler et al., 1988). The population of *Calymene magnifica* apparently had grown dramatically between these two cruises and surrounded the mussel beds. Populations of filter-feeding invertebrates (serpulids, anemones, anchored siphonophores) had crashed and the scavenger populations (*Phymorhynchus* and *Munidopsis*) were considerably more abundant. Between visits in 1985 and 1990, the community had changed very little, although the peripheral fauna had moved increasingly into the active area.

Venting instability is related to spreading rate. Moving southward on the EPR, the spreading rate increases from 60 mm per year at 21°N to 162 mm per year at 21°S. It is likely that this gradient in spreading rate parallels the intensity of vent flow alterations. The temporal evolution at 13°N and 9°50'N is obviously constrained by stochastic events: eruptions or rearrangement of subsurface plumbing by tectonic events, the clogging of major conduits, or the intrinsic instability of hydrothermal convection at fast-spreading ridges leading to major shifts in venting activity. On a longer time scale, periods of relative stability of venting are interspersed with highly unstable periods, when some sites shift position or some entire fields collapse. These unstable periods favour the settlement and dominance of fast-growing species such as vestimentiferans. In contrast, stable periods favour the slow growing *Calymene magnifica*, which appears to be the species of bivalve most sensitive to variations in venting, and *Bathymodiolus thermophilus*. This latter species was able to survive the drastic reduction in venting which was observed over several years at 13°N, and is thus able to cope with relative instability. Variability of habitat conditions remains the major factor affecting the observed biogeographical patterns. When the spatio-temporal instability is long-lasting, the communities never reach a stable configuration and remain in a juvenile stage. Conversely, in more stable environments (e.g. the Rose Garden vent field), interspecific competition becomes the most important factor in community regulation. Johnson et al. (1994), noted that in areas of intense hydrothermal venting around large stands of vestimentiferan tube worms, the animals appear to have little impact on the water chemistry. However, in areas of more modest flow, such as in mussel beds, the animals substantially reduce the sulphide content of the venting. These mechanisms might lead to the exclusion of *Riftia* from stable environments by competition for resources, by larviphagy, or more likely by exclusion of *Riftia* larvae from suitable environments. It is clear that the ability of *Bathymodiolus* sp. to overcome early settlers like vestimentifera in stable venting conditions, must be seriously considered when comparing the faunal composition between fast and slow spreading ridges, where venting patterns are characterized by differing degrees of venting stability.

The colonization rates after disturbances, the observation of early settlement of *Calymene magnifica* coincident with the revitalization of the Genesis vent site at 13°N, and the infrequency of abiotic active vent sites on the EPR suggest that the propagule supply is not a limiting factor for the settlement and development of vent communities. Instead, population settlement and development is more influenced by local factors such as habitat suitability and intraspecific competition for space and resources. Because of the temperature and the low organic concentration, the deep-sea larvae might prolong their longevity till reaching suitable habitat (Mullineaux, 1995). Active sites on fast spreading ridges are not uncommon, and the distance between them is likely shorter than was previously thought. Long-lasting vent fields, acting as propagule reservoirs, might be present on ridge adjacent seamounts (Fouquet et al., 1996). Mullineaux et al. (1996), studying experimental basalt block colonization, showed that many species display broad settlement ranges, indicating that larvae were capable of colonizing zones where adults are unable to persist. The same study suggested that initial colonization by *Tevnia* facilitates subsequent colonization by *Riftia*. These results demonstrate that, even at the settlement and recruitment levels, biological interaction influences temporal successions, even if the pattern of venting remains the dominant factor in explaining the temporal evolution of vent communities.

Because there are vent communities in several stages of evolution in the same area on the EPR between 17°-21°S, an international effort to study this region in the near future would provide valuable information. Collaborative event detection research with geoscientists using acoustic detection methods would also provide a better estimate of the frequency of eruptions on the EPR sectors. Last but not least, a better exploration of the EPR by manned submersible and ROV remains an essential preface for a better understanding of the dispersion patterns and genetic fluxes of hydrothermal vent populations.

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