A review of the distribution of hydrothermal vent communities along the northern Mid-Atlantic Ridge: dispersal vs. environmental controls

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Abstract

Until 1985, seven vent fields were described from the Mid-Atlantic Ridge (MAR). An eighth field, Mount Saldanha (36° N), discovered in 1998, showed unusual geological and biological settings. Vent sites on the MAR exhibit varied environmental conditions, resulting from depth variation of the axis and associated physical parameters, and different source rocks. These could be considered as first order (i.e. most dominant) factors affecting the composition of vent communities on the MAR, in contrast to the East Pacific Rise (EPR) where geographical isolation appears to be a major determinant of faunal differences. In this paper, the geological setting and vent fluid composition of the fields are considered together with their community composition to tentatively ascertain the order of a hierarchy between dispersal and environmental control. The deepest fields (>3000 m) are rather stable systems. The shallower fields, especially Rainbow and Menez Gwen, present some evidence of instability in time and space. The variability in fluid composition is related to phase separation processes (boiling/distillation of subsurface vent fluids) and to the nature of the basement rocks. Depending on depth, phase separation produces gas-enriched and metal-depleted fluids (Menez Gwen, Lucky Strike) or metal-enriched brines (Rainbow, TAG). In addition, high methane content characterises the fluids formed in ultramafic rocks (Rainbow, Logatchev) compared to basaltic rocks. The discrepancy in mineral particulate fluxes at Lucky Strike and Menez Gwen, on one hand, and TAG and Rainbow, on the other, is correlated to the predominance of the vapour or brine phase. The semi-quantitative description of the faunal composition of the different vent fields displays a continuum from *Rimicaris*-dominated to *Bathymodiolus*-dominated assemblages. Rather than geographic or bathymetric zonation, this gradation appears to be related to the metal content of the fluids. In addition, the penetration of non vent species into the vent environment increases with decreasing hydrostatic pressure and/or metal content in the fluids. Similarity analysis between vent communities shows that similarity is strongest between Menez Gwen and Lucky Strike (the shallowest fields), less significant between these sites and Rainbow, and weakest for Snake Pit. The inverse relationship between filter feeding organisms and metal concentration in vent fluids could result from a hindrance of mussel bed development by particulate or toxic metal fluxes, and has to be further investigated. Conversely, high metal and particulate content would less affect the more mobile *Rimicaris* populations. Considering specific similarities of endemic fauna between the four best known hydrothermal vents, the distance between vent fields appears to be a first order parameter. Nevertheless, within the proximity of the Azores Triple Junction area, and in the absence of geographical discontinuity, the similarity between fields stays rather low suggesting faunal islands that have distinct composition and habitat requirements.

Introduction

Light penetrates only ∼300 m into the ocean and the deep-sea environment is devoid of local photosynthetic production, which usually fuels the ecosystems of the Earth. Deep-sea benthic communities are fuelled by surface primary production, which is partially mineralised during its descent to the deep-sea floor. Given this limitation of energy inputs to the deep sea, the biomass is generally low (i.e. <1 g wet weight

/m^2) and the deep-sea environment is usually considered as a desert (life in the deep-sea habitat is scarce because its food is scarce). Conversely, deep-sea environments are generally known for the high diversity found amongst the mostly small-bodied invertebrates inhabiting the sediments.

In contrast to the rest of the deep sea, the hydrothermal vent assemblages, discovered first at the Galápagos Spreading Centre (GSC) at 2500 m water depth, are spectacular in their biomass, distribution and composition (Hessler & Smithey, 1983). Since 1977, faunal assemblages, similar to those discovered at GSC, have been sampled at other locations on the East Pacific Rise (EPR) (Lutz & Kennish, 1993), Juan de Fuca Ridge (Tunnicliffe, 1988), Mid-Atlantic Ridge (MAR) (Van Dover, 1995), and the spreading centres of Western and South-western Pacific Back Arc Basins (Hessler et al., 1987; Desbruyères et al., 1994). The deep MAR exploration began in 1985 and is, presently, restricted to a section delimited by Vema Fracture Zone (11° N) to the south and the Azores Plateau (38° N) to the north, with the exception of few indications of activity (only dense beds of sponges observed) at the Iceland periphery (see Van Dover, 1995 for review). Between these two latitudes, seven vent fields have been localised and studied (Fig. 1, Table 1) with variable sampling effort ranging from a few dives (e.g. Logatchev and Broken Spur vent fields) to long series of diving cruises (e.g. Snake Pit and Lucky Strike vent fields). This discrepancy in data makes comparison difficult between vent field communities.

'Hydrothermal communities' thriving on chemoautotrophic bacterial production are strictly linked to reduced fluid emission. Clustered around vents, they are roughly distributed on the mesoscale in a linear arrangement along the ridge axis. Because active hydrothermalism occupies only a small portion of the ridge axis at any one time, that portion of the hydrothermal habitat that can support life is discontinuous in space. Distribution patterns are affected greatly by the shape and size of the underlying magma chamber, and related spreading rates (Cann et al., 1994). Discontinuity in vent emission rate has been observed directly (Haymon et al., 1993; Desbruyères, 1998) or inferred from radiochronological data (Lalou et al., 1989, 1990) in different ridge dynamic contexts.

When studying the faunal composition of vent communities, the most basic pattern to emerge is an inverse relationship between faunal similarity and distance between vent fields (Hessler & Lonsdale, 1991). The increase in number and size of ridge axis dis-

continuities, as well as increasing distance between vent fields, will result in faunal differences partially because of the geographic isolation of breeding groups and genetic pools. Several works dealing with hot vent biogeography, and mainly based on dispersion in a linear fragmented habitat, have been published recently using plate tectonic history (Tunnicliffe, 1988, 1991, 1996; Hessler & Lonsdale, 1991; Van Dover, 1995; Tunnicliffe & Fowler, 1996; Tunnicliffe et al., 1996, 1998). This model only applies to communities having fairly homogenous habitats, uniform bathymetry, unique source rocks and linear heat sources, such as observed on fast spreading ridges such as the EPR. The situation is much more complex for the slow spreading Mid-Atlantic Ridge where the local conditions affected by changing source rocks, and depth variations of the axis (proximity of hot spot), might be first order factors affecting the composition of vent communities.

This paper aims to describe the patterns of the vent distribution and habitat diversity on the MAR between 11° N and 38° N. It aims also to compare community composition to determine the relative importance of dispersal vs. environmental controls. The characteristics of the studied areas, with depth ranging from 800 to 3800 m and source rocks varying from basaltic to ultramafic rocks, are of importance in structuring vent communities.

Cruises

The work presented here is based chiefly on the most recent dives made at the Azores Triple Junction during cruises DIVA 2 (1994), MARVEL (1997), PICO & SALDANHA (1998) with the manned submersible Nautile. Nevertheless, complementary data were also collected during former cruises of the Nautile (HYDROSNAKE, MICROSMOKE) and Alvin (MAR'93), on different MAR vent fields.

Distribution of hot hydrothermalism along Mid-Atlantic Ridge between 11° and 38° N (Fig. 1)

Present knowledge of the vent distribution relies on a complex sequence of (1) swath bathymetry and side scan sonar, (2) hydrocast sampling, CTD and transmissometer-nephelometer measurements, (3) dredging of sulphide and source rocks, (4) camera deep-towing, and (5) submersible operations. These methods have allowed the study of hydrothermal fields that have been primarily localised by the detection
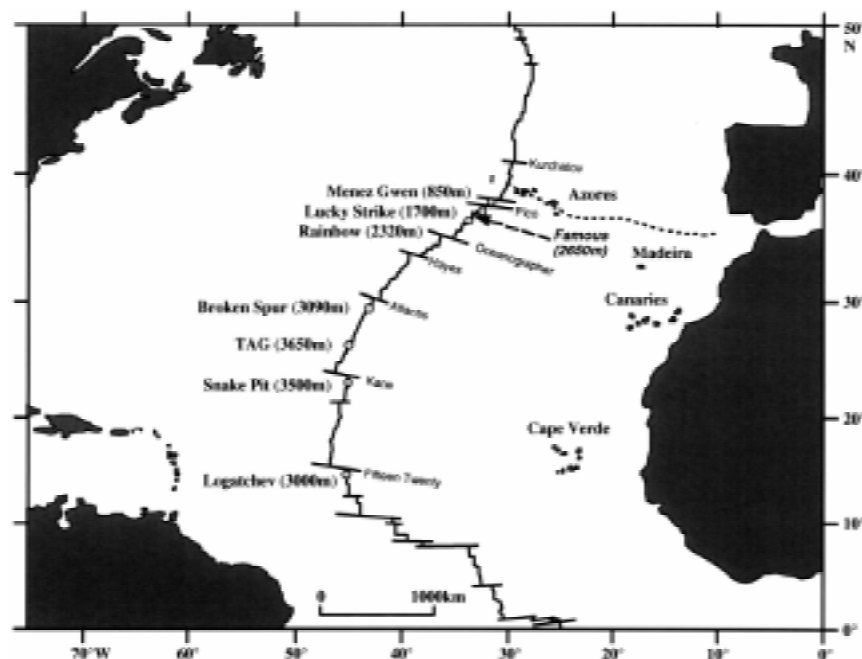
Figure 1. Location map of the eight active hydrothermal vent fields known to date on the Mid-Atlantic Ridge between Equator and the Azores Archipelago. The major Transform Faults, which constitute the principal isolation structures, are also shown.

of hydrothermal tracers (manganese, hydrogen, methane) in seawater. Experience and theory predict that at slow-spreading centres, the style of volcanism and hydrothermalism provides for relatively stable but isolated vent systems (Cann et al., 1994). TDM[1] CH_4 anomalies and bathymetry data on two sections of the Mid-Atlantic Ridge (German & Parson, 1998) inferred that the frequency of venting is at least one vent field every ∼110 km between 12° N and 26° N, and one vent field every 25–30 km along axis between 36° and 38°N. The distribution of individual sites among the vent fields is likely to differ between MAR and EPR, being less numerous in the first case but larger in size and more stable in time (Cann et al., 1994). The above estimation, relying on major tracer anomaly, pays no attention to small-sized phenomena such as low temperature diffuse venting.

In fact, some conspicuous vent fields (e.g. Menez Gwen) were found in areas without significant hydrothermal signals in the water column because of the special fluid pattern encountered. A new kind of hydrothermal vent, known as a methane vent, was recently observed on the MAR. Its occurrence and biological importance are still unknown and deserves further investigation. This type of vent was found after

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[1] Total dissolved manganese.

strong anomalies of methane were detected (Charlou et al., 1997) at the southern end of the FAMOUS segment (36 °30′ N). This area was later surveyed and sampled during the FLORES and MARVEL diving cruises, but no visible hydrothermal manifestation or typical hydrothermal vent fauna was then discovered. During the Portuguese-French SALDANHA cruise in 1998, the area was revisited and six dives with the Nautile were made. A submarine hill of about 700 m altitude, on the southern tip of the FAMOUS segment (Mount Saldanha, 36° 33′ N, 33° 26′ W and 2300 m depth), was explored thoroughly and finally, at its summit, a discharge of clear, warm, gas-bearing fluid was discovered. This discharge originates from small orifices through the sediment, covering an area of at least 50 m^2 (Barriga et al., 1998). The summit and flanks of Mount Saldanha are covered with very fine sediment. The orifices through which the vent fluid escapes contain metallic oxides and sulphates (Barriga, 1999). Such important methane anomalies were detected also in the southern end of the Lucky Strike segment but, up to the present time, no submersible dive has taken place there.

The biological setting of this new active site is completely different from those found at Rainbow, Lucky Strike and Menez Gwen fields. The most striking feature is the absence of benthic vent macrofauna

Table 1. Location of vent fields observed on the M. A. R. between 11° N and 38° N

Vent field	Latitude N	Longitude W	Depth	References
Logatchev	14° 45′	44° 58.7′	2930 – 3020	Gebruk et al. (1997b)
Snake Pit	23° 23′	44° 56.1′	3 480	Segonzac (1992)
T.A.G.	26° 08′	44° 49.6′	3635 – 3670	Rona et al. (1993)
				Van Dover (1995)
Broken Spur	29° 10′	43°1 0.4′	3050 – 3875	Van Dover (1995)
				Murton et al. (1995)
Rainbow	36° 13′	33° 54.1′	2260 – 2350	Fouquet et al. (1997)
Mount Saldanha	36° 33′	33° 28′	2300	
Lucky Strike	37° 17′	32° 16.3′	1620 – 1730	Langmuir et al. (1993)
				Van Dover et al. (1996)
Menez Gwen	37° 51′	31° 31.2′	840 – 865	Fouquet et al. (1997)
				Fouquet et al. (1999)

in the active site. In some orifices, thin whitish filaments were observed undulating with the fluid. These could well be methanotrophic bacteria, but this remains to be confirmed. Another interesting feature is the presence of large concentrations of hairy, round tetractinellid sponges, possibly close to the genus *Cinachyra*, in the flanks and near the summit of Mount Saldanha. Further away, large concentrations of sessile invertebrates, in particular hexactinellid sponges, hydroids, gorgonians, alcyonarians and stalked crinoids, can be found on the edge of basaltic crests where currents are important. The mutual influence of enrichment by chemoautotrophic local production and/or topographical effect is unknown and deserves further study in the near future.

Habitat heterogeneity

At a regional scale, vent habitats among MAR fields differ mainly in their fluid chemistry (including particulate content) and mineral deposit pattern. These groups of factors are deeply influenced by water depth and the geology of source rocks and hydrothermal deposits.

Geological settings

According to Fouquet (1997), the size and morphology of the sulphide deposits are controlled by the permeability of the seafloor, the temporal stability of the discharge, the existence of geological caps over the system and the water depth which affects the phase separation. The Atlantic deep sites (Logatchev, Snake Pit, TAG, Broken Spur) are mainly massive sulphide mounds with focused discharges of high temperature

fluid venting from chimneys or fractures [for reviews, see Van Dover (1995) and Gebruk et al. (1997a)]. They are rather stable systems. For example, radiochronological dating (Lalou & Brichet, 1981; Lalou et al., 1990, 1993) of sulphide documented several hydrothermal episodes at the same place over a period of 26 000 years at TAG. Conversely, Rainbow vent field comprises more than 30 groups of active small sulphide chimneys spread over 15 000 m^2. Because of the great number of inactive edifices observed in the same area, and the changes in individual smokers at an interval of 1 year, the discharge in this vent field is likely to be unstable in time and place, a character often attributed to fast-spreading ridges. Lucky Strike vent field is clustered around a lava lake (caldeira) (Fouquet et al., 1995). Twenty seven vent sites have been observed in the border of this caldeira. At the scale of individual mounds comprising clusters of a few vent openings, the presence of impermeable cap rocks (slabs) prevents the mixing and dilution of fluid in ambient seawater. Hydrothermal solutions are conductively cooled and precipitate sulphides before their emission on the seafloor (Fouquet, 1997). This subsurface circulation could be a favourable zone of thermophilic biological production, and flocs of bacterial mats have been observed, emerging from cracks and warm vent openings. In Menez Gwen vent field, barite and anhydrite dominate the surface precipitates and hydrothermal chimneys are situated at the top of sulphate mounds. This shallow system can be affected by explosive volcanic activity (Fouquet et al., 1999) on an area of several square kilometres as disclosed by the distribution of volcanic ejecta on the bottom

(ash, sand and lapilli). According to Fouquet et al. (1994), the Menez Gwen is, geologically speaking, very young (few decades?): chimneys are very small, growing directly on fresh pillow lava.

Hydrothermal fluids and mixing zone chemical characteristics

Deep-sea hydrothermal communities live in the interfacial zone where hydrothermal fluid mixes turbulently with bottom seawater. This fluctuating environment provides a cyclical access to reduced chemical species (H_2S, CH_4) provided by vent fluid and seawater oxidised compounds (especially O_2), both of which are required for chemolithoautotrophic bacterial primary production (Fisher, 1990; Tunnicliffe, 1991; Childress & Fisher, 1992). In other respects, this environment is enriched in potentially toxic species (sulphide and heavy metals) to which the organisms are exposed.

The chemical characteristics of habitats can be derived, in the first instance, from the dilution of a pure vent fluid in seawater. They also depend on abiotic and biotic processes occurring in the subsurface and within the mixing zone (Johnson et al., 1988; Sarradin et al., 1999). Characterisation of the medium surrounding the communities thus provides the more relevant way to compare the different habitats. However, data related to the mixing zone are characterised by large spatial and temporal variability, and are limited to a few hydrothermal fields. End-member fluid concentrations, extrapolated from hot fluids collected on smokers, provide a more complete and consistent database on which a first differentiation can be established.

Hydrothermal fluids are seawater which has been chemically altered during its passage through the oceanic crust at elevated temperature and pressure. Two main processes control fluid chemistry (Von Damm et al., 1995). At high temperature and pressure, saline solutions can undergo phase separation processes which produce metal-rich brines and a gas-enriched vapour phase. Fluid chemistry is also controlled by seawater-rock interaction undergone at high temperature and pressure. In fact, vent fluids often issue as a mixture of the vapour phase, brine and (altered) seawater.

Chemical composition of these vapour and brine contributions depends on the temperature and pressure conditions met during the hydrothermal circulation (Edmond et al., 1995; Douville et al., 1999) and the nature of the underlying rocks. In particular, fluid emissions occurring in ultramafic rock (Rainbow, Logatchev), as distinguished from basaltic systems are characterised by high methane content resulting from serpentinization (Donval et al. 1997).

The concentration of most of the major chemical components in vent fluid end-members is summarised in Table 2. These parameters can be considered as characteristics of the processes controlling the hydrothermal emissions, highlighting differences between sites. Furthermore, some of these species, if not all, are directly or indirectly related to biological activity. H_2S, CO_2, CH_4 being the source of carbon and energy for chemoautotrophic bacteria are essential to the functioning of the ecosystem. pH is expected to play a role in biotic and abiotic processes occurring in the mixing zone (Scott et al., 1994; Toulmond et al., 1994; Goffredi et al., 1997). Iron and manganese, the most abundant transition metals in the MAR hydrothermal fluids (James et al., 1995b; Douville et al., 1997), as in other MOR fluids (Von Damm, 1995), can be regarded as major sources of mineral particles. Iron and manganese enrichments are also usually associated with enrichment of other transition metals, potentially toxic to organisms. Zinc and copper are the next most concentrated transition metals in proportions ranging between 1 and 10% of the iron contents (Douville et al., op. cit.). Several other transition metals (e.g. Cd, Pb, Ag, Sb) have been also found in MAR fluids at concentrations ranging from a few nanomoles per kilogram to a few tens of nanomoles per kilogram of fluid (Douville et al., 1997).

Snake Pit, TAG and Lucky Strike vent fluids are well documented with data coming from several diving cruises, enabling inter-annual and intra field comparison. For the other fields, especially Rainbow, Broken Spur and Logatchev, the data are scarcer and do not necessarily account for the potential variability within a field.

The Menez Gwen fluids exhibit a uniform chemical composition. Chloride depletion and CH_4 enrichment indicates a dominant contribution of the vapour phase resulting from phase separation (Douville et al., 1999). This gas enrichment is consistent with the fact that Menez Gwen is considered a young site at the beginning of its activity. Menez Gwen is located in a basaltic environment, methane is produced by outgassing of carbon from the mantle and is related to the carbon-enriched character of basalt (Charlou et al., 1997). In addition, the low pH and low Fe and Si concentrations are consistent with a short duration of

Table 2. End-member temperature (°C) and concentrations of chemical species (mmol kg^{-1}) for the different MAR vent fields (MG: Menez Gwen (Douville et al., 1997, 1999; Fouquet et al., submitted; Charlou et al., 2000); LS: Lucky Strike (Von Damm et al., 1998; Langmuir et al., 1997; Donval et al., 1997; Douville et al., 1997; Fouquet et al., submitted); Rb: Rainbow (Charlou et al., 1997; Donval et al., 1997; Douville et al., 1997, 1999; Charlou et al., 2000, submitted); BS: Broken Spur (James et al., 1995a; Fouquet et al., submitted); T.A.G.: Trans Atlantic Geotraverse (Charlou & Donval, 1993; Von Damm, 1995; Edmonds et al., 1996; Rudnicki & Elderfield, 1992; Charlou et al., 1996; Gamo et al., 1996); SP: Snake Pit (Von Damm, 1995; Campbell et al., 1988; Jean-Baptiste et al., 1991; Edmond et al., 1995; Rudnicki and Elderfield, 1992); Lg: Logatchev (Charlou et al., 1997, submitted)

Site	MG	LS	Rb	BS	T.A.G.	SP	Lg
T	265–284	152–333	360–365	356–364	270–363	335–356	>353
pH	4.2–4.8	3.5–4.9	2.8–3.1		2.5–3.4	3.7–3.9	<3.3
Si	8.2–11.2	9.1–17.5	6.9–8.0		18–22	18–20	7–8.2
Cl$^-$	360–400	410–540	>750	469	633–675	550-563	515–522
CO$_2$	17–20	8.9–28	<16		2.9–4.1	10.63	
H$_2$S	1.5–2	1.4–3.3	1–2.5	9.3	2.5–6.7	2.7–6.1	<1
CH$_4$	1.35–2.63	0.5–0.97	2.2–2.5	0.065	0.14–0.62	0.046–0.062	2.1
Fe	0.002–0.018	0.13–0.86	24	1.68–2.16	1.64–5.45	1.8–2.56	2.50
Mn	0.068	0.45	2.25	0.26	1	0.49	0.33

fluid-rock interaction linked to a shallow circulation system induced by the Azores Hot Spot (Douville et al., 1999).

A high variability in fluid composition between vents was observed at Lucky Strike and two sources of fluids were hypothesised (Von Damm et al., 1998). Lucky Strike vent fluids have chlorinities equal or depleted with respect to ambient seawater and are thought to have undergone phase separation (Von Damm et al., *op. cit.*). Lucky Strike is associated usually with Menez Gwen when comparing vent fluid characteristics. Both are basalt-hosted sites, strongly affected by recent volcanic activity and shallow circulation systems. The vapour phase enrichment is, however, more moderated at Lucky Strike than at Menez Gwen. The unusual aspect of Lucky Strike fluid chemistry is the relatively high pH and low concentration of Fe, Mn and Zn. This was attributed to reaction with an altered substrate, depleted in these elements (Von Damm et al., *op. cit.*).

Rainbow fluids are uniform in composition and influenced by phase separation, which generates stable Cl-rich fluids indicating a high brine contribution (Douville et al., 1997). Compared to the Menez Gwen field, little evidence of recent volcanic activity or hydrothermal activity was found at Rainbow. Hydrothermal circulation is considered to be tectonically controlled and activated by exothermic serpentinization processes (Douville et al., 1997). Serpentinization is the cause of high methane concentration in fluids. Transition metal (Fe, Mn, Cu) content in Rainbow fluids is the highest observed in the MAR hydrothermal area. This metal enrichment is likely to be related to the formation of Cl-complexes at the high temperature reached by these fluids (Douville et al., 1999).

Broken Spur is located in a basaltic substratum. Hydrothermal activity within this field was shown to be controlled by a combination of recent volcanic activity and tectonic activity (Murton et al., 1995). Fluid depletion in chloride (–14%) is attributed to supercritical phase separation.

Sampled TAG fluids are inferred to be from the same source of fluid (Von Damm et al., 1998). As for Rainbow, high chlorinity and metal content are attributed to phase separation (Douville et al., 1997). Hydrothermal circulation through the basaltic layer carries CO$_2$ and CH$_4$ of magmatic origin (Charlou et al., 1996). The Snake Pit fluids have almost the same composition and temperature as fluids collected in the TAG area, suggesting that the factors controlling the chemistry of the major elements are similar (Jean-Baptiste et al., 1991).

Like Rainbow, Logatchev is located in an ultramafic environment. Composition of hot fluids confirms that serpentinization is a major process producing high methane flux (Charlou et al., 1997).
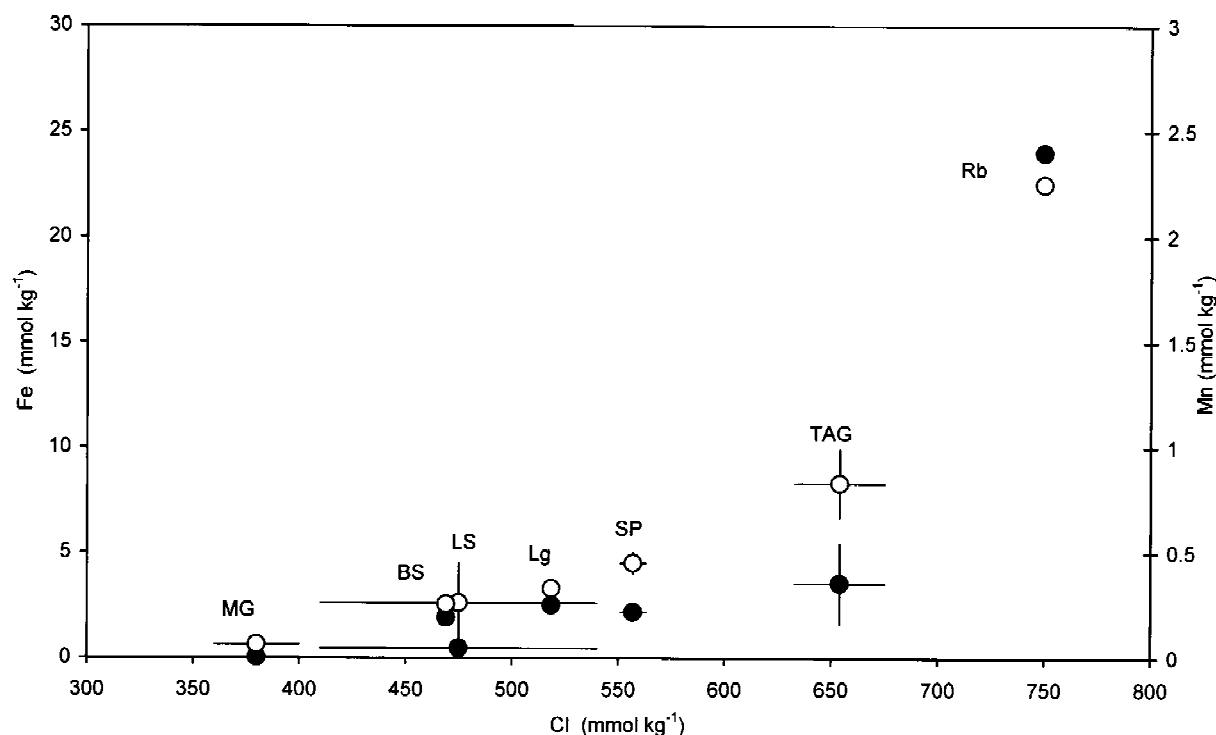
Figure 2. Iron (black circles) and manganese (open circles) concentrations versus chloride concentration in the end-member fluids of the MAR hydrothermal fields (when more than one data set is available, error bars indicate the range of end-member concentrations determined for one site). Chloride concentration in seawater is about 550 mmol kg^{-1}. End-member chloride concentrations above this value indicates a high brine contribution, and fluid depleted in chloride compared to seawater should be enriched in the vapour phase.

Comparison of end-member chemical composition between fields

The above observations, and characteristics listed in Table 2, enable the sites to be distinguished with regards to their end-member fluid composition. Figure 2 shows that manganese and iron covary with chloride as expected from metal enrichment in the brine following phase separation processes. The opposite trend predicted for CH_4 content is less noticeable. Rainbow differs clearly from the other sites with a high methane content associated with the highest chlorinity and metal content. Methane enrichment in the fluids of Logatchev vents, which is also hosted in an ultramafic environment, was also highlighted (Charlou et al., 1997).

As shown in Figure 3, CH_4 enrichment (Logatchev, Rainbow, TAG) corresponds to H_2S depletion in the fluids and this inverse relation is verified for all the studied MAR vent fields.

Particle fluxes

The flux of mineral and organic particles in the vicinity of vents is a major ecological factor both in terms of nutrition and toxicity. Mineral particulate flux can alter the feeding activity of filter feeding and deposit feeding animals and, when accumulating on the bottom, may change edaphic properties and affect larval or post-larval settlement. In the studied areas, fluid aspect ranges from clear shimmering fluids at Menez Gwen to black particle loaded fluids at Rainbow and TAG. Quantification (Table 3) of particulate flux was made using sediment traps positioned with the submersible in the close vicinity of vents. A sediment trap moored off the vent fields gave the pelagic input reference.

The total particle fluxes measured with sediment traps (Khripounoff & Albéric, 1991) are of the same magnitude at the two deepest sites studied. At the shallow fields (Menez Gwen and Lucky Strike), total fluxes are ten times smaller than those of TAG and Rainbow. The same trends were observed for the particulate sulfur contribution. The particulate organic carbon flux was of the same order of magnitude (9–48 mg m^{-2} d^{-1}) in all the vent fields studied.
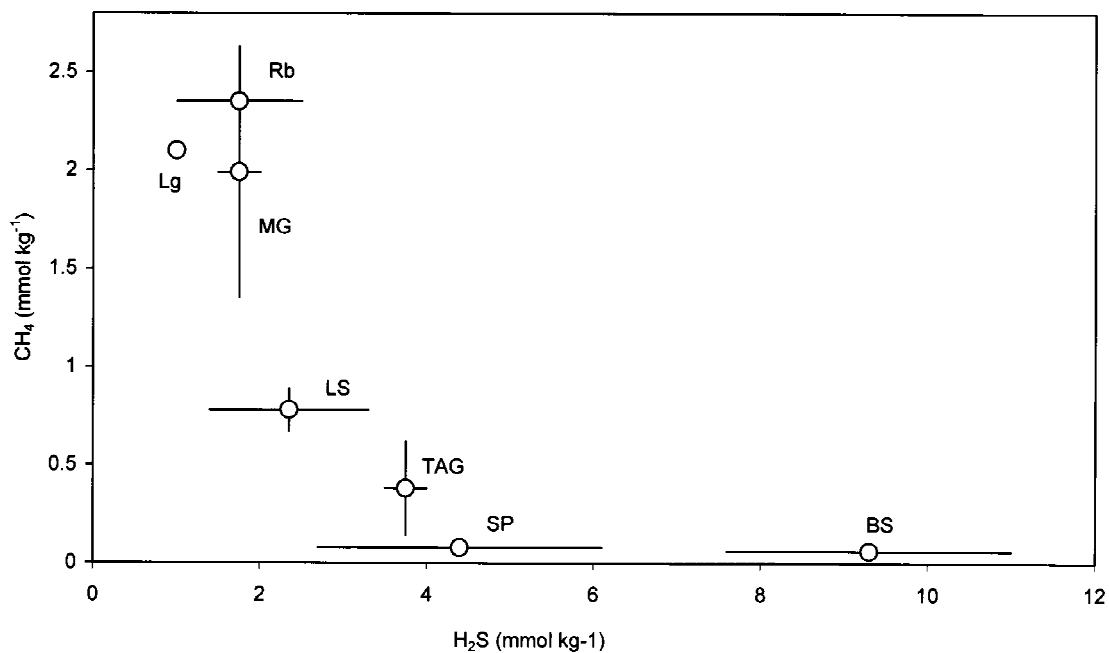
Figure 3. Methane concentration versus chloride concentration in the end-member fluids of the MAR hydrothermal fields.

Table 3. Particle fluxes (raw data not corrected for current headings) measured by sediment traps at four hydrothermal vent fields on the Mid-Atlantic Ridge

Site	Location from the vent	Total flux mg m^{-2} d^{-1}	Organic C flux mg m^{-2} d^{-1}	Inorganic C flux mg m^{-2} d^{-1}	Total Nitrogen flux mg m^{-2} d^{-1}	Total S flux mg m^{-2} d^{-1}
TAG	2 m northward	9024.7	48.8	not detected	4.46	2733.7
	pelagic reference	11.3	0.49	0.95	0.05	0.2
Rainbow	2 m Southwest	6890	9.3	not detected	0.9	1171
	Pelagic reference	11.2	0.62	1.32	0.07	0.04
Lucky Strike	2 m southward	264.5	12.06	9.4	2.0	29.0
	Pelagic reference	7.7	0.55	0.75	0.09	0.07
Menez Gwen	2 m southward	704	11.26	not detected	0.85	126.7
	Pelagic reference	28.5	2.51	2.18	0.41	0.11

Table 4. Schematic description of the hydrothermal vent communities from the known hydrothermal fields on MAR based on published observations and personal data. Numbers (ranging from 1 to 5) between square brackets are visual estimation of the distribution and dominance of megafauna: [1], rare; [2], rare / patchy; [3], common, [4] dominant/patchy, [5] Exclusive

	Dominant species on chimneys walls	Dominant species on chimneys bases	Dominant species on surrounding blocs within active area	Dominant accompanying species	Dominant carnivorous	Dominant peripheral species
Logatchev (Gebruk et al., 1997a; Gebruk et al., 1997b)	*Bathymodiolus cf. puteoserpensis* [3] + *Branchipolynoe seepensis* [3] / *Rimicaris exoculata* [2]	*Bathymodiolus cf. puteoserpensis* [3] + *Branchipolynoe seepensis* [3]		*Ophioctenella acies* [3] / *Mirocaris keldyshi* [3]	*Segonzacia* sp.	Actinaria gen. sp. [2]
Snake Pit (Segonzac, 1992; Segonzac et al., 1993)	*Rimicaris exoculata* [4]	*Chorocaris chacei* [2] / *Alvinocaris markensis* [1]	*Bathymodiolus puteoserpensis* [1] + *Branchipolynoe seepensis* [1] / *Ophioctenella acies* [1]	*Pseudorimula midatlantica* / *Peltospira* sp.	*Segonzacia mesatlantica* [2] / *Pachychara thermophilum* [2]	*Parasicyonis ingolfi* [2] / *Candelabrum serpentarii* [1] / *Chaetopterus* sp. [1]
TAG (Gebruk et al., 1997a; Van Dover, 1995)	*Rimicaris exoculata* [4]	*Chorocaris chacei* [2] / *Alvinocaris markensis* [1]	*Ophioctenella acies* [1]	*Stygiopontus pectinatus*	*Segonzacia mesatlantica* / *Pachychara thermophilum* [1]	*Chaetopterus* sp. / *Parasicyonis ?* sp. [3] / *Munidopsis* sp.
Broken Spur (Murton et al., 1995; Gebruk et al., 1997a)	*Rimicaris exoculata* [2]	*Mirocaris fortunata* [1]	Spionid polychaetes [2] / *Bathymodiolus puteoserpensis* [1] & *Bathymodiolus azoricus* / *Branchipolynoe seepensis* [1] / *Ophioctenella acies* [2]		*Segonzacia mesatlantica* [2]	*Chaetopterus* sp. / Actiinaria gen. sp.
Rainbow (Desbruyères et al., subm)	*Rimicaris exoculata* [3] / *Mirocaris fortunata* [2]	*Mirocaris fortunata* [2] / *Chorocaris chacei* [1]	*Bathymodiolus azoricus* [2] + *Branchipolynoe seepensis* [1]	*Amatys lutzi*	*Segonzacia mesatlantica* [2]	*Chaetopterus* sp. [1] / *Prionospio* sp. [2]
Lucky Strike (Desbruyères et al., subm) (Van Dover et al., 1996)	*Bathymodiolus azoricus* [5] + *Branchipolynoe seepensis* [5] / *Chorocaris chacei* [2] / *Mirocaris fortunata* [3]	*Bathymodiolus azoricus* [5] + *Branchipolynoe seepensis* [5] *Mirocaris fortunata* [3]	*Bathymodiolus azoricus* (young specimens) [3] + *Branchipolynoe seepensis* [3]	*Amathys lutzi* / *Lepetodrilus* n. sp.	*Segonzacia mesatlantica* [2]	*Candelabrum phrygium* [2]
Menez Gwen (Desbruyères et al. subm) (Colaço et al., 1998)		*Bathymodiolus azoricus* [3–5] according to the vent sites *Mirocaris fortunata* [2–3] *Chorocaris chacei* [1]	*Bathymodiolus azoricus* [3–5] according to the vent sites *Mirocaris fortunata* [2–3] *Chorocaris chacei* [1]	*Protolyra valvatoidae*	*Chaceon affinis* [2] / *Segonzacia mesatlantica* [1]	*Eudendrium* sp. / *Grammaria abietina*

MAR hydrothermal vent communities

Faunal composition of the hydrothermal vent communities on MAR was described previously (Grassle 1986; Moskale, 1992; Segonzac, 1992; Van Dover 1995; Murton et al., 1995; Van Dover et al., 1996; Saldanha et al., 1996; Gebruk et al., 1997a; Desbruyères et al., in press). Several phylogenetic analyses, based on molecular techniques, have been made on the dominant species along the MAR and between ridges in order to resolve relationships (Comtet, 1998; Shank et al., 1998a, 1999; Chevaldonné et al., 1998; Jollivet et al., 1998). Nevertheless, part of the taxonomic work is still in progress and the following faunal description could be subject to future variations in taxonomic content, at least at the level of accompanying species; for an updated species list see Desbruyères et al. (submitted). Based on a 'landscape approach', used previously in MAR hydrothermal vent fields by Gebruk et al. (1997a), Table 4 gives a global scheme of the dominant species in vent communities along the ridge axis from Logatchev to Menez Gwen vent fields. A continuum from *Rimicaris*-dominated assemblages to *Bathymodiolus*-dominated assemblages comes out when considering the whole range of variations within MAR hydrothermal vent communities. The MAR vent communities, ordered according to their faunal composition, range from TAG to Menez Gwen assemblages: TAG ↔ Snake Pit ↔ Rainbow ↔ Broken Spur ↔ Logatchev ↔ Lucky Strike ↔ Menez Gwen. Compared to other vent field assemblages, Broken Spur and Logatchev appear to be substantially impoverished in terms of abundance. The two dominant taxa are associated with autotrophic bacteria: *Bathymodiolus* species (Mytilidae) are sessile organisms with endosymbionts belonging to sulphide-oxidising chemoautotrophs and methanotroph bacteria (Cavanaugh et al., 1992; Fiala-Médioni et al., 1996). Nevertheless, although anchored by byssal filaments, *Bathymodiolus* is capable of migration along sulphide gradients and is also able to grow on methane alone as demonstrated by Dando et al. (submitted). Although symbiotrophic, *Bathymodiolus* spp. still behave as filter feeding organisms, requiring a constant flow of water through their gills. *Rimicaris exoculata* (Bresiliidae) is a mobile swimming species and its source of nutrition is still debated, but probably (Segonzac et al., 1993; Polz et al., 1998; Rieley et al., 1999) largely reliant on bacterial epibionts living inside the branchial chamber and also on gut microflora. Based on stable isotope analysis, Colaço et al. (submitted) recognise, among all the
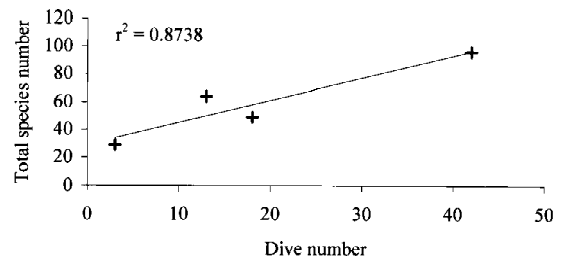

Figure 4. Number of species collected on the four studied vent fields against the number of dives on each field. The total number of species ranges from 29 for Rainbow to 96 for Lucky Strike.

MAR vent fields considered in this study, an obvious dichotomy of the trophic web based on either *Bathymodiolus* spp. beds being significantly depleted in ^{13}C or *Rimicaris* swarms being substantially enriched in ^{13}C. In a first analysis, the gradation between the two assemblages, based on dominant populations among vent communities, cannot be related to geographic distances or to an obvious bathymetric zonation. When considering the relationship between the chemical environment and the characteristics of the faunal assemblages, a high level of metals and high chlorinity of the fluid is associated with *Rimicaris*-dominated communities, while low levels are related to *Bathymodiolus*-dominated communities. In a first attempt, when considering our data on mineral particle fluxes, among the four studied vent fields, *Rimicaris*-dominated assemblages are characteristic of high mineral particle fluxes while *Bathymodiolus*-dominated assemblages are characteristic of fluids depleted in mineral particles. The very high production of inorganic particles at TAG and Rainbow can not only affect the filtration of the mussels, but also juvenile growth as demonstrated previously in *Mercenaria mercenaria* (Bricelj et al., 1984).

MAR geographic patterns in hydrothermal vent fauna

The taxonomic work on MAR hydrothermal vents, on which the present biogeographic analysis relies, is still in progress both for classical taxonomy and molecular phylogenetic analyses, and may still evolve in the future. Our biogeographical study is based on the analysis of a presence/absence matrix referring to the theory that the distribution of taxa represents information on its history over an evolutionary time scale. The species list has been made from that published in Desbruyères & Segonzac (1997), and updated from recent papers and from unpublished results kindly communicated by taxonomists. Species have been separated into 'hydrothermal' and 'penetrating'. A species has
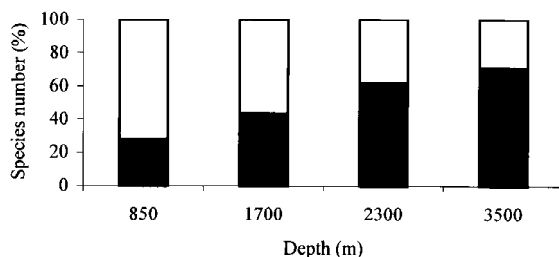
Figure 5. Relative numbers of hydrothermal (black) and penetrating (white) species against depth inside the hydrothermal vent influence area.

been considered 'hydrothermal' if it is known only from hydrothermal vent environments and if it lives close to fluid emissions. Thus, each new species found in active areas has been considered as 'hydrothermal'. Conversely, each species known to occur in the normal deep-sea habitats has been considered as 'penetrating'. This led us to distinguish 67 'hydrothermal' and 105 'penetrating' species among those sampled on MAR in this environment. An important bias in such a study is caused by the differences in sampling effort in each vent field. The number of species increases with the number of dives, which is used as an estimation of the sampling effort (Fig. 4). This trend is amplified by the fact that the poorly dense vent fields deserve less sampling effort due to scientific profitability of dives. This is the reason why we considered herein only the four best sampled fields (Menez Gwen, Lucky Strike, Rainbow and Snake Pit). Even with such care, our results give only a provisional image of what we know at the time of the analysis.

Relation between depth and faunal composition

As expected, the deepest sites are dominated by 'hydrothermal' species whereas 'penetrating' species are the main component of the shallowest field (i.e. Menez Gwen), where 'hydrothermal' species represent only 28% of the community (Fig. 5).

The penetration of non-hydrothermal fauna inside the vent habitat may be a consequence of phase separation caused by the decrease of hydrostatic pressure leading to a non-metal loaded fluid as revealed by the low metal/chlorinity content (see Fig. 2) rather than a direct bathymetric effect. This explanation, based on the low toxicity of metal-depleted hydrothermal fluids, was proposed for the first time by Valdès & Bouchet (1998) for the occurrence of a nudibranch (*Dendronotus*) in the Lucky Strike vent field.

Similarity analysis

In order to analyse species distribution between the four best-known vent fields, we used the Sorensen similarity coefficient:

$$I_s = \frac{2a}{2a + b + c},$$

where *a* is the number of species found in the two vent fields, *b* the number of species found only in the first vent field, and *c* the number of species found only in the second vent field. Results are given in Table 5.

Similarity values are very low when only the 'penetrating' species are considered. This means that these deep-sea species are different from one field to another. As they are those found in the common deep-sea environment, the observed differences are likely to be due to differences in the zonation patterns between the four fields, but may also result from edaphic characteristics of the peripheral areas (soft bottom vs. hard bottom).

Similarities between hydrothermal vent communities are higher when only the 67 'hydrothermal' species are considered. Their significance level has been tested using a Monte Carlo procedure (Sokal & Rohlf, 1980). As recommended by Jackson & Somers (1989), we performed 10 000 random permutations of the initial matrix of presence/absence data. The similarity coefficient was calculated after each permutation. The probability that similarity is due to chance, is then the ratio between the number of times the recalculated coefficient is superior to the observed one (i.e. when the similarity by chance is greater than the observed one) and the number of permutations. Results are given in Table 6.

These results show that the hydrothermal fauna in Snake Pit is clearly different from that of the three other fields (*p*>0.6 for each of the three similarities). The most significant similarity between faunas (*p*<0.01) is observed for the closest fields (Lucky Strike and Menez Gwen, separated by 49 nautical miles), whereas the similarities between these fields and Rainbow are less significant (*p* value ranging from 0.05 to 0.1). These values have been used to draw a similarity tree using the simple linkage clustering method (Fig. 6a). When considering the total fauna, similarity trees are different, grouping Rainbow and Snake Pit on one hand, Lucky Strike and Menez Gwen on the other hand, although the similarities are less significant (Fig. 6b). The 'penetrating' species composition is likely to be controlled by depth whereas

Table 5. Sorensen similarity coefficients and geographic distances: above diagonal: 'hydro-thermal' species and geographic distances in nautical miles; under diagonal: 'penetrating' species and total species

	Snake Pit	Rainbow	Lucky Strike	Menez Gwen
Snake Pit	1	0.3396 / 199	0.3896 / 300	0.3396 / 349
Rainbow	0.1600 / .02821	1	0.4667 / 101	0.4444 / 151
Lucky Strike	0.0588 / 0.2345	0.0615 / 0.2560	1	0.5333 / 49
Menez Gwen	0.0667 / 0.1947	0.0702 / 0.2151	0.2800 / 0.3750	1

Table 6. Probability that the similarity is due to chance, calculated after 10 000 permutations of the presence/absence data matrix

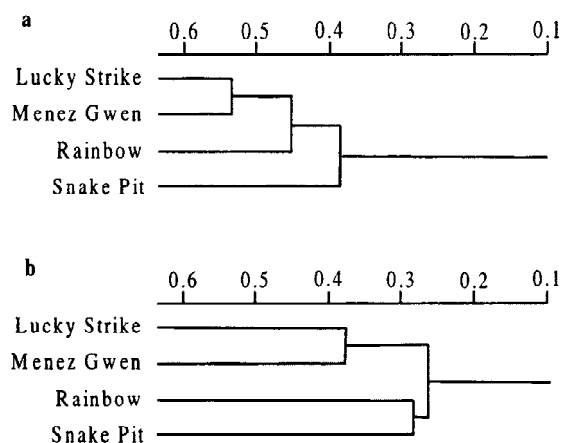|	Snake Pit	Rainbow	Lucky Strike	Menez Gwen
Snake Pit	–			
Rainbow	0.6977	–		
Lucky Strike	0.9999	0.1015	-	
Menez Gwen	0.6808	0.0509	0.0072	–

Figure 6. Similarity trees based on the Sorensen similarity coefficient. These trees were drawn using the simple linkage clustering method (a) hydothermal species, (b) all species.

'hydrothermal' species composition is controlled by the chemistry of the fluid.

Discussion and conclusion

The occurrence of hot hydrothermal venting on MAR between 12° N and 38° N, as revealed by chemical tracer detection, is more important than previously thought, mainly in the northernmost part where the frequency of occurrence is close to that described previously on fast-spreading ridges. A new kind of warm methane venting was observed on the Famous segment (Saldanha vent site) and deserves further studies. This new hydrothermal site is not colonised by endemic hydrothermal species, but by filamentous bacterial mats and tetractinellid sponges (*Cynachira*). Hexactinellid sponges (Euplectellidae) were also observed at the periphery of active vents in the North Fiji Basin (Desbruyères et al., 1994) and methanotrophic *Cladorhiza* (Desmospongiae) were abundant at Barbados cold seeps at c.a. 5000 m (Vacelet & Boury-Esnault, 1995; Olu et al., 1997). Although the distribution of the phenomenon is unknown, several clues lead us to think that many methane vent fields could be present in the vicinity of the Azores Triple Junction. Nevertheless, because of its faunal composition, it seems unlikely that this new kind of methane venting could serve as stepping stones between hot vent fields.

A continuum between *Rimicaris*-dominated and *Bathymodiolus*-dominated assemblages emerges from our 'landscape approach' based on semi-quantitative data. Bathymetric zonation or geographic distance between vent fields cannot explain this continuum. Most likely it is related to the metallic content (dissolved and particulate) of the end-member fluid. The development of mussel beds could be hindered by iron oxide precipitation and/or heavy mineral particle fluxes being deleterious both to filter feeding beha-

viour and larval settlement. Among the seven vent fields considered, only Broken Spur does not follow this trend, possibly not only due to an incomplete series of chemical samples within a heterogeneous vent field (James et al., 1995a). Nevertheless, no relation is obvious among studied MAR vent fields with respect to abundance of organisms in communities and Fe/H_2S ratio as suggested previously by Von Damm (1995). Our hypothesis of an inverse relationship between filter feeding organisms and mineral particles has to be tested experimentally. Conversely, *Rimicaris* populations are able to thrive in an environment with high concentration of metals, possibily not only because of their ability to escape from contamination, but also to detoxify the environment through symbiotic relationships. Tyler & Young (1999) assume that young individuals and berried females of *Rimicaris* may live away from the vent influence or in less toxic parts of the habitat (Shank et al., 1998b). The absence of swarms of *Rimicaris* in shallowest vent fields remains enigmatic as only few individuals were sampled at the Lucky Strike vent field. This absence may result from interspecific competition with mussels for access to habitat, which for both, it is the porous parts of the chimney walls according to Segonzac et al. (1993). The end member fluid chemistry provides a first estimate of the major ecological structuring factors at the scale of the ridge. Nevertheless, further work on fluid chemistry, at the level of population, by *in-situ* analysis is still needed as well as measurements of chemical fluxes (dissolved and particulate) at the very proximity of organisms to assess the microscale factors involved.

Specific similarities between the four best known vent fields give a complex image, which results from dispersal and recruitment parameters. Larval biology, hydrodynamic patterns and distance between vent fields influence dispersal. Propagule availability and local environmental conditions influence recruitment. Examination of the species list demonstrates an increase in non-endemic species ('penetrating') within the vent habitat at the approach of the Azores Plateau where depth decrease from 2300 m in the Rainbow vent field to 840 m in the Menez Gwen vent field. This increase results probably from a decrease in fluid toxicity as revealed by metallic content and sulphide concentration. When considering the cladogram of specific similarities of endemic fauna between the four best known hydrothermal vents, the influence of the distance between vent fields appears to be a first order parameter. Transform faults may represent major barriers to dispersal of vent species along the ridge. Between 14° 45′ N and 37° 51′ N, only three major transform faults (Kane, Oceanographer and Famous) break the ridge ranging from 145 to 20 km in length (Van Dover, 1995). Within the Azores Triple Junction area, the geographic proximity, and the absence of conspicuous discontinuities between vent fields, allows the exchange of propagules of the vent endemic species when bathymetric variations, induced by the proximity of the hot spot, introduce zonation differences among non-endemic assemblages. Nevertheless, when considering presence/absence matrix, the faunal similarity between the different vent fields remains relatively low ($\leq$30% of hydrothermal species only are shared between two vent fields). One cannot consider MAR vent communities, or even the Azores Triple Junction communities, as a single biogeographical entity but as a series of distinct faunal islands having different composition and habitat requirements.

Acknowledgements

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