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Chemical environment of the hydrothermal mussel communities in the Lucky Strike and Menez Gwen vent fields, Mid Atlantic Ridge

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Abstract: Water samples were collected around the communities of a hydrothermal mussel, *Bathymodiolus* sp., in the Lucky Strike (1700 m depth) and Menez Gwen (850 m depth) areas, Mid Atlantic Ridge, and analysed for chemical constituents. The environment surrounding the organisms consists in sea water (88 to 100%) mixed with hydrothermal fluid with pH between 6.2 and 8, ΣS (H_2S + HS^-) concentrations from 0 to 62 µmol l^{-1}. High dissolved organic carbon (DOC) concentrations suggest a highly productive ecosystem. Production of ammonium and DOC, consumption of nitrate and sulfide in the vicinity of the organisms are among the environmental changes found in relation with local biological activity. Concentrations of Cu and Pb were high, implying that the organisms need to have efficient strategies of adaptation.

An empirical distinction between the extreme sizes of the mussels (> 6 cm and < 3 cm) reveals that the size distribution of the communities is related to the presence of different environments: the large size classes are present closer to the fluid exits, with higher ΣS concentrations, than the small size classes. This could indicate differences in the growth rate related to the availability of the energy sources, competition for energy and space, and/or different settlement periods.

Résumé : *Environnement chimique des communautés de moules hydrothermales sur les sites Lucky Strike et Menez Gwen, Ride Médio-Atlantique*. Des échantillons d'eau ont été prélevés autour des moules hydrothermales *Bathymodiolus* sp., aux sites de Lucky Strike et Menez Gwen, ride Médio Atlantique. L'environnement de ces organismes est caractérisé par un pH compris entre 6.2 et 8, des concentrations en ΣS de 0 à 62 µmol l^{-1}. La zone de mélange eau de mer (88-100 %) /fluide hydrothermal est modifiée par les organismes avec une production de carbone organique dissous et d'ammoniac, et une consommation de nitrate et de ΣS à proximité des organismes. Les concentrations en Cu et Pb sont élevées suggérant la nécessité pour ces modioles de développer des stratégies d'adaptation efficaces.

Une distinction empirique des classes de taille révèle que la distribution des organismes est reliée à l'environnement. Les colonies de moules de grande taille sont à proximité des sources de fluide, dans un milieu plus riche que celui des moules de petite taille. Cette ségrégation spatiale des tailles pourrait indiquer des différences de taux de croissance, une compétition pour l'énergie et l'espace et/ou des périodes de recrutement différentes.

Keywords : environment, sea water, hydrothermal vents, mussels

Introduction

Deep sea hydrothermal vents are characterized by a set of unique environmental parameters. The chemical

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interactions between the magma source and the surrounding sea water produce strongly reducing hot waters with various chemical compositions. Biological communities associated with this hydrothermal activity reflect the peculiarities of the composition of the environment around the vents. They are functionally dependent on the association between the macroorganisms and their symbiotic chemoautotrophic bacteria and on the reduced chemicals present in the fluid (sulfide, methane) for energy and the oxygen of sea water (Fisher, 1990).

Biological communities are present within areas where the thermal and chemical gradients due to the mixing of hot hydrothermal fluid with cold sea water enable the availability of both reduced (sulfide, methane) and oxidized (oxygen, nitrate) compounds. Such a zone is subject to rapid and large spatio temporal variations of the environmental conditions, as has been shown for temperature (Chevaldonné et al., 1991), silicate and sulfide with gradients up to 2-10 µmol l^{-1} ΣS cm^{-1} on *Riftia pachyptila* clumps (Johnson et al., 1988). However, most studies till now have focused on the composition of the hot fluids from the vents. The chemical composition of the water surrounding the organisms remains yet to be adequately documented. The objective of the present work is to describe the chemical environment of the mussel clumps occurring at the Lucky Strike and Menez Gwen hydrothermal areas. This is a first step to elucidate the trends which govern the functioning of the ecosystem, the microdistribution of the organisms and the interactions between fluid and organisms.

Materials and methods

The data presented in this paper were obtained during the DIVA 2 cruise (June 1994, on the N.O. Nadir and Nautile) in two hydrothermal areas, Lucky Strike and Menez Gwen (Fig. 1), located on the Mid Atlantic Ridge (MAR).

I. The Lucky Strike area,

(37°17 N, 1700 m), is located around a central lava lake and presents both high temperature active black smokers (324°C) and lower temperature diffuse flow (170°C). The biological communities are dominated by the mussel *Bathymodiolus* sp. (Von Cosel et al., 1999), uniformly covering the hydrothermal structures or distributed in patches around the vents and in the cracks. Some of these mussel beds were covered with white filamentous mats. Shrimps (*Mirocaris fortunata* Martin & Christiansen, 1995 and *Chorocaris chacei* Williams & Rona, 1986) and bythograeid crabs (*Segonzacia mesatlantica* Williams, 1988) were present on the smoker walls and the mussels beds. An extensive description of the geological and biological settings of this hydrothermal field is given in Fouquet et al. (1995) and Van Dover et al. (1996).

II. The Menez Gwen area,

(37°50 N, 840-870 m), located near the top of a young volcano, was discovered during the DIVA 1 cruise. This site is apparently very young, with small chimneys and hot (281°C) and clear fluid diffusing through the volcano surface. Mussel (*Bathymodiolus* sp.) patches of mixed sizes were found along with shrimps (*Mirocaris fortunata* and *Chorocaris chacei*) and bythograeid crabs (*Segonzacia mesatlantica*) in the vicinity of the diffusing fluids (Colaço et al., 1998). A geological description of this site is given in Fouquet et al. (1995).

III. Sampling

Water samples were collected from five sites (Sintra, Isabel, Eiffel Tower, PP7 and Elisabeth) in the Lucky Strike area and one in the Menez Gwen area (Fig. 1). They were collected using 750 ml titanium syringes (Von Damm, 1983), initially designed for sampling the hot fluids, and manipulated by the French submersible Nautile. The Ti syringes were rinsed with deionized water between each use. Sampling was done in and around the mussel clumps. Samples were also taken in the fluid exits ("vent") and in the bottom sea water. The water surrounding the organisms results from of a mixture of sea water and hydrothermal fluid characterized by steep chemical gradients at a cm scale. The samples obtained will represent the environmental conditions (fluid and sea water) but possibly with a certain amount of dilution by extra sea water due to instability during sampling. The results thus would systematically differ from true local environmental conditions but may still present a reasonable picture of the chemical conditions to which the animals are exposed. Temperatures were recorded with the temperature probe set on the arm of the submersible. Temperature measurements and water sampling were not simultaneous. Table 1 presents the procedures of sample treatment and the analytical methods employed.

IV. Fluid dilution

Endmember concentrations were estimated (from table 2) using Mg as conservative tracer of the fluid dilution by sea water (concentration in sea water for the reference and extrapolation of the data to zero Mg to estimate the pure fluid concentration, Von Damm, 1983). This assumption has been verified in the Lucky Strike area, except in the Statue of Liberty area where Mg concentrations were estimated around 10 mmol kg^{-1} and remained unexplained yet (Langmuir et al., 1997). The relative position of the sample concentration and the estimated dilution curve may

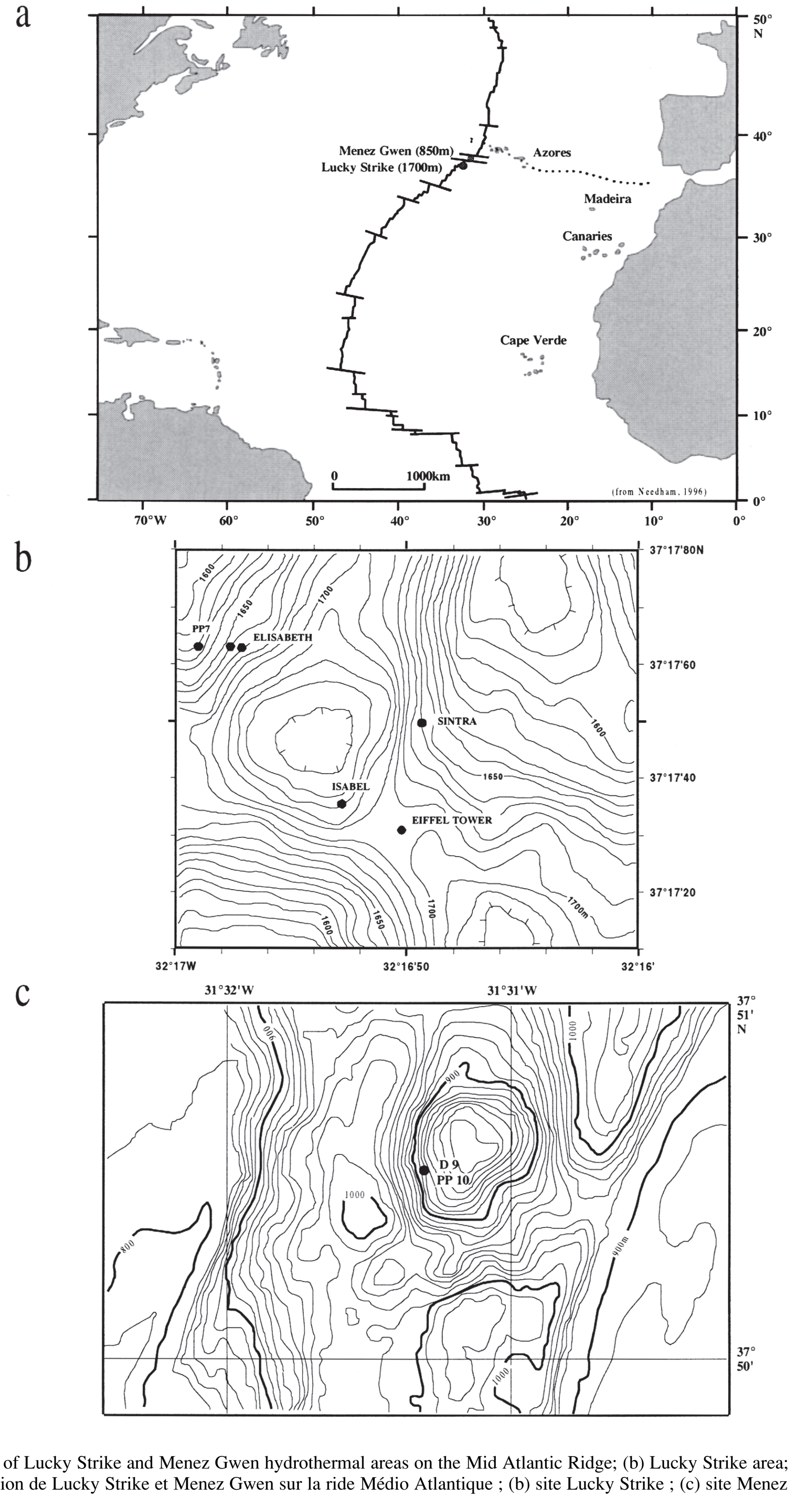

Figure 1. (a) Location of Lucky Strike and Menez Gwen hydrothermal areas on the Mid Atlantic Ridge; (b) Lucky Strike area; (c) Menez Gwen area.
Figure 1. (a) Localisation de Lucky Strike et Menez Gwen sur la ride Médio Atlantique ; (b) site Lucky Strike ; (c) site Menez Gwen.

Table 1. Sample treatment and analytical methods.
Tableau 1. Traitement des échantillons et méthodes analytiques.

Parameter	Preservation method	Analytical method	Remark
pH	analysis on board	potentiometry electrode for sulfidic medium	25°C
ΣS ($H_2S + HS^-$)	analysis on board	colorimetry (Fonselius, 1983)	TRIS buffer DL° = 0.5µmol l^{-1} rsd = 5%
DOC	filtration, freezing	High T combustion Shimadzu TOC 500	rsd = 5%
nutrients*	freezing	colorimetry, segmented flow	rsd = 5%
Mg, Ca	HNO_3 suprapur®, 20 µl in 20 ml, ambient T	ion selective electrode, EDTA complex	rsd = 3%
Cu, Pb total dissolvable metal	HNO_3 suprapur®, 20 µl in 20 ml, ambient T	Potentiometric stripping analysis (Riso et al., 1997)	Cu rsd = 5% Pb rsd =5%

° DL detection limit
*: PO_4^{3-}, NH_4^+, NO_3^- + NO_2^-

therefore suggest production or chemical and / or biological consumption.

V. Spatial distribution

Water samples were sorted as a function of the location and whenever possible of the size of the mussels. The latter was estimated from the video records of each dive, using the diameter of the sampler inlet as reference. The water samples were then classified into the following six categories: vent (in the fluid exit), reference (bottom sea water), clumps of large (> 6 cm) mussels, clumps of small (< 3 cm) mussels, clumps of mussels with various lengths and clumps of mussels covered with a white filamentous mat.

Results and Discussion

I. The sites

Table 2 provides a comprehensive account of the results. Fig. 2 gives a rough description of the main sampling sites along with the distribution of mussels around the fluid sources (chimneys and fissures). PP7 (Fig. 2a) is characterized by a chimney and flange like structure with pools of hot fluids underneath the overhangs. Populations of large mussels were found on the flange near the main hot fluid exit whereas smaller individuals were present on the outer part of the flange and on the chimney edge. Mussels shells occurred on the lower (inactive) part of the chimney. Eiffel tower (Fig. 2b) is a large edifice, nearly uniformly covered with dense and large mussel communities around the numerous high temperature vents and close to the numerous fissures with diffusing fluid. Large mussels were mostly found near the fluid exits whereas smaller ones covered the less active side of the edifice. Menez Gwen (Fig. 2c) was colonized by small and sporadic patches of mussels around the smokers and the fluid diffusers.

II. Fluid dilution

1. Mg concentrations are sometimes higher (up to 56.3 mmol l^{-1}) than the reference (52.8-53.5 mmol l^{-1}) in the vicinity of the organisms. A similar unexplained scatter of the data around the sea water values has also been observed elsewhere for Mg by Gamo et al. (1996) and for O_2 vs silicate and ΣS vs silicate for discrete samples by Johnson et al. (1994).

2. pH : Changes in pH are caused not only by a dilution of the hydrothermal fluid by bottom sea water but also by the titration of a complex acid (hydrothermal fluid) by a complex base (sea water). The extrapolated endmember pH (3.8-4.0) is in good agreement with the values found in the literature of 4.0-4.9 in the Lucky Strike area (Langmuir et al., 1997). The oxidation of variable amounts of ΣS during sample transfer and analysis would also cause a reduction in pH.

Mussels are observed at pH values ranging from 6.2 to 8. Shrimps are observed moving very close to the flowing hot fluid where the pH may be lower.

3. Total sulfide ΣS (fig 3 a) : The extrapolated endmember concentrations are between 2 and 3.2 mmol l^{-1} and are in good agreement with Langmuir et al. (1997) who calculated endmember concentrations of 1.4-3.3 mmol kg^{-1} in the Lucky Strike area.

Mussels were present in a fluid containing 0-60 µmol l^{-1} ΣS, comparable to the ranges of 0 to 330 µmol l^{-1} (average 27 µmol l^{-1}) found by Johnson et al. (1994) on *B. thermophilus* in the Rose Garden (Galapagos Rift). A few values are below the estimated dilution curve in the vicinity of the organisms suggesting an important removal (up to 100 µmol l^{-1}) of hydrogen sulfide from the medium. This sulfide loss may originate from different ways: chemical oxidation with oxygen and precipitation with the metals present in the fluid (Von Damm, 1983). Jannasch & Mottl (1985) observed the coexistence of O_2 and ΣS in the mixing zone. The half-life for sulfide oxidation is about 26±9 h at 25°C, pH = 8 in air saturated and metal free solutions (Millero et al., 1987) and chemical oxidation may not be the

Table 2. Concentrations of some chemical constituents in the Lucky Strike and Menez Gwen hydrothermal areas.
Tableau 2. Composition chimique des échantillons prélevés sur Lucky Strike et Menez Gwen.

SITE (chimney)	Sample	n°	T°C	pH	ΣS	$PO_4^{3^-}$	NO_2^-	NH_4^+	NO^{3^-} + NO_2^-	Mg	Cu	Pb	Ca	DOC
					μ	μ	μ	μ	μ	m	μ	n	m	μ
LS (Eiffel T)	+ Bact	08D3		7.64	0.5	0.96	0.04	0.15	17.9	54.1	0.74±0.01	2.7±0.1	10.1	121
LS (Eiffel T)	+ Bact	09D1		7.46	0.5	2.59	0.1	1.16	16.8	55.4	0.82±0.01	16±1	10.7	210
LS (Eiffel T)	+ Bact	09G1		7.60	<0.5	1.22	0.07	0.45	18.1	52.6	0.091±0.01	2.6±0.2	9.9	192
LS (Eiffel T)	Small	10D3		7.74	<0.5	ns	ns	ns	ns	51	ns	ns	10.7	ns
LS (Eiffel T)	Small	10G3		8.02	<0.5	1.18	0.42	0.84	10.4	53.5	nm	9.0±0.5	10.7	257
LS (Eiffel T)	+ Bact	21G1		7.76	0.5	ns	ns	ns	ns	53.5	ns	ns	9.8	ns
LS (Eiffel T)	Small	22G3		7.78	<0.5	ns	ns	ns	ns	47.9	ns	ns	10.5	ns
LS (Eiffel T)	Small	18D3	9.6-11	7.32	1	ns	ns	ns	ns	53.9	ns	ns	10.6	95
LS (Eiffel T)	Small	18G3	9-10	7.21	1	0.69	0.06	0.31	16	53.3	0.44±0.01	3.7±0.2	10.5	177
LS (Eiffel T)	Big	21D1		7.00	1	ns	ns	ns	ns	52.5	ns	ns	10.5	ns
LS (Eiffel T)	Small	22D3		7.80	1	ns	ns	ns	ns	53.6	ns	ns	10.2	ns
LS (Eiffel T)	M	04G3		7.20	2	ns	ns	ns	ns	nm	2.0±0.1	8.0±0.4	10.4	422
LS (Eiffel T)	+ Bact	17G3	6-10.6	7.53	3	ns	ns	ns	ns	56.3	ns	ns	10.8	ns
LS (Eiffel T)	Big	18D1	10	6.93	3	ns	ns	ns	ns	54.9	ns	ns	10.9	ns
LS (Eiffel T)	Big	18G1	13	7.02	3	0.62	0.08	0.92	16	nm	ns	ns	10.7	381
LS (Eiffel T)	Big	21D3		6.62	21	ns	ns	ns	ns	51.9	ns	ns	10.1	ns
LS (Eiffel T)	M	04D3		6.68	42	1.08	0.09	0.61	17.3	nm	0.02±0.001	0.96±0.04	11.2	140
LS (Eiffel T)	Vent	17D3		5.26	700	ns	ns	ns	ns	39.9	ns	ns	16.4	ns
LS (Eiffel T)	Vent	21G3	323	5.05	1540	ns	ns	ns	ns	33.4	ns	ns	20	ns
LS (Isabel)	Vent	03D3		7.04	9	0.87	0.04	0.35	18.1	53.7	ns	ns	10.1	ns
LS (Isabel)	Vent	03G3		4.79	170	0.4	0.07	4.4	17.7	26	ns	ns	21.6	ns
LS (PP7)	+ Bact	07D1	7.4-11	7.60	0.5	1.22	0.06	0.45	10.9	55.3	0.16±0.01	9.0±0.5	10.3	183
LS (PP7)	REF	07G1	6.07	7.66	0.5	0.99	0.01	0.21	17.9	53.5	0.020±0.001	1.21±0.05	10.8	169
LS (PP7)	+ Bact	20G3		7.49	0.5	ns	ns	ns	ns	53	ns	ns	10.5	ns
LS (PP7)	Big	25G3		7.82	0.5	ns	ns	ns	ns	53.2	ns	ns	9.9	ns
LS (PP7)	Big	06G3		6.93	3	1.08	0.12	0.44	12.2	51	0.27±0.01	32±1	10.4	257
LS (PP7)	+ Bact	20D3		7.26	3	ns	ns	ns	ns	54.6	ns	ns	10.5	ns
LS (PP7)	Big	25D3		7.62	4	ns	ns	ns	ns	53	ns	ns	10.7	ns
LS (PP7)	Big	07G3	6.7-8.0	6.19	62	0.99	0.02	0.29	13.9	52.6	ns	ns	11	160
LS (PP7)	Vent	06D3	162	5.23	690	0.1	0.2	2.95	13.5	38.7	ns	ns	18.7	109
LS (PP7)	Vent	07D3	53-68	4.57	2360	0.4	0.0	6.75	7.79	20	ns	ns	29.4	114
LS (Sintra)	Vent	02G3		5.80	11	ns	ns	ns	ns	49.6	0.091±0.001	21±1	14.2	130
LS (Sintra)	Vent	02D3		5.67	16	ns	ns	ns	ns	48.8	0.039±0.001	20±1	15.4	ns
LS(Elisab.)	Small	19G1	6-7	7.55	0.5	ns	ns	ns	ns	53.4	0.35±0.01	6.0±0.3	10.5	ns
LS(Elisab.)	Small	23G1		7.59	<0.5	ns	ns	ns	ns	nm	ns	ns	10.8	ns
LS(Elisab.)	Big	24D3		7.17	<0.5	ns	ns	ns	ns	56	ns	ns	10.6	ns
LS(Elisab.)	Big	24G3		7.46	<0.5	ns	ns	ns	ns	53.2	ns	ns	10.1	ns
LS(Elisab.)	Big	19D1		6.50	1	ns	ns	ns	ns	54.1	0.22±0.01	11.0±0.5	10.9	ns
LS(Elisab.)	Small	23D3		7.22	1	ns	ns	ns	ns	52.2	ns	ns	10.6	ns
LS(Elisab.)	Small	23G3		7.34	1	ns	ns	ns	ns	nm	ns	ns	10.5	ns
Menez G	+ Bact	13D3		7.83	<0.5	1.27	0.08	0.33	16.4	55	0.063±0.001	4.2±0.2	10.5	216
Menez G	+ Bact	13G3		7.88	<0.5	0.92	0.09	0.58	16	55.9	nm	3.5±0.2	10.6	259
Menez G	M	14G3	15	7.45	0.5	1.89	0.09	1.71	13.6	54.1	ns	ns	10.4	360
Menez G	M	15D3	10	7.62	<0.5	ns	ns	ns	ns	50.7	ns	ns	10.6	ns
Menez G	M	15G3		7.68	<0.5	ns	ns	ns	ns	nm	ns	ns	10.6	ns
Menez G	Big	12D3		7.14	2	ns	ns	ns	ns	52.7	0.41±0.01	14.0±0.5	10.4	ns
Menez G	Big	12G3		7.53	2	ns	ns	ns	ns	49.8	0.25±0.01	4.1±0.2	10.9	ns
Menes G	Big	16G3	11-21	6.74	3	ns	ns	ns	ns	50.9	ns	ns	10.7	ns
Menez G	M	26D3		7.84	3	ns	ns	ns	ns	53	ns	ns	10.6	ns
Menez G	Big	11G3	11.3	7.68	11	1.59	0.06	0.43	16.8	56.3	0.16±0.01	nm	11.9	647
Menez G	M	14D3	11-26	6.70	17	ns	ns	ns	ns	52.7	0.33±0.01	nm	11.5	ns
Menez G	M	26G3		7.79	18	ns	ns	ns	ns	50.4	ns	ns	10.4	ns
Menez G	Vent	16D3		5.79	240	ns	ns	ns	ns	47.4	ns	ns	13.4	ns
Menez G	Vent	11D3	279	4.90	1100	ns	ns	ns	ns	23.7	ns	ns	22.3	ns
sea water	REF	19D3	6.0	7.80	<0.5	1.22	0.09	0.49	18.2	52.8	ns	ns	10.4	143
sea water	REF	19G3	6.0	7.82	<0.5	ns	ns	ns	ns	53.5	nm	0.34±0.02	9.9	ns

m: mmol l^{-1} μ: μmol l-1 n: nmol l^{-1} nm not measured ns : no sample T°C indicative temperature
LS: Lucky strike Menez G.: Menez Gwen Ref: reference sample, bottom sea water
M: mussels mixed Length Small: small mussels L< 3 cm
Big: big mussels L > 6 cm +Bact: mussels covered with a white and filamentous mat

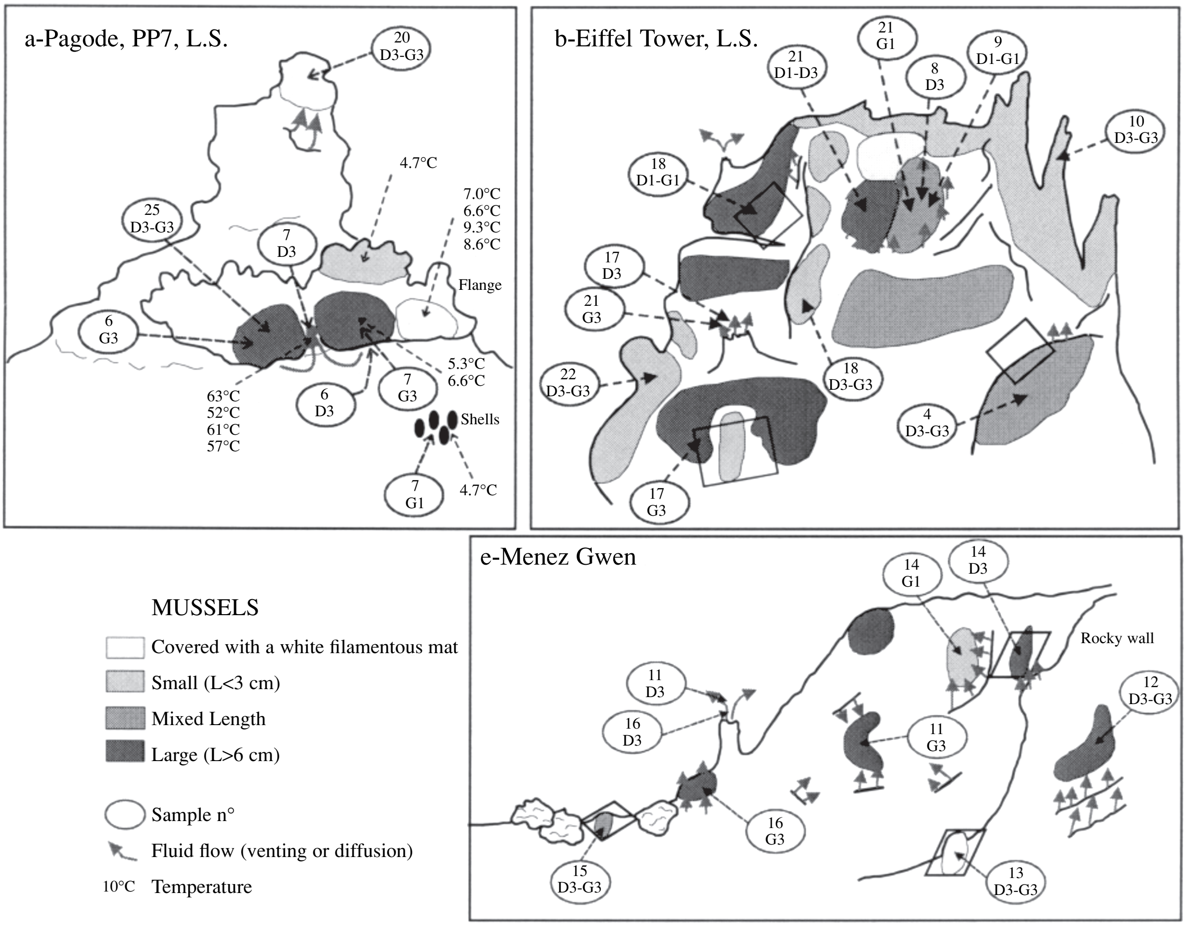

Figure 2. Simplified view of the sampling sites profiles.
(a) PP7, Lucky Strike; (b) Eiffel Tower, Lucky Strike; (c) Menez Gwen.
Figure 2. Représentation simplifiée des profils des sites échantillonnés.
(a) PP7, Lucky Strike ; (b) Tour Eiffel, Lucky Strike ; (c) Menez Gwen.

main process of sulfide removal. Sulfide can also be consumed as an energy source during the symbiotic chemoautotrophic processes (Fisher, 1990). Using an *in situ* chemical analyzer in the Galapagos Spreading Center, Johnson et al. (1988) observed a decrease of the sulfide concentration correlated with the population density of *B. thermophilus*. The sulfide loss estimated in this study is in the same range and may be partly attributed to an uptake by the mussels communities.

4. N species (Fig. 3b, c): extrapolated endmember concentrations ranged from 0-2 for nitrate to 8-10 µmol l^{-1} for ammonia. NH_4^+ values are comparable with the range (3.6 and 20.3 µmol l^{-1}) found by Tunnicliffe et al. (1986) in the North Pacific Explorer Ridge.

The estimated mixing lines showed an increase of the nitrate + nitrite concentrations from the source to the sea water and a concomitant, but non quantitative, decrease of ammonia. Jannasch et al. (1985) and Johnson et al. (1988) suggested that the nitrate from sea water is transformed to nitrite and ammonia with increasing temperature, with a zone of coexistence of the three species between 2 and 8 °C. According to Aminot & Kérouel (1995) ammonium and nitrate, in the absence of biological reactions, are quite chemically stable and should not undergo spontaneous chemical oxidation or reduction in sea water. Thus changes in their concentrations, in the absence of organisms, should only be due to a conservative mixing of the hydrothermal fluid with sea water.

Most of the concentrations obtained in the vicinity of the organisms, where Mg concentrations were close to the sea water value, showed a departure from the mixing lines: concentrations of ammonium were above (up to + 1.5 µmol l^{-1}), and those of nitrate below (down to -8 µmol l^{-1}) that of sea water, suggesting a production of ammonium and a consumption of nitrate + nitrite by the organisms. This hypothesis is supported by Johnson et al.

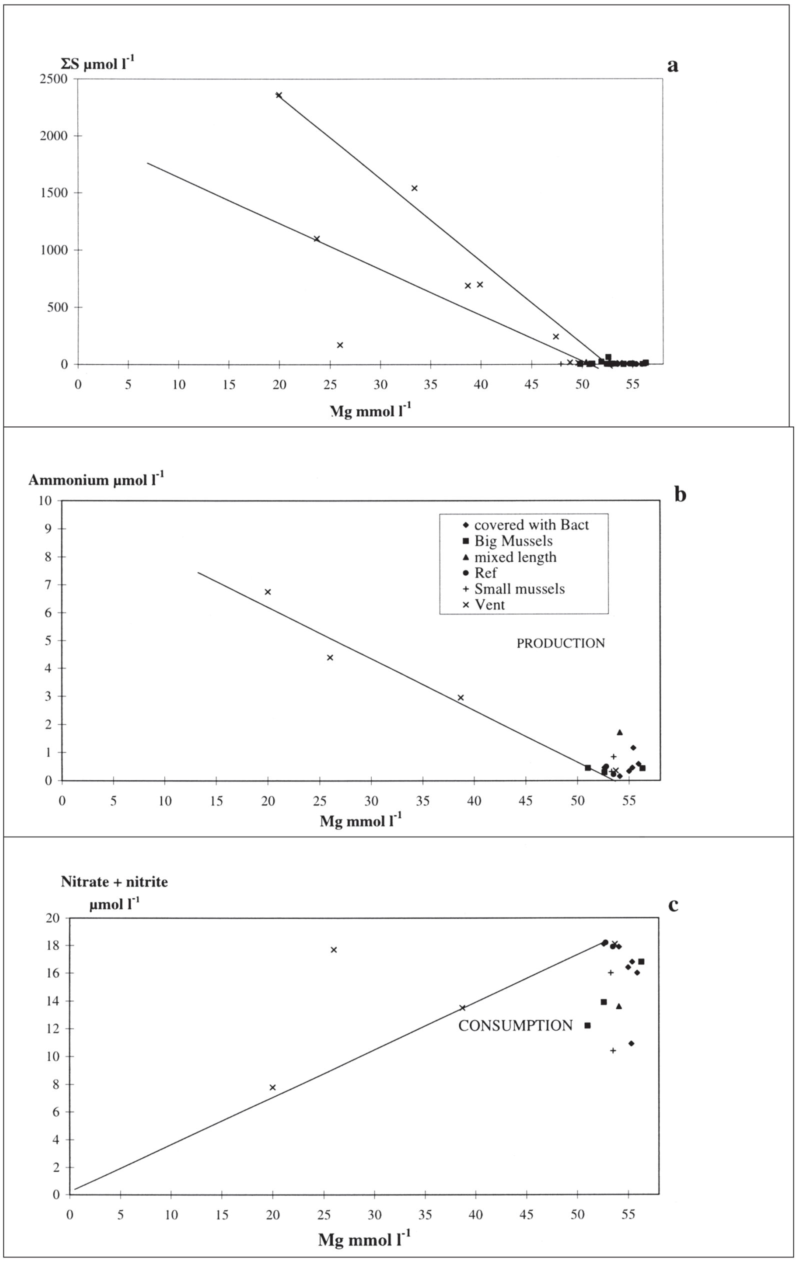

Figure 3. Estimation of the hydrothermal fluid dilution using Mg as mixing index.

(a) ΣS (H_2S + HS^-) vs Mg; (b) ammonium (NH_4^+) vs Mg; (c) nitrate (NO_3^-) + nitrite (NO_2^-) vs Mg. Ref. reference sample, bottom sea water ; vent : fluid emission

Figure 3. Estimation de la dilution du fluide hydrothermal en utilisant Mg comme indicateur de mélange. (a) ΣS (H_2S + HS^-) vs Mg ; (b) ammonium (NH_4^+) vs Mg ; (c) nitrate (NO_3^-) + nitrite (NO_2^-) vs Mg. Ref. échantillon de référence, eau de mer du fond ; vent : émission du fluide.

(1988) who observed in situ nitrate consumption. Similarly, the ammonium increase could have occurred because it is a major waste product of marine invertebrate metabolism. For example *Riftia pachyptila* has been observed (Childress et al., 1991) to excrete ammonium in laboratory experiments.

The nitrogen flux appears to be complicated as production and consumption were not observed in the same samples suggesting a lateral dispersion of the compounds. Johnson et al. (1988) made a similar remark in the case of O_2 and ΣS which were consumed in different areas within the mussels communities. More important, a mass balance cannot be achieved yet without information on N_2 and N_2O (Lilley et al., 1982).

5. *PO_4^{3-}*: the data obtained in the present study are distributed around the reference values, with a concentration decrease in the hydrothermal fluid rich samples, suggesting low phosphate concentrations in the pure fluid. Tunnicliffe et al. (1986) measured concentrations ranging from 2 to 3 µmol l^{-1} in the North Pacific Explorer Ridge. According to Sedwick et al. (1992), dissolved phosphate can be scavenged from sea water by iron oxyhydroxides. Three samples (9D1, 11G3 and 14G3) had a higher phosphate concentration. This might be due to an excretion by animals or reflect a scatter caused by a possible entrainment of hydrothermal precipitates in the sampler (Feely et al., 1990).

6. *Ca*: the extrapolated endmember concentration for this area is between 32 and 40 mmol l^{-1} and is comparable to values found in other locations in the MAR (Campbell et al., 1988 ; Jean-Baptiste et al., 1991; James et al., 1995; Massoth et al., 1989) ranging from 10 to 47 mmol l^{-1}.

7. *Dissolved Organic Carbon (DOC)*: results obtained in this study show a net increase of DOC in the vicinity of the organisms. This increase is distinctly higher than what would be expected if there were contamination or analytical errors, and is suggestive of a high productivity of the ecosystem.

8. *Cu and Pb* (total dissolvable metal): the estimation of endmember concentrations was not possible because of the large scatter in the data. This variability can be linked to the great affinity of those metals to form sulfide precipitates and the possible precipitation in the sampler. However these data are a first

attempt to characterize the metallic environment of the hydrothermal organisms and further analysis should differentiate between the dissolved and particulate phase with an in situ filtration of the sample (work in progress). Godfrey et al. (1994) observed at TAG site that lead concentrations decreased rapidly away from the source because of its precipitation as lead sulfide. Cu and Pb behave like Fe, Co, Zn, Cd and Hg (Von Damm, 1983) and will form insoluble precipitates with sulfides in plumes (Trefry & Trocine, 1985), to build chimneys, and on conduit surfaces. Measured or extrapolated endmember concentrations in the literature show great variability, with concentrations ranging between 0.02 and 44 µmol l^{-1} for copper (4-7 nmol l^{-1} in sea water) and 0.6 to 10000 nmol l^{-1} for lead (0.01 nmol l^{-1} in sea water) (Massoth et al., 1989; James et al., 1995; Butterfield et al., 1990).

Because of the high variability of the concentrations and the great diversity of the sampling sites, it was not possible to relate the distributions of metals and the organisms. However the environment is enriched in these metals. The concentrations of copper were always higher in the vicinity of the "big mussels" than in the sea water and were more or less constant (0.26 ± 0.09 µmol l^{-1}, Table 2). A comparison of these values with the concentrations of copper reported for surface [Pb, 0.07-2.7 nmol l^{-1} (Riso et al., 1993), Cu, 1.5-8 nmol l^{-1} (Riso et al., 1988)] and deep Atlantic water [Pb, 0.005-0.02 nmol l^{-1} (Yeats & Campbell, 1983), Cu, 2-5 nmol l^{-1} (Bruland & Franks, 1983)] shows that hydrothermal organisms are subjected to Cu and Pb concentrations up to 1000 times greater than in oceanic waters. The mussels need to have developed a high tolerance or adaptive strategies to colonize such highly toxic areas. The measurements of the concentration factors for hydrothermal mussels are currently underway.

The environment surrounding the mussel communities is schematically described in Fig 5: the hydrothermal fluid enriched the medium in sulfide, ammonia, Cu and Pb, with higher temperature and lower pH. The sea water (88-100%) brings magnesium and nitrate. This mixing zone is finally modified by the organisms with an elimination of sulfide and nitrate and a production of DOC and ammonia.

II. Distribution of the organisms and chemical parameters

Fig. 4 shows the prevalence of different micro-environments (microhabitat) linked to the patchy distribution of each class of organisms, suggesting a relationship between the size class and the distribution along the chemical gradient. The samples studied appeared to be distributed in the following order from the vent exit to sea water: large sized mussels, mixed sized, small sized (mussels covered with a white filamentous mats being in the

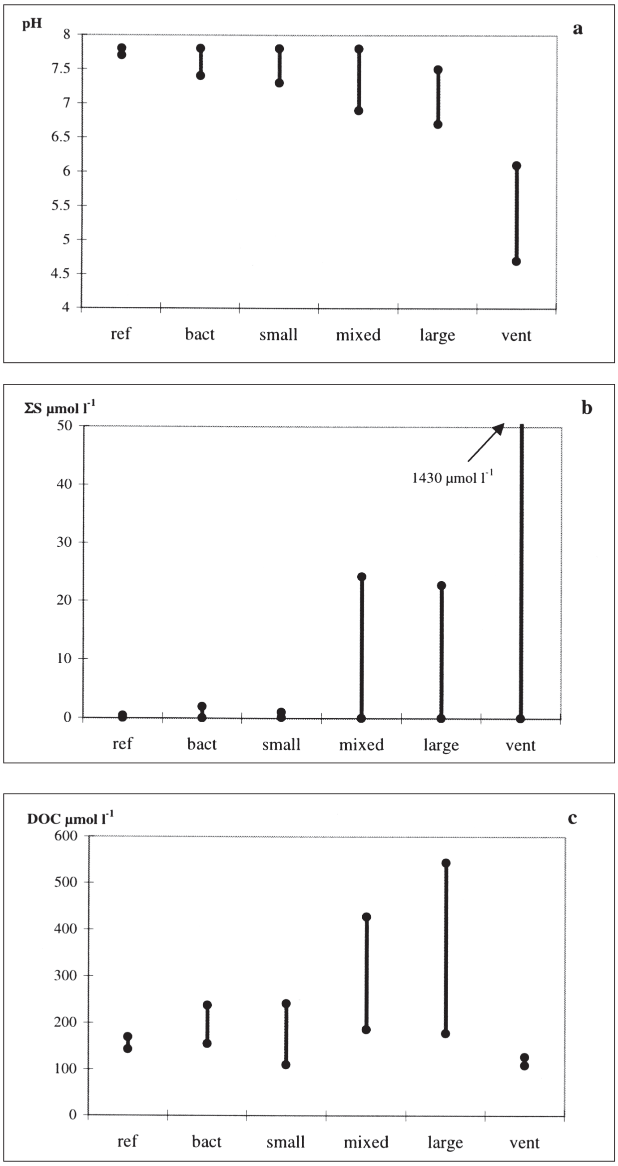

Figure 4. Distribution of mussels vs chemical parameters of the environmental milieu (the interval is built using the mean+standard deviation and mean -standard deviation).

(a) pH; (b) total sulphide (H_2S + HS^-); (c) dissolved organic carbon.

ref: reference sample, bottom sea water; bact: mussels covered with white filamentous mats; small: small sized mussels; mixed: mixed sized mussels; large: large sized mussels; vent: fluid emission.

Figure 4. Distribution des modioles en fonction de la composition chimique du milieu environnant (l'intervalle est construit en utilisant la moyenne – l'écart type et la moyenne + l'écart type).

(a) pH; (b) sulfure total (H_2S + HS^-) ; (c) carbone organique dissous.

ref : échantillon de référence, eau de mer du fond ; bact : modioles recouvertes d'un revêtement de filaments blancs ; small : petites modioles ; mixed : modioles de tailles variées; large : grandes modioles ; vent : émission du fluide.

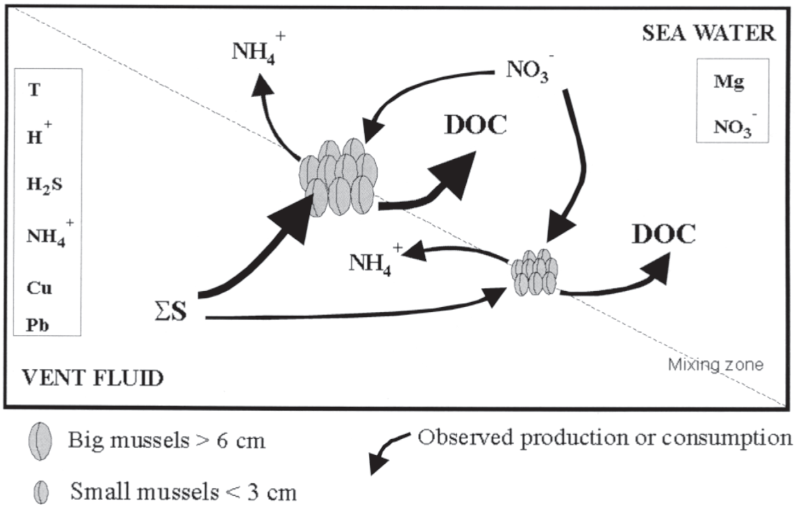

Figure 5. Schematic description of the chemical environment of hydrothermal mussels at Lucky Strike and Menez Gwen showing: 1. inputs from the hydrothermal fluid and seawater, 2. production and consumption by the mussels communities (arrows), 3. spatial segregation of the size along the chemical gradient.

Figure 5. Description schématique de l'environnement chimique des modioles hydrothermales de Lucky Strike et Menez Gwen montrant : 1. les apports de l'eau de mer et du fluide hydrothermal, 2. la consommation et la production par les communautés de modioles (flèches), 3. la ségrégation spatiale des tailles le long du gradient chimique.

same concentrations ranges as small sized mussels). The increase of dissolved organic carbon (DOC) concentration followed the same trend with a higher production near the colonies of large sized mussels. This suggested a higher productivity in these communities.

The second point arising from this figure is the increase in standard deviation with pH decrease or sulfide concentration increase. A statistical study was made on these results (table 3): comparison of variance (Fisher test) and of mean (Student test for equal or unequal variances). A difference in the variance between two groups can be indicative of the variability of the environment surrounding the organisms and particularly of the amount of hydrothermal fluid present. The mixing zone is characterized by a steady state (small variance) in its cold part which is mainly bottom sea water. When the hydrothermal fluid content increases, the variability of the system increases with constant switching from cold sea water to variable hydrothermal inputs. The organisms are therefore subjected to more variable chemical conditions.

Difference in the means is more difficult to observe as it can be hidden by the high variances obtained. However significant results were obtained between groups demonstrating the presence of different microhabitats especially between the extreme size classes (small and large mussels).

This result reinforces the trends observed during sampling: large size classes seem to be settled closer to the fluid emission (high sulfide, temperature and low pH)

Table 3. Results of the Fisher and Student tests for the comparisons of variances and means respectively.

Tableau 3. Résultats des tests de Fisher et Students pour les comparaisons de variances et moyennes.

			Fisher	test			Student	test	
class 1	class 2	pH	ΣS	DOC	Mg	pH	ΣS	DOC	Mg
sea water	+ white mat	0.387	0.120	0.594	0.199	0.198	0.345	0.281	0.109
sea water	small mussels	0.186	0.555	0.317	***0.077***	0.250	0.238	0.761	0.472
sea water	mixed length	***0.069***	**0.001**	0.175	0.125	0.196	***0.094***	0.266	0.300
sea water	big mussels	***0.068***	**0.001**	0.128	***0.092***	**0.028**	0.086	0.265	0.818
+ white mat	small mussels	0.246	**0.019**	0.259	0.170	0.655	0.465	0.632	**0.011**
+ white mat	mixed length	**0.014**	**0.000**	**0.032**	0.503	0.212	0.114	0.325	**0.007**
+ white mat	big mussels	**0.009**	**0.000**	**0.006**	0.226	**0.001**	0.116	0.217	**0.031**
small mussels	mixed length	0.152	**0.000**	0.460	0.655	0.305	0.105	0.250	0.877
small mussels	big mussels	0.120	**0.000**	0.263	0.745	**0.010**	0.102	0.216	0.450
mixed length	big mussels	0.955	0.887	0.695	0.812	0.185	0.713	0.723	0.390

0.072 significant difference for $p < 0.1$
0.012 significant difference for $p < 0.05$

whereas smaller ones are confined to the outer parts with lower sulfide concentrations, pH and temperature values nearer to those of the bottom sea water. Comtet & Desbruyères (1998) studied the size frequency distribution and confirmed the existence of an intra-site variability of the size structure. This spatial segregation of the sizes could be related to the availability of the hydrothermal fluid and to the nutritive supply (distance from the vent) inducing a competition for energy and space. Larger individuals were present in an environment richer in reduced compounds leading to a possible higher growth rate. Smith (1985) observed a decrease of density of *Bathymodiolus thermophilus* when getting away from the effluent in the Galapagos Rift. This decrease of density was concomitant with a decrease of the O_2 consumption rate, of the concentration of particulate organic carbon and of the nutritional state that may be related with the decrease of nutritive supply. Fisher et al. (1988) observed the same trends with more chemoautotrophic bacteria associated with the gills, more chemoautotrophic carbon content in the tissues and a slightly better overall conditions in mussels sampled in a more active venting area than in mussels found in the peripheral area suggesting a higher contribution of the autotrophic process in the more active site. These observations: higher concentrations of reduced compounds, of dissolved organic carbon, possible higher concentrations of particulate organic matter (Smith, 1985) leading to the hypothesis of a higher growth rate are coherent with the nutritional strategies developped by *Bathymodiolus* sp. Fiala-Medioni et al. (1986) and Page et al. (1991) observed that both autotrophic and heterotrophic processes were possible in *Bathymodiolus* sp. This species can thus follow three nutritional strategies: autotrophy using the reduced compounds present in the surrounding water, filter feeding of particulate organic matter (POM) and even uptake of dissolved organic matter (Fiala-Medioni et al., 1986). Page et al. (1991) stated that the relative contribution of POM to mussel nutrition is unknown but may be the main source of nutrition at a distance from the vent effluent. Where sulfide are higher, POM may be a less important source of C but could still provide supplemental C and / or nutrients not provided by the endosymbionts. These mussels have developped different nutritional stategies allowing them to survive in different environmental conditions.

The importance of the fluid availability is also in agreement with the videoscopic observations i.e. the density and distribution of the organisms appears to be related to the geomorphology of the site or, more precisely, the spatial variability of the fluid emission (based on subjective videoscopic observations). Eiffel Tower has numerous fluid exits through small chimneys or fissures and cracks inhabited by large communities whereas Menez Gwen is characterized by higher fluid flows, a different substratum and perhaps a lower availability of fluids and is inhabited by sparse communities.

The second hypothesis preferred by Comtet et al. (1998) suggests a spatio temporal variability in the recruitment rather than differences in growth rate. This spatio temporal variability in the recruitment could be explained (Comtet et al., 1998) by the variability of the hydrothermal activity leading to the formation of micro habitats more or less suitable for the settlements of young mytilids and by intraspecific interactions such as feeding competition between adults and postlarvae and intraspecific larviphagy.

Finally this spatial segregation in size could indicate movement of the mussels along the sulfide gradients during their growing phase. Mussels have been observed to align themselves along a sulfide gradient in simulated in situ conditions (P. Dando, pers. com.). Large size mussels have also been sampled settled on artificial substrate recovered one year after mooring, confirming this hypothesis of moving mussels.

Conclusion

Notwithstanding the limitations of sample quality (uncertainties of the concentrations due to dilution during sampling) and the necessity to develop specific sampling devices, some preliminary results on the chemistry of the waters surrounding the hydrothermal vents were obtained and schematized in Fig. 5.

1. The Lucky Strike and Menez Gwen mussels live in a dilute hydrothermal medium, with pH between 6.2 and 8, hydrogen sulfide concentration between 0 and 62 µmol l^{-1} and high DOC concentrations.
2. The size distribution appears to be related to environmental conditions, with patches of big mussels closer to the vents than smaller mussels. This distribution may reflect either the functioning of the ecosystem (need and competition for energy originating from chemical compounds) or different settlement periods.
3. The microenvironment surrounding the organisms is not only modified by temperature, chemical reactions and dilution with sea water but also by the organisms themselves as evidenced by high DOC production, sulfide consumption, and anomalies in phosphate distribution. Nitrate consumption and ammonia production are separated in space, reflecting a possible lateral dispersion of the hydrothermal fluid by the mussels. This might influence the flux of compounds through the chemical food chain and the distribution of the organisms.
4. The environment is enriched in Cu and Pb, with concentrations up to 1000 times higher than in oceanic waters with living mussel communities. Further studies on the tolerance of hydrothermal mussels to such high metal

concentrations will help in understanding their adaptive strategies.

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References

Aminot A. & Kérouel R. 1995. Reference material for nutrients in sea water: stability of nitrate, nitrite, ammonia and phosphate in autoclaved samples. *Marine Chemistry,* **49**: 221-232.

Bruland K.W. & Franks R.P. 1983. Mn, Ni, Cu, Zn and Cd in the Western North Atlantic. *Trace metals in sea water.* Series N.C. NY, Plenum Press. **9**: 395.

Butterfield D.A., Massoth G.J., McDuff R.E., Lupton J.E. & Lilley M.D. 1990. Geochemistry of hydrothermal fluids from axial seamount hydrothermal emissions study vent field, Juan de Fuca ridge: subseafloor boiling and subsequent fluid-rock interaction. *Journal of Geophysical Research,* **95** (B8, august 10): 12895-12921.

Campbell A.C., Palmer M.R., Klinkhammer G.P., Bowers T.S., Edmond J.M., Lawrence J.R., Casey J.F., Thompson G., Humphris S., Rona P. & Karson J.A. 1988. Chemistry of hot springs on the Mid-Atlantic Ridge. *Nature,* **335** (6 - october): 514-519.

Chevaldonné P., Desbruyères D. & Le Haître M. 1991. Time-series of temperature from three deep-sea hydrothermal vent sites. *Deep-Sea Research,* **38** (11): 1417-1430.

Childress J.J., Fisher C.R., Favuzzi J.A., Kochevar R.E., Sanders N.K. & Alayse A.M. 1991. Sulfide driven autotrophic balance in the bacterial symbiont containing hydrothermal vent tubeworm, *Riftia pachyptila* Jones. *Biological Bulletin,* **180**: 135-153.

Colaço A., Desbruyères D., Comtet T. & Alayse A.M. 1998. Ecology of the Menez Gwen hydrothermal vent field(Mid Atlantic Ridge/Azores Triple Junction). *Cahiers de Biologie Marine,* **39**: 237-240.

Comtet T. & Desbruyères D. 1998. Population structure and recruitment in mytilid bivalves from the Lucky Strike and Menez Gwen hydrothermal vent field (37°17’N and 37°50’N on the Mid-Atlantic Ridge). *Marine Ecology Progress Series,* **163**: 165-177.

Feely R.A., Geiselman T.L., Baker E.T., Massoth G.J. & Hammond S.R. 1990. Distribution and composition of hydrothermal plumes particles from the ASHES vent field at axial volcano, Juan de Fuca ridge. *Journal of Geophysical Research,* **95** (B8): 12855-12873.

Fiala-Medioni A., Alayse A.M. & Cahet G. 1986. Evidence of in situ uptake and incorporation of bicarbonate and amino acids by hydrothermal vent mussel. *Journal of Experimental Marine Biology and Ecology,* **96**: 191-198.

Fisher C.R. 1990. Chemoautotrophic and methanotrophic symbioses in marine invertebrates. *Aquatic Sciences,* **2** (3, 4): 399-436.

Fisher C.R., Childress J.J., Arp A.J., Brooks J.M., Distel D., Favuzzi J.A., Felbeck H., Hessler R., Johnson K.S., Kennicutt II M.C., Macko S.A., Newton A., Powell M.A., Somero G.N. & Soto T. 1988. Microhabitat variation in the hydrothermal vent mussel, *Bathymodiolus thermophilus,* at the Rose Garden vent on the Galapagos Rift. *Deep-Sea Research,* **35** (10/11): 1769-1791.

Fonselius S. H. 1983. Determination of hydrogen sulfide. *Methods of sea-water analysis.* Grasshof K. Ed., Verlag Chemie: 73-84.

Fouquet Y., Ondreas H., Charlou J.L., Donval J.P., Radford-Knoery J., Costa I., Lourenco N. & Tivey M.K. 1995. Atlantic lava lakes and hot vents. *Nature,* **377** (21 september): 201.

Gamo T., Chiba H., Masuda H., Edmonds H.N., Fujioka K., Kodama Y., Nanba H. & Sano Y. 1996. Chemical characteristics of hydrothermal fluids from the TAG mound of the mid-Atlantic ridge in August 1994: implications for spatial and temporal variability of hydrothermal activity. *Geophysical Research Letters,* **23** (23): 3483-3486.

Godfrey L.V., Mills R., Elderfield H. & Gurvich E. 1994. Lead behaviour at the TAG hydrothermal vent field, 26°N, Mid-Atlantic Ridge. *Marine Chemistry,* **46**: 237-254.

James R.H., Elderfield H. & Palmer M.R. 1995. The chemistry of hydrothermal fluids from the Broken Spur site, 29°N, Mid Atlantic Ridge. *Geochimica et Cosmochimica Acta,* **59** (n° 4): 651-659.

Jannasch H.W. & Mottl M.J. 1985. Geomicrobiology of deep-sea hydrothermal vents. *Science,* **229**: 717-725.

Jean-Baptiste P., Charlou J.L., Stievenard M., Donval J.P., Bougault H. & Mevel C. 1991. Helium and Methane measurements in hydrothermal fluids from the mid-Atlantic ridge : the Snake Pit at 23°N. *Earth and Planetary Science Letters,* **106**: 17-28.

Johnson K.S., Childress J.J., Hessler R.R., Sakamoto-Arnold C.M. & Beelher C.L. 1988. Chemical and biological interactions in the Rose Garden hydrothermal vent field, Galapagos spreading center. *Deep-Sea Research I,* **35** (10/11): **1723-1744.**

Johnson K.S., Childress J.J., Beelher C.L. & Sakamoto C.M. 1994. Biogeochemistry of hydrothermal vent mussel communities : the deep sea analogue to the intertidal zone. *Deep Sea Research I,* **41** (N° 7): 993-1011.

Langmuir C., Humphris S., Fornari D., Van Dover C., Von Damm K., Tivey M.K., Colodner D., Charlou J.L., Desonie D., Wilson C., Fouquet Y., Klinkhammer G. & Bougault H. 1997. Hydrothermal vents near a mantle hot spot: the Lucky Strike vent field at 37°N on the Mid-Atlantic ridge. *Earth and Planetary Science Letters,* **148**: 69-91.

Lilley M.D., de Angelis M.A. & Gordon L.I. 1982. CH_4, H_2, CO and N_2O in submarine hydrothermal vent waters. *Nature,* **300** (4 november): 48-50.

Massoth G.J., Butterfield D.A., Lupton J.E., McDuff R.E.,

Lilley M.D. & Jonasson I.R. 1989. Submarine venting of phase-separated hydrothermal fluids at Axial Volcano, Juan de Fuca Ridge. *Nature,* **340** (31 august): 702-705.

Millero F.J., Hubinger S., Fernandez M. & Garnett S. 1987. Oxidation of H_2S in sea water as a function of temperature, pH and ionic strength. *Environmental Science and Technology, **21**:* 439-443.

Page H.M., Fiala-Medioni A., Fisher C.R. & Childress J.J. 1991. Experimental evidence for filter-feeding by the hydrothermal vent mussel *Bathymodiolus thermophilus. Deep Sea Research,* **38** (n°12): 1455-1461.

Riso R., Quentel F., Madec C., Le Corre P. & Birrien J.L. 1988. Le cuivre et le cadmium dans le front interne cotier de l'Iroise (Atlantique Nord Est, côte de Bretagne). *Oceanologica Acta,* **11** (n° 3): 221-226.

Riso R.D., Le Corre P., Birrien J.L. & Quentel F. 1993. Seasonal variation of copper, nickel and lead in Western Brittany coastal waters (France). *Estuarine, Coastal and Shelf Science,* **37**: 313-327.

Riso R.D., Le Corre P. & Chaumery C.J. 1997. Rapid and simultaneous analysis of trace metals (Cu, Pb, and Cd) in sea water by potentiometric stripping analysis. *Analytica Chimica Acta,* **351**: 83-89.

Sedwick P.N., McMurtry G.M. & Macdougal J.D. 1992. Chemistry of hydrothermal solutions from Pele's vents, Loihi Seamount, Hawaï. *Geochimica et Cosmochimica Acta,* **56**: 3643-3667.

Smith K.L. 1985. Deep-sea hydrothermal vent mussels : nutritional state and distribution at the Galapagos Rift. *Ecology,* **66** (n° 3): 1067-1080.

Trefry J.H. & Trocine R.P. 1985. Iron and copper enrichment of suspended particles in dispersed hydrothermal plumes along the mid atlantic ridge. *Geophysical Research Letters,* **12** (N° 8): 506-509.

Tunnicliffe V., Botros M., De Burgh M.E., Dinet A., Johnson H.P. & McDuff R.E. 1986. Hydrothermal vents of Explorer Ridge, northeast Pacific. *Deep-Sea Research,* **33** (3): 401-412.

Van Dover C.L., Desbruyeres D., Segonzac M., Comtet T., Saldanha L., Fiala Medioni A. & Langmuir C. 1996. Biology of the Lucky Strike Hydrothermal field. *Deep-Sea Research I,* **43** (n° 9): 1509-1529.

Von Cosel R., Comtet T. & Krylova E. 1999. A new species of *Bathymodiolus* from hydrothermal vents on the Mid Atlantic Ridge. *Veliger,* (in press).

Von Damm K.L. 1983. Chemistry of submarine hydrothermal solutions at 21°North, East Pacific Rise and Guaymas Basin, Gulf of California, University thesis, Massachussett Institute of Technology and Woods Hole Oceanographic Institute.

Yeats P.A. & Campbell J.A. 1983. Ni, Cu, Cd and Zn in the Nortwest Atlantic Ocean. *Marine Chemistry,* **12**: 43.