



## Chemical and thermal description of the environment of the Genesis hydrothermal vent community (13°N, EPR)

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**Abstract:** The objective of this study is to describe the chemical and physical environment surrounding the vent organisms at the Genesis site (EPR, 2640 m). The main chimney is colonized by *Riftia pachyptila*, fishes Zoarcidae and crabs Bythograeidae. The top of the smoker is covered with tubes of polychaetes Alvinellidae, the frontier zone by limpet gastropods. Temperature measurements and water sampling were made on an axis along the chimney.

The environment was characterized using relationships between chemical concentrations and temperature to provide a chemo-thermal model of the site. Discrete temperature ranges were 1-1.6°C in sea water, 1.6-10°C among *Riftia* plumes (up to 25°C at the tube base), 7-91°C close to the alvinellid tubes, fluid emission was 262-289°C. This study describes the habitat of Alvinellidae emphasizing its chemical ( $\Sigma S$  [ $H_2S + HS^- + S^{2-}$ ] 3-300  $\mu mol\ l^{-1}$ ,  $CO_2$  3.5-6  $mmol\ l^{-1}$ , pH 5.7-7.5) and thermal specificities compared to the *Riftia* ones ( $\Sigma S$  4-12  $\mu mol\ l^{-1}$ ;  $CO_2$  2-3.5  $mmol\ l^{-1}$ ; pH 5.8-7.7). The size of *Riftia* allowed us to define its environment at the organism (temperature gradient along the tube 0.5-1°C  $cm^{-1}$ ) and population scales (temperature difference between organisms from the same clump: 10-20°C). Such spatial heterogeneity may play a significant role in the animal physiology and calls for further investigations.

**Résumé :** Description des conditions chimiques et thermiques de l'environnement des communautés biologiques du site hydrothermal Genesis (13°N, ride Est-Pacifique). Le but de ce travail est de décrire l'environnement physico-chimique des organismes hydrothermaux sur le site Genesis (EPR, 2 640 m). La cheminée principale est colonisée par *Riftia pachyptila*, des poissons Zoarcidae et des crabes Bythograeidae. Le sommet du fumeur est couvert de polychètes Alvinellidae, la zone frontière par des gastéropodes patelliformes.

Un modèle reliant la température et la concentration en  $\Sigma S$  et  $CO_2$  est proposé. Les valeurs discrètes de températures s'échelonnent depuis 1-1,6 °C dans l'eau de mer, 1,6-10 °C autour de l'organe branchial de *Riftia* et jusqu'à 25 °C à la base des tubes. Elles atteignent 7-91°C à proximité des alvinellidés et 262-289 °C pour le fluide pur. Un environnement spécifique pour chaque communauté d'organismes est présenté : autour des Alvinellidae  $\Sigma S$  3-300  $\mu mol\ l^{-1}$ ,  $CO_2$  3,5-6  $mmol\ l^{-1}$ , pH 5,7-7,5 ; autour de *Riftia pachyptila*  $\Sigma S$  4-12  $\mu mol\ l^{-1}$  ;  $CO_2$  2-3,5  $mmol\ l^{-1}$  ; pH 5,8-7,7. La taille de *R. pachyptila* a permis de préciser cet environnement à l'échelle de l'organisme (gradient de 0,5-1 °C  $cm^{-1}$  le long du tube) et de la communauté (différence de 10-20 °C au sein d'un même bouquet d'individus). Les travaux ultérieurs devront porter sur le rôle physiologique de cette hétérogénéité spatiale.

**Keywords :** hydrothermal ecosystem, hydrogen sulphide, carbon dioxide, temperature.

### Introduction

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In the absence of light, the food-web of deep-sea hydrothermal communities is based mainly on the

chemolithoautotrophic bacterial primary production. A large part of the dominant primary consumers is associated with autotrophic bacteria in closed symbiotic systems relying on a periodical access to reduced and oxygenated compounds (Childress et al., 1992; Fisher, 1990; Tunnicliffe, 1991). The sessile primary consumers are living in the turbulent mixing zone where the environmental conditions are constantly switching from hydrothermal to sea water dominated conditions. As Johnson et al., (1986, 1988a) demonstrated using in situ chemical measurements, the mixing gradient within interfacial region is steep and environmental conditions vary at the centimetre scale. Temporal studies using thermal probes demonstrate also (Johnson et al., 1988b) that, at the scale of micro-habitats, temperature is extremely variable on time scales from few seconds (turbulence) to days (harmonic of the tidal signal) (Chevaldonné et al., 1991; Chevaldonné et al., 1992). The definition of physical and chemical environment of organisms in fluctuating micro-environment is thus deeply affected by the scale of measuring and sampling and by procedures and strategies. In situ chemical analysis is probably the most accurate tool when considering microbiotope definition, but it must be associated with temporal series due to its sensitivity to micro-hydrodynamics conditions. Because of the variability of this turbulent environment, discrete sampling of hydrothermal water is by far less resolving but provide a wider range of possible analysis. Nevertheless it gives averaged values which can be used for comparison between micro-habitats only.

The main objective of this study is to compare the gross physical and chemical conditions surrounding two of the most prominent populations of worms (*Riftia* and *Alvinella*) living within a typical vent field area (Genesis) at 13°N/EPR. These two species were described by Fustec et al. (1987) to be dominant organisms among two different megafaunal assemblages based on in situ observation, faunal analysis and discrete temperature measurements. Our aim is to characterize and to compare the two micro-habitats in term of ecological settings as well as thermal and chemical characteristics.

## Material and Methods

All the sampling and experiments were done during the HOT 96 French-American cruise (9° and 13°N, East Pacific Rise, February and March 1996) on the N/O Nadir hosting the submersible Nautille. During this cruise, 10 dives out of 31 were partially or totally devoted to the study of the Genesis site (12°48.63N, 103°56.41W, depth 2639-2647 m).

750 ml titanium syringes (Von Damm, 1983) were used for the sampling of hot vent fluid. A new device (Fig. 1)

based on evacuated bottles was used for the first time to collect water samples in the vicinity of the animals. The 150 ml Whitey Teflon coated bottle is equipped with two valves, the first one (Swagelock, 1/4 turn) to open the bottle with the main arm of the submersible, allowing the sample to enter through a stainless steel tubing (o.d. 1/8", l = 20 cm), the second one (Swagelock, needle valve) to distribute the sample on board. The system is manipulated by the two arms of the submersible. The filling is obtained using the difference between the inner and outer pressure.

Water sampling and temperature measurements were made on several points along an axis (Fig. 2) including the main smoker, the animal communities and the surrounding cold sea water. Table 1 presents the chemical treatment and analytical methods used during the water samples analysis. pH was measured on board using an electrode for sulphidic medium, at 25 °C. Dissolved gases (CO<sub>2</sub> and CH<sub>4</sub>) were analysed using a new method described in Sarradin et al. (1996) and based on an headspace injection, separation by gas chromatography with column selection and detection on a 3 detectors device. Hydrogen sulphide was determined by the methylene blue method (Fonselius, 1983), Mg with an ionic selective electrode after complexation with EDTA. The sampling points performed on the site are summarized in Fig. 2.

Discrete temperature measurements were obtained with a probe held by the Nautille arm. These values were corrected during the cruise using a comparison with a standard reversal thermometer. The long term measurements (30 days) were obtained from 3 HOBO probes (C. Fisher, pers. com.) placed on 3 different clumps of *Riftia pachyptila* (Jones, 1981) (Fig. 2).

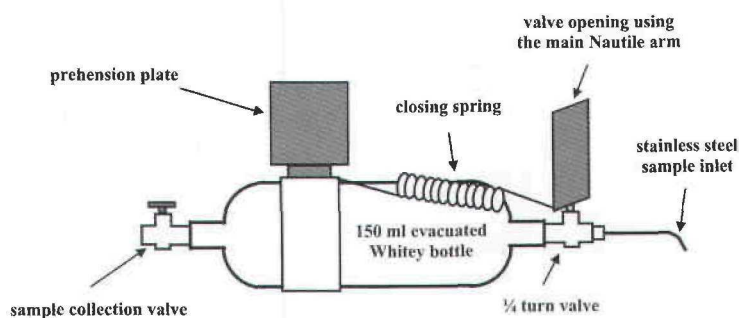
The description of the associated communities (Fig. 2) was obtained from the video records of the Nautille (mobile camera) as previously described (Fustec et al., 1987).

## Results

### I. Ecological setting

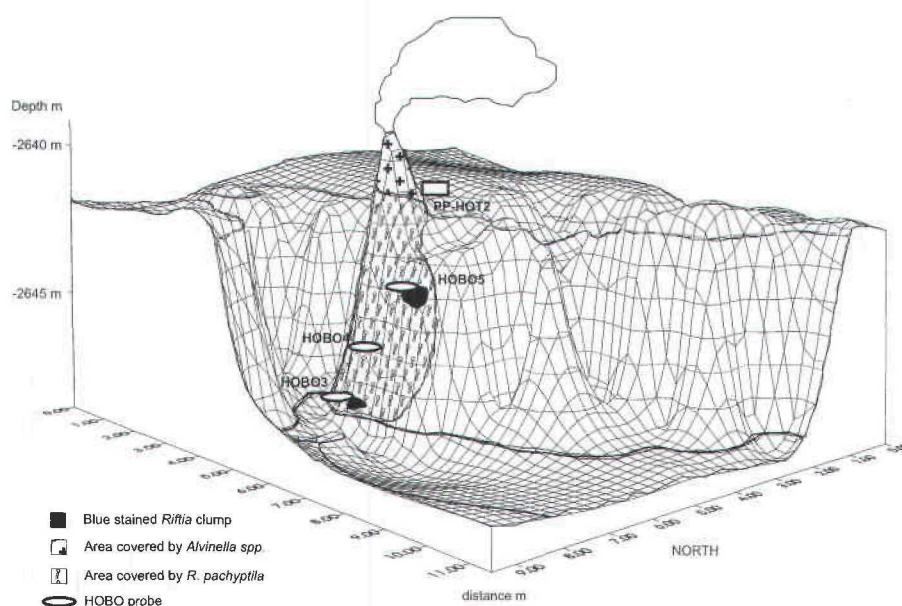
A schematic 3D view of the site is proposed in Fig. 2. The black smoker of the site, identified by the PP HOT2 marker, set down by the submersible during the cruise, was venting a clear hot fluid (262 to 269°C). It is 9 m high and is built on the 5 m high upright wall oriented NW-SW delimiting the western side of the Genesis hydrothermal vent field. The upper part of the chimney (2638 m depth at its highest point) is located above the plateau like a 4 m high needle.

The top 2 m of the chimney (3.5 m<sup>2</sup>) were totally covered with alvinellid worms including *Alvinella pompejana* (Desbruyères & Laubier, 1980), *A. caudata* (Desbruyères & Laubier, 1986) and *Paralvinella grasslei* (Desbruyères &



**Figure 1.** Schematic view of the water sampling device.

**Figure 1.** Schéma du dispositif de prélèvement.



**Figure 2.** 3D map of the Genesis chimney, ecological setting and location of the sampling points.

**Figure 2.** Carte 3D de la cheminée principale de Genesis, description écologique et points de prélèvement.

**Table 1.** Sample treatment and analytical methods.

**Tableau 1.** Traitement des échantillons et méthodes analytiques utilisées.

| Parameter   | Preservation method  | Analytical method                                | s*     |
|---|--|--|--------|
| pH  | analysis on board  | potentiometry<br>electrode for sulphidic medium  | 0.1 pH |
| $\Sigma\text{CO}_2$ , $\text{CH}_4$                                 | analysis on board  | Head space-GC-HWD FID<br>(Sarradin et al., 1996) | 10 %   |
| $\Sigma\text{S}$ ( $\text{H}_2\text{S}+\text{HS}^-+\text{S}^{2-}$ ) | analysis on board  | colorimetry<br>(Fonselius, 1983)                 | 10 %   |
| Mg  | $\text{HNO}_3$ suprapur, 20 $\mu\text{l}$ in 20 ml sample, ambient T | ion selective electrode, EDTA complex            | 3 %    |

s\* relative standard deviation (standard deviation for pH)



Laubier, 1982) (700 ind m<sup>-2</sup>). Crabs belonging to *Bythograea thermydron* (Williams, 1980) and *Cyanograea praedator* (de Saint Laurent, 1984) (20-30 ind m<sup>-2</sup>) were crawling at the surface and the top of the chimney.

The frontier zone between the populations of *R. pachyptila* and *Alvinella* spp. was localized on the needle between 2641 and 2640 m. This brown oxidized zone was colonized by small sized *Tevnia jerichonana* (Jones, 1985) vagile polynoid polychaetes and numerous amphipods. Large populations of limpets (300-600 ind m<sup>-2</sup>) were also observed. The crenellated shells of these gastropods were different from that of the limpets *Lepetodrilus* spp. covering the *R. pachyptila* tubes.

Some small sized *R. pachyptila* were present one metre below the top of the chimney (2639 m) either isolated or gathered in small clumps of 5-6 individuals in cracks. Populations of this species of Vestimentifera were observed from the base of the wall to the half height of the needle (area 26.5 m<sup>2</sup>, 2640 m depth) with densities ranging from 300 to 700 ind m<sup>-2</sup>. The HOB0 probe n°4 was set where the largest density of *R. pachyptila* was found (2644 m). The 2 other HOB0 probes were set at 2646 m (HOB0 3), and 2643 m (HOB0 5). The densities of Zoarcidae fishes *Thermarces cerberus* (Rosenblott & Cohen, 1986) and crabs *Bythograea thermydron* were in this area about 22 and 17 ind m<sup>-2</sup> respectively. Serpulid polychaetes were covering the basaltic scree at the most basal part of the wall (2647 m).

## II. Chemical environment

The main pattern of the chemical environment surrounding the vent communities is summarized in Table 2. A chemical

**Table 2.** pH and chemical concentrations in the water samples from Genesis.

**Tableau 2.** pH et concentrations mesurées dans les échantillons provenant de Genesis.

| dive | sampling point       | pH  | ΣS<br>μmol l <sup>-1</sup> | ΣCO <sub>2</sub><br>μmol l <sup>-1</sup> | Mg<br>mmol l <sup>-1</sup> |
|------|----------------------|-----|----------------------------|--|----------------------------|
| 11   | sea water            | 7.9 | 1                          | 1920                                     | 52.5                       |
| 28   | sea water            | 7.9 | 4                          | 2290                                     | 52.0                       |
| 28   | <i>Riftia</i>        | 6.5 | 5                          | 2300                                     | 50.1                       |
| 10   | <i>Riftia</i> HOB0 3 | 7.2 | 8                          | 3220                                     | 54.0                       |
| 8    | <i>Riftia</i> HOB0 3 | 7.7 | 9                          | 2700                                     | 49.0                       |
| 11   | <i>Riftia</i> HOB0 4 | 5.9 | 17                         | 2030                                     | 51.4                       |
| 8    | <i>Riftia</i> HOB0 4 | 6.6 | 13                         | 3550                                     | 53.3                       |
| 28   | <i>Riftia</i> HOB0 4 | 6.8 | 7                          | 2600                                     | 50.2                       |
| 8    | <i>Alvinella</i>     | 5.7 | 348                        | 5990                                     | 49.7                       |
| 28   | <i>Alvinella</i>     | 6.5 | 5                          | 3450                                     | 51.1                       |
| 28   | smoker               | 4.6 | 2870                       | 28050                                    | 24.7                       |

Sampling points are defined as follows: "sea water", ambient sea water; "*Riftia*", among *R. pachyptila* clumps, close to the plume; "HOB0" sampled among *Riftia* clumps using HOB0 probes as markers; "*Alvinella*" sampled among *Alvinella* spp., the sample inlet at 1 to 3 cm to the tubes, "smoker", in the venting fluid.

gradient can be observed along the chimney, with specific concentration ranges for each population, corresponding to their respective location. Traces of methane were found in some samples with concentrations ranging from 0.1 to 0.5 μmol l<sup>-1</sup>. Traces of hydrogen sulphide were also found in the surrounding sea water. Such samples being collected by the submersible just before its arrival on the active site, these traces may result from the presence of small amount of hydrothermal fluid in the collected area (sampling in the plume). Scatter in the Mg concentrations around the sea water value was observed on the whole set of data with concentrations up to 54.0 mmol l<sup>-1</sup>.

Endmember concentrations were estimated from the whole set of data presented in Table 3 using Mg as conservative tracer of the fluid dilution by the sea water (linear extrapolation of the compound concentration vs. Mg concentration to zero Mg to estimate the pure fluid concentration) (Von Damm, 1983; Campbell et al., 1988). The endmember concentrations presented in the literature for 9° and 13°N are gathered in Table 4 and are in ranges similar to the values estimated during the present cruise.

## III. Temperature, (Fig. 3)

Table 5 gathers the temperature data obtained along the chimney of Genesis, for the discrete values. The large temperature range (1-1.6°C) obtained in sea water reflects the possible influence of the hydrothermal plume a few meters away from the active site. HOB0 probes were used as point marker for the discrete data obtained from the temperature probe from the Nautille arm. Except for one measure, the discrete data reflect the temperature surrounding the upper part of the tube worm *Riftia*. Long term measurements at the base of *Riftia* are summarized in Table 6. HOB0 probes were located along the chimney axis in *Riftia* clumps (Fig. 2). HOB0 4 was set where the largest density of organisms was observed (2644 m, up to 700 ind m<sup>-2</sup>). HOB0 5 was located in the upper part of the chimney (2643 m) whereas HOB0 3 (2646 m) was at the frontier zone with the ambient sea water.

## Discussion

### I. Tracers of dilution

Magnesium is often used as a conservative tracer of the dilution of the hydrothermal fluid by the sea water (Von Damm, 1983; Campbell et al., 1988), i.e. it is not modified by chemical or biological reactions and is only submitted to dilution process. Temperature can also be a conservative tracer which may only be underestimated as conductive heat flow may reduce temperature (Johnson et al., 1988b). Linear fits between these parameters were found on different sites

**Table 3.** pH and chemical concentrations values in the water samples from 9 and 13°N, used to estimate endmember concentrations.

**Tableau 3.** valeurs de pH et des concentrations mesurées dans les échantillons provenant de 9 et 13 °N, utilisées pour estimer la concentration du fluide natif.

| dive n° | pH  | ΣS μmol l <sup>-1</sup> | CO <sub>2</sub> μmol l <sup>-1</sup> | CH <sub>4</sub> μmol l <sup>-1</sup> | Mg mmol l <sup>-1</sup> |
|---------|-----|-------------------------|--------------------------------------|--------------------------------------|-------------------------|
| 8       | 5.7 | 348                     | 5990                                 | 0.1                                  | 49.7                    |
| 8       | 7.7 | 9                       | 2700                                 | <LD                                  | 49.0                    |
| 8       | 6.6 | 13                      | 3550                                 | 0.5                                  | 53.3                    |
| 10      | 7.2 | 8                       | 3220                                 | <LD                                  | 54.0                    |
| 11      | 7.9 | 1                       | 1920                                 | <LD                                  | 52.5                    |
| 11      | 5.9 | 17                      | 2030                                 | <LD                                  | 51.4                    |
| 14      | 7.6 | 12                      | 3460                                 | 0.1                                  | 54.2                    |
| 14      | na  | 4                       | 3080                                 | <LD                                  | 53.6                    |
| 14      | 7.6 | 0.1                     | 3710                                 | <LD                                  | 54.0                    |
| 15      | 5.4 | 544                     | 12030                                | 4                                    | 47.2                    |
| 15      | 5.7 | 118                     | 8410                                 | 4                                    | 49.4                    |
| 15      | 6.2 | 26                      | 4010                                 | <LD                                  | 51.4                    |
| 16      | 6.5 | 175                     | 3980                                 | 5                                    | 51.7                    |
| 16      | 6.6 | 217                     | 3790                                 | 4                                    | 52.2                    |
| 19      | 6.4 | 2                       | 2320                                 | <LD                                  | 52.5                    |
| 19      | 6.4 | 2.5                     | 2750                                 | <LD                                  | 51.1                    |
| 20      | 6.0 | 57                      | 4610                                 | 2                                    | 51.4                    |
| 20      | 6.0 | 26                      | 5400                                 | 2.5                                  | 49.3                    |
| 20      | 7.3 | 3                       | 2450                                 | <LD                                  | 52.8                    |
| 20      | 5.7 | 10                      | 6320                                 | 3                                    | 51.3                    |
| 21      | 7.0 | 35                      | 2550                                 | 1                                    | 54.7                    |
| 21      | 6.7 | 25                      | 2620                                 | 3                                    | 49.8                    |
| 21      | 7.1 | 10                      | 2500                                 | 3                                    | 51.0                    |
| 22      | 6.4 | 1                       | 3610                                 | 2                                    | 51.7                    |
| 22      | 7.5 | 0.5                     | 2710                                 | 1                                    | 50.0                    |
| 23      | 6.5 | 1                       | 2000                                 | <LD                                  | 48.0                    |
| 23      | 6.1 | 3                       | 2910                                 | 0.1                                  | 50.7                    |
| 24      | 7.5 | 4                       | 1770                                 | <LD                                  | 52.4                    |
| 25      | 7.7 | 2                       | 2380                                 | <LD                                  | 53.0                    |
| 25      | 6.3 | 46                      | 3870                                 | <LD                                  | 52.8                    |
| 25      | 7.3 | 2                       | 2400                                 | <LD                                  | 50.5                    |
| 26      | 6.2 | 128                     | 4020                                 | 2                                    | 51.8                    |
| 26      | 6.6 | 15                      | 2990                                 | <LD                                  | 49.7                    |
| 27      | 7.3 | 2                       | 2550                                 | <LD                                  | 52.6                    |
| 28      | 6.8 | 7                       | 2600                                 | <LD                                  | 50.2                    |
| 28      | 4.6 | 2870                    | 28050                                | 12                                   | 24.7                    |
| 28      | 6.5 | 5                       | 2300                                 | <LD                                  | 50.1                    |
| 28      | 7.9 | 4                       | 2290                                 | <LD                                  | 52.0                    |
| 28      | 6.5 | 5                       | 3450                                 | <LD                                  | 51.1                    |
| 29      | 7.2 | 2                       | 2620                                 | <LD                                  | 51.1                    |

na : not analysed

LD : detection limit

from the EPR at 21°N and Galapagos sites (Von Damm et al., 1983).

Considering that both magnesium and temperature are conservative tracers of the fluid dilution and that the data are not collected simultaneously, a theoretical estimation of the concentrations surrounding the organisms was made, using the following relationships (Table 7):

compounds concentrations = f(Mg concentrations) and

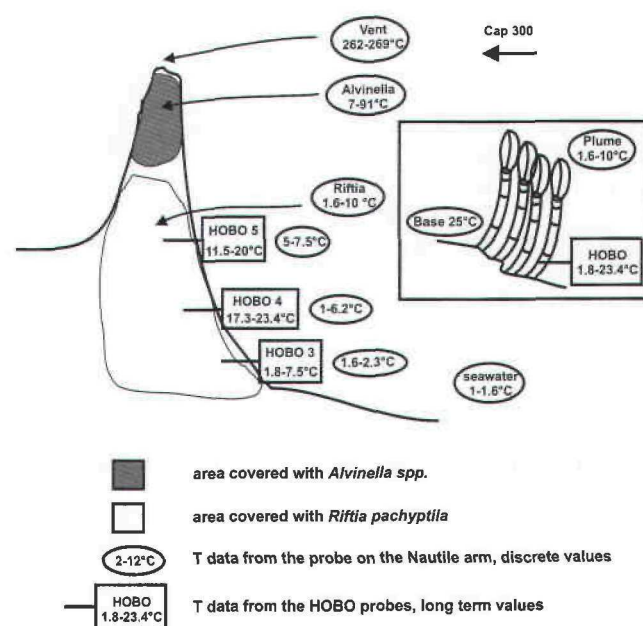
temperature = f(Mg concentrations)

**Table 4.** Estimations of the endmember pH and concentrations values of the hydrothermal fluid from 9° and 13°N, EPR.

**Tableau 4.** pH et concentrations estimés du fluide hydrothermal natif à 9 et 13 °N, EPR.

| References               | site         | pH      | ΣS mmol l <sup>-1</sup> | CH <sub>4</sub> μmol l <sup>-1</sup> | CO <sub>2</sub> mmol l <sup>-1</sup> |
|--------------------------|--------------|---------|-------------------------|--------------------------------------|--------------------------------------|
| <b>this study *</b>      | 13°N         | 3.5-4.0 | 4.5-5.3                 | 20-30                                | 50-55                                |
| (Childress et al., 1993) | 13°N         | 3.51    | 5.9                     | -                                    | 40.1                                 |
| (Michard et al., 1984)   | Genesis 13°N | -       | 6.5                     | -                                    | -                                    |
| (Charlou et al., 1996)   | 13°N         | -       | 2.9-8.2                 | 27-54                                | 11.8-18.4                            |
| (Merlivat et al., 1987)  | 13°N         | 3.5-4   | -                       | -                                    | 14-18                                |
| (Von Damm et al., 1995)  | 9°45 N       | -       | 10-70                   | -                                    | -                                    |
| sea water                |              | 7.8     | 0                       | 0.0003                               | 2.3                                  |

\* estimated from Table 3.



**Figure 3.** Temperature measurements along the Genesis chimney.

**Figure 3.** Mesures de température le long de la cheminée principale de Genesis.

This lead to the final relationship:

compounds concentrations = f(temperature).

Temperature being a suitable parameter to be determined both in space and time, this relationship allowed us, using a limited set of chemical data, to estimate theoretical concentrations around the organisms corresponding to the measured temperatures (Table 8).



**Table 5.** Corrected temperatures from the probe set on the Nautilie arm, discrete values, HOBO probes were used as markers.

**Tableau 5.** Valeurs corrigées de température obtenues par la sonde de température située sur le bras du Nautilie, les sondes HOBO sont utilisées comme marqueur.

| Measurement point |       |        | T °C    |
|-------------------|-------|--------|---------|
| sea water         |       |        | 1-1.6   |
| <i>Riftia</i>     | plume | HOBO 3 | 1.6-2.3 |
| <i>Riftia</i>     | plume | HOBO 4 | 1.6-2   |
| <i>Riftia</i>     | plume | HOBO 5 | 5-7.5   |
| <i>Riftia</i>     | plume |        | 1.6-10  |
| <i>Riftia</i>     | base  |        | 25      |
| <i>Alvinella</i>  |       |        | 7-91    |
| smoker            |       |        | 262-289 |

**Table 6.** Long term temperature data: 30 days, HOBO probes, located inside the *Riftia* clumps, at the base of the tubes.

**Tableau 6.** Mesures de température à long terme, 30 jours, sondes HOBO placées dans les massifs de *Riftia*, à la base des tubes.

| Genesis, 13°N |               | mean °C | min °C | max. °C | mean range °C* | max. range °C** |
|---------------|---------------|---------|--------|---------|----------------|-----------------|
| sea water     |               |         | 1      | 1.6     |                |                 |
| HOBO 3        | <i>Riftia</i> | 3       | 1.8    | 7.5     | 3              | 5.7             |
| HOBO 4        | <i>Riftia</i> | 20.5    | 17.2   | 23.4    | 3.5            | 6.2             |
| HOBO 5        | <i>Riftia</i> | 16      | 11.5   | 20      | 3              | 8.5             |

\* average range on 1 day \*\* (T max. - T min) on 30 days

**Table 7.** Linear fittings obtained from Fig. 3 and used to estimate the concentrations from the temperature data; T is temperature in °C.

**Tableau 7.** Régressions obtenues à partir de la figure 3 et utilisées pour estimer les concentrations à partir des données de température (T en °C).

|   |  |                                 |
|---|--|---------------------------------|
| $\Sigma S \text{ } \mu\text{mol l}^{-1}$    | $[\Sigma S] = -95 [\text{Mg}] + 5000$      | $[\Sigma S] = 17.4T - 27.8$     |
| $\text{CO}_2 \text{ } \mu\text{mol l}^{-1}$ | $[\text{CO}_2] = -910 [\text{Mg}] + 50000$ | $[\text{CO}_2] = 0.166T + 2.03$ |
| $\text{Mg mmol l}^{-1}$                     | $T = -5.48 [\text{Mg}] + 289$              | $[\text{Mg}] = -0.183T + 52.8$  |

Taking into account only the dilution process, the theoretical  $\Sigma S$  concentrations among the organisms might range between 0-100  $\mu\text{mol l}^{-1}$  over the *Riftia* population and up to 1000  $\mu\text{mol l}^{-1}$  over Alvinellidae. An additional vertical chemical gradient is present along the tube of *Riftia*, the fluid around the plume being more dilute than that around the base. In the same way, the  $\text{CO}_2$  concentrations might be in the range of 2200-3500  $\mu\text{mol l}^{-1}$  over the Vestimentifera population and reach up to 17000  $\mu\text{mol l}^{-1}$  over *Alvinella*, with still a similar distal apical gradient along the *Riftia* tube length.

When compared to the calculated data (Table 8), experimental data appeared to be in the same range for  $\text{CO}_2$  and underestimated for  $\Sigma S$ . Methodological factors may be involved in such difference. Analytical bias may be excluded as our estimated endmember concentrations are in the range of previous published ones (Table 4). Chemical modifications following the sampling (Campbell et al., 1988) or spontaneous oxidation (Millero et al., 1987) may reduce the  $\Sigma S$  concentrations. The exact sampling point location is also critical as space microvariations are important for both temperature and chemical species (Johnson et al., 1988a). The temperature gradient can be up to 3°C cm<sup>-1</sup> at 13°N (Chevaldonné et al., 1991) and the sulphide gradient in the order of 10  $\mu\text{mol l}^{-1}$   $\Sigma S$  cm<sup>-1</sup> among the tube worm community (Johnson et al., 1988a). Finally, the filling procedure of our system being very fast (150 ml in a few seconds), surrounding sea water can be forced in the sampler by the depression, resulting in dilution of the samples. This dilution of the sample can only be detected by a comparison of the measured temperature and the Mg concentration at the sampling point.

Biological factors are also important in the surrounding variations (Johnson et al., 1988a; Hessler et al., 1988) as organism consumption, uptake and bioaccumulation are acting in the chemical modification of the surroundings. Johnson et al. (1988 a) estimated, from Scanner measurements, that the values of sulphide removed by the organisms were about 30-80  $\mu\text{mol l}^{-1}$ , while initial environmental concentrations ranged from 100 to 200  $\mu\text{mol l}^{-1}$ .

**Table 8.** Extrapolation of the chemical concentrations around the organisms using temperature as tracer of dilution.

**Tableau 8.** Estimation des concentrations chimiques autour des organismes en utilisant la température comme traceur de dilution.

|                             | Measured T °C | Calculated $\Sigma S \text{ } \mu\text{mol l}^{-1}$ | Measured $\Sigma S \text{ } \mu\text{mol l}^{-1}$ | Calculated $\text{CO}_2 \text{ } \mu\text{mol l}^{-1}$ | Measured $\text{CO}_2 \text{ } \mu\text{mol l}^{-1}$ |
|-----------------------------|---------------|---|---|--|--|
| <i>Alvinella</i> *          | 7-91          | 94-1560   | 5-300   | 3200-17000   | 3500-6000  |
| <i>Riftia</i> plume *       | 1.6-10        | 0-140   | 5-17  | 2300-3700  | 2000-3500  |
| <i>Riftia</i> base HOBO 3** | 1.8-7.5       | 4-100   | -   | 2330-3280  | -  |
| <i>Riftia</i> base HOBO 4** | 17.2-23.4     | 270-380   | -   | 4880-5900  | -  |
| <i>Riftia</i> base HOBO 5** | 11.5-20       | 170-320   | -   | 3940-5350  | -  |

\* discrete values, \*\* long term values

The hydrothermal micro-environment is characterized by spatial and temporal variability, and chemical modification by the organisms. Temperature appears to be a good tracer easy to set at the spatio-temporal scale giving an overview of the ecosystem, but does not take into account the modification of the medium by the organisms. A complete description of the environment must gather both thermal and chemical information. A model relating temperature and chemistry can be a useful tool to give estimates of the environment using measured temperature data.

## II. Habitat specificity (Fig. 4)

A specific environment for each biological community can be highlighted, bearing in mind that chemical data represent a partial aspect of the real environment. The main chemical and physical characteristics surrounding the Alvinellidae

and the Vestimentifera are summarized in Fig. 4. The Genesis environment exhibits overlapping in the observed ranges especially in the lower values representing the periodical supply of oxygenated sea water. However this overlapping is not followed by a continuous distribution of the organisms along the gradient but on the contrary by a marked spatial segregation, the frontier between the two populations consisting of a brown mineralized zone colonized by small *Tevnia jerichonana*. This segregation may reflect the upper values of the chemical ranges obtained as maximal sustainable values for each population (in concentrations and/or duration).

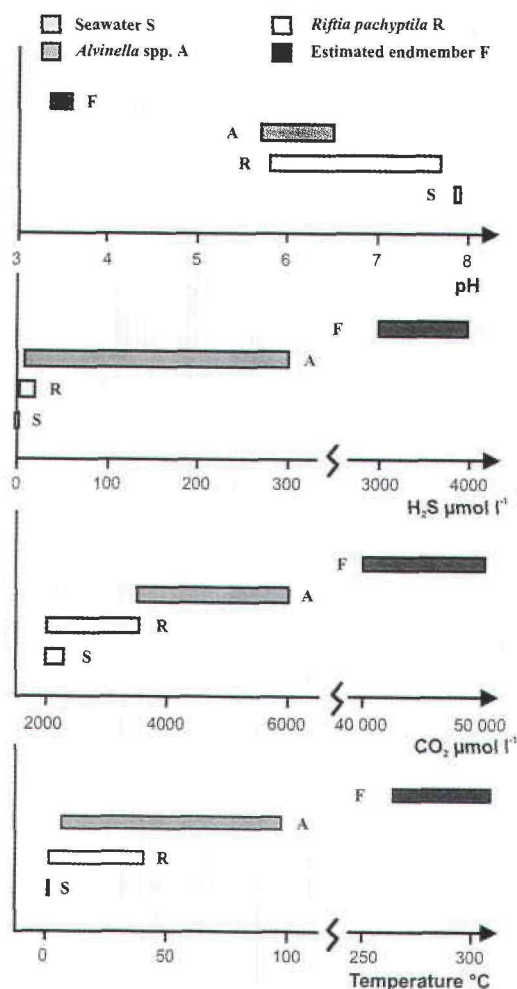
When compared to previous data, it is obvious that our results corroborate the average temperature range of the Vestimentifera from diffuse vents (Johnson et al., 1988a, 1994). Surprisingly a larger thermal range is found for the Alvinellidae habitat (7-91 °C gradient) about 50°C higher than the data previously obtained in the same conditions by Fustec et al. (1987). Chevaldonné et al. (1992) and Desbruyères et al. (1997) recorded an environmental temperature of 20-50 °C at the external part of the populations, and up to 70-80 °C when the probes were pushed inside the Alvinellidae tube masses.

### 1. *Alvinella* environment

The obtained data are a first attempt to describe the chemical environment of Alvinellidae: pH 5.7 to 7.5,  $\Sigma S$  3-300  $\mu\text{mol l}^{-1}$ ,  $\text{CO}_2$  3500-6000  $\mu\text{mol l}^{-1}$  and temperature from 7-90°C. The temperature and chemical ranges are large and comparable to those presented in Desbruyères et al. (1997), using pooled data from 13°N and this suggests a very fluctuating medium with steep gradient imposed by the proximity of the vent and rare input of pure sea water. Even though such results have to be confirmed, they corroborate other data on the high temperature these animals may punctually withstand (Chevaldonné et al., 1992) and the assumptions that they can face occasional blasts of hot water (Tivey et al., 1990; Tunnicliffe et al., 1993; Juniper, 1994). However this environment has to be described at a finer scale, taking into account the interior of the tube as *A. pompejana* seems to spend most of its time in its tube (Desbruyères et al., 1997). This behaviour can be explained by several reasons including protection from the external environment, satisfying the physiological requirements of the epibiotic bacterial associations or foraging on bacterial mats within the tube (Chevaldonné et al., 1993). However questions are arising from these results on the tube permeability to chemicals and on its efficiency as thermal buffer.

### 2. *Riftia* environment

*Riftia* plume environment can be characterized as follows: pH 5.8-7.7,  $\Sigma S$  4-12  $\mu\text{mol l}^{-1}$ ,  $\text{CO}_2$  2000-3500  $\mu\text{mol l}^{-1}$  and



**Figure 4.** Chemical concentrations and temperatures measured in the vicinity of the organisms from Genesis.

**Figure 4.** Gammes de concentrations et de températures obtenues autour des organismes de Genesis.



temperature 1.6–10°C. *Riftia* clumps are subjected periodically to non hydrothermal sea water (1.6°C) and the temperature variation on a same point is near 3°C day<sup>-1</sup>. Maximum temperature ranging from 2.9 to 14°C with corresponding sulphide concentrations from 7.1 to 330 µmol l<sup>-1</sup> and a corresponding chemical gradient of 2–10 µmol l<sup>-1</sup> ΣS cm<sup>-1</sup> were obtained over the Vestimentifera from Rose Garden at the Galapagos (Johnson et al., 1988a). The coexistence of O<sub>2</sub> and ΣS in the temperature range 2–8 °C was also noticed by these authors. At the Genesis vent site, Childress et al. (1993) observed that the fluid analysed among the *Riftia* tubes represents between 93.5 to 95% dilution of the pure hydrothermal fluid by sea water, with a temperature among *Riftia* of 19 ± 0.1 °C, and chemical parameters: pH = 6.22 ± 0.1, ΣS = 86 ± 20 µmol l<sup>-1</sup>, CO<sub>2</sub> = 4700 ± 500 µmol l<sup>-1</sup>. Our data are in the same range as those obtained previously keeping in mind the already discussed bias and the variety of sampling devices used (Ti syringe, scanner or evacuated bottle). Higher ΣS and CO<sub>2</sub> concentrations were obtained in the literature, with smaller variation range for pH. However, endmember estimations were similar for pH and CO<sub>2</sub>, being quite smaller for ΣS.

*Riftia* fields are also characterized by thermal and chemical gradients within the clumps along the chimney. Different organisms from a same area may experience a 10–20°C variation (Table 5 & 6, Fig. 3) leading to high differences in the sulphide or CO<sub>2</sub> concentrations they face. The maximum temperatures were noticed where the density of organisms was highest.

A thermal gradient was also observed along the Vestimentifera tubes. This gradient can be estimated to 0.5–1°C cm<sup>-1</sup> for an animal inhabiting a tube of 20 cm in length, which represents less than one third the gradient estimated for the alvinellid surroundings (Chevaldonné et al., 1991). A difference of about 10°C seems to be the average thermal apico basal gradient the *Riftia* are facing as indicated by the literature (Childress et al., 1984; Johnson et al., 1988a, b). Such gradients seem therefore important for the worm physiology considering especially that the metabolite uptake occurs at the plume level (Childress et al., 1984, 1993) and that the optimal temperature required for the metabolism of carbon fixation of the symbionts ranged from 10 to 30°C (Belkin et al., 1986; Scott et al., 1994).

As a conclusion, an extensive description of the hydrothermal ecosystem needs both thermal and chemical data strengthened by their spatial and temporal scales. This ecosystem is characterized by the presence of steep chemical and thermal gradients with populations distributed discontinuously along the gradient. *Alvinella* spp. is present in the hotter part of the gradient and is probably subjected to the higher range of variations of this environment. *Riftia pachyptila* populations are also subjected to large

environmental variations among the populations and along the tube for each individual.

These data underline the physiological importance of the interactions between the organisms and their surroundings and more accurate analyses are needed to clarify the microgradients experienced by the vent organisms. Further studies are underway to obtain more accurate data and to conceive new devices adapted to the codetermination of physical and chemical analysis of these organisms' microhabitats.

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