



Community structure and temperature dynamics within a mussel assemblage on the Southern East Pacific Rise

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Abstract: The composition, biomass and diversity of the fauna in a *Bathymodiolus thermophilus* mussel assemblage colonizing diffuse flow areas on the SEPR is described and compared with biological characteristics of other hydrothermal assemblages. The spatio-temporal dynamics of temperatures over fine scales within the mussel habitat are characterized using newly-developed statistical approaches. Temperature data obtained from two adjacent habitats (a cirriped assemblage and a bare substratum) are compared. The results of the temperature data show that the mean temperature and the temperature variations were significantly higher in the mussel assemblage (mean temperature: $4.12 \pm 1.85^\circ\text{C}$) in comparison with $2.40 \pm 0.14^\circ\text{C}$ in the cirriped assemblage and $2.20 \pm 0.23^\circ\text{C}$ on the bare substratum. Discrete temperature measurements showed that temperature data varied both at a broad and fine scales in the mussel assemblage. Finally, analysis of the temperature periodic variability in the mussel assemblage during a 4-day period showed significant periodic modulations near $T = 24\text{h}$. Although not significant, a second trend is also observed around $T = 12\text{h}$. This work represents a step forward to the understanding of species distribution patterns at vents.

Keywords: Hydrothermal vents • Mussel assemblage • *Bathymodiolus thermophilus* • Diversity • Biomass • Temperature dynamics • East Pacific Rise

Introduction

The Southern East Pacific Rise (SEPR) is among the fastest spreading ridge in the world and is characterized by a marked instability in hydrothermal venting likely associated with recent volcanic activity (Embley, 1998). The local hydrothermal systems are more closely spaced than those of slow spreading ridges, insuring habitat continuity that

should favour fauna dispersal (Van Dover, 2002). The first explorations of the 17-19°S region (Desbruyères et al., 1982) indicated the coexistence of faunal assemblages similar to those present in the ecological succession stages identified on the East Pacific Rise (EPR, Desbruyères, 1998; Shank et al., 1998) but to date, very few ecological studies have focused on the structure and functioning of SEPR communities (Van Dover, 2002).

The main goal of this study was to compare the biological and environmental characteristics of different faunal assemblages found on the SEPR with other hydrothermal assemblages, including those found on the EPR. Here, we focus on the composition, biomass and diversity of the fauna as well as on the dynamics of temperatures over fine spatial and temporal scales in a *Bathymodiolus thermophilus* Kenk & Wilson, 1985 assemblage. Comparison with temperature data obtained from two adjacent habitats was done. According to our hypothesis, the mussel assemblage should colonize areas of higher temperatures. Newly-developed statistical approaches were used to extract the spatial and temporal variability of temperature data within these diffuse flow habitats. This work represents a step forward to the understanding of species distribution patterns at vents.

Materials and Methods

The BIOSPEEDO cruise was held in April/May 2004 on the SEPR. The Oasis study site (17°25'N; 113°18'S) was located at 2600 metre depth. At this site, a mosaic of three distinct assemblages was observed on large diffuse flow areas. The first assemblage, referred here as to the mussel assemblage, was visibly dominated by *Bathymodiolus thermophilus*. This assemblage was surrounded by a second assemblage dominated by stalked *Neolepas/Leucolepas* cirripeds. A third assemblage was formed by large vesicomylid clams distributed along fissures. Patches of bare substratum were also observed. Because of time limitations, only the mussel assemblage was studied in details and therefore, only the data pertaining to this assemblage is described. Video imagery, temperature data and faunal samples were collected during two dives with the manned submersible Nautille deployed from the R/V L'Atalante.

Discrete temperature measurements

To evaluate variation in temperature data within the mussel assemblage, a small-scale (ca. 0.25 m²) temperature coverage was done (n = 48) with the Nautille temperature probe (Fig. 1). Spatial variability of the temperature within this assemblage was assessed using a polynomial regression (i.e. trend-surface analysis), in which the standardized coordinates of the sampling units (X and Y) were used to generate polynomial functions (Borcard et al., 1992). For instance, the polynomial function using the X coordinates allowed one to model a linear trend, whereas the a second-order term such as X², is used to fit a spatial structure in the form of a parabola (Borcard & Legendre, 2002). To identify the polynomial functions that best described the spatial variability of the temperature

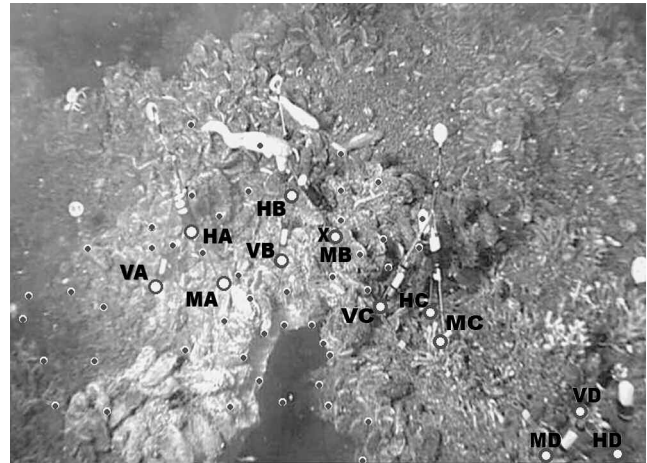


Figure 1. Small-scale temperature mapping within the *Bathymodiolus thermophilus* faunal assemblage at the Oasis diffuse flow site, SEPR. The small dots represent 48 discrete temperature measurements in the *Bathymodiolus* mussel habitat whereas the larger dots indicate different sampling units in which temperature measurements were recorded during four days. Four tripods (A, B, C, D), carrying three autonomous temperature probes each (Micrel (M), Vemco (V) or Hobo (H)), were deployed.

Figure 1. Cartographie à petite échelle de la température dans l'assemblage de *Bathymodiolus thermophilus* sur le site Oasis, un site d'émissions diffuses, SEPR. Les petits points représentent 48 mesures discrètes de température alors que les plus gros indiquent les unités d'échantillonnage où la température a été enregistrée en continu pendant quatre jours. Quatre tripodes (A, B, C, D) supportant trois capteurs autonomes de température chacun (Micrel (M), Vemco (V) ou Hobo (H)) ont été déployés.

measurements, a stepwise procedure (SPSS, 1999) was carried out using temperature as the dependent variable and the polynomial functions as independent variables. The threshold probabilities for the partial *F* statistics used in the selection were $p = 0.05$ to include and $p = 0.10$ to remove a variable.

Temperature spatio-temporal dynamics

The assessment of short-term variations of temperature within the mussel assemblage as well as within two adjacent habitats was done using the records from a series of four tripods (A, B, C, D), each of them recording on a three day period (Fig. 1). Each tripod had three autonomous temperature probes (Micrel (M), Hobo (H) and Vemco (V)), providing a total of 12 probes (4 tripods x 3 probes). Eight of the 12 probes were placed within the mussel assemblage (MA, MB, MD, VA, VB, VC, HA, HB), two of them were installed in a cirriped assemblage (MC, VD) and the last two probes (HC, HD) were deployed on a bare substratum. The temperatures were averaged over thirty

minutes (average of 120, 180 and 9 measurements for M, V and H probes respectively), giving a total of 146 temperature estimates for each probe. An analysis of variance with random factors was performed to test if there was a significant statistical difference of temperature between the three habitats. Analysis of the periodic variability of the temperature estimates was conducted using periodograms (Legendre & Legendre, 1998) created with R package (Legendre & Vaudor, 1991). Periodograms can be described as graphs in which measures of amplitude (entropy) are plotted as a function of the time (i.e. periods). The contingency periodogram developed by Legendre et al. (1981) are particularly suited for the analysis of short time series. Identification of the significant periods in the contingency periodogram was tested using the Wilk's χ^2 statistic (Legendre & Legendre, 1998). Since multiple tests were performed, a Bonferroni correction ($\alpha' = \alpha / \text{number of simultaneous tests}$) was used.

Faunal sampling

A discrete, semi-quantitative faunal sample was taken in the mussel assemblage, using the submersible claw and the suction sampler to clear the surface area. The size of the surface sampled (0.035 m²) was estimated using captured video frames of the sampled area (Sarrazin & Juniper, 1999). The faunal sample was passed through a 63 μm sieve and retained material was preserved in buffered 10% formalin for 48 hours and stored in 70% ethanol. Species composition in the mussel assemblage was characterized for all faunal components, including the meiofauna. Large mobile predators (fish, crab) were not included in this study. The density and biomass (wet and dry weights and ash free dry weights) of the mussels were also determined. Different diversity indices (species richness, Fisher's α , Shannon H') were calculated for the mussel assemblage using Primer© software (Clarke & Gorley, 2001).

Results

Discrete temperature measurements

The discrete temperature measurements within the mussel assemblage ranged from 2°C to 8.7°C with an average of $3.8 \pm 1.7^\circ\text{C}$ (\pm standard deviation). Two polynomial functions (X and Y^3), explaining 33% of the temperature total variability, were identified using the polynomial regression analysis (third order). The two functions were grouped into a spatial model describing the structure of the temperature estimates (Fig. 2). According to the model, the temperature estimates were on average 1.9°C greater near the vent source (Fig. 2).

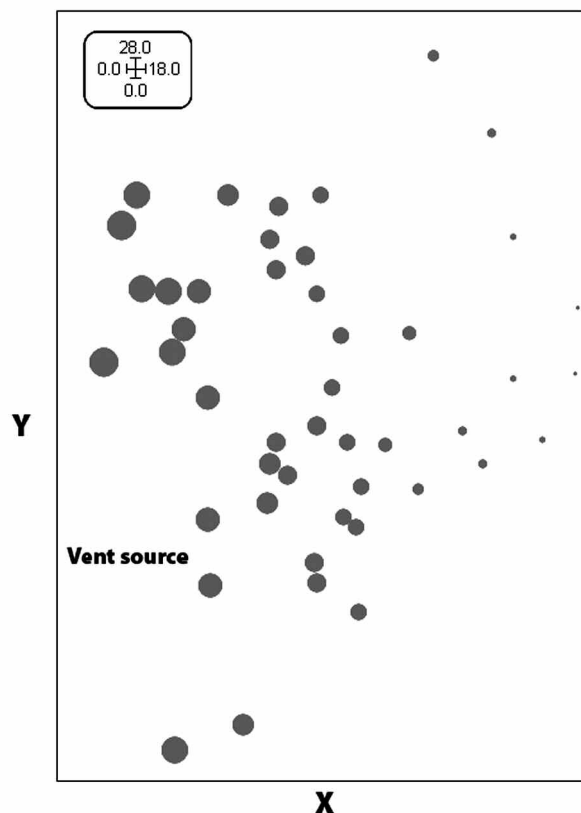


Figure 2. Map of the study site showing the forecasted values of the temperature estimates based on the polynomial regression analysis. The size of the bubbles is proportional to the forecasted values.

Figure 2. Carte du site d'étude montrant la distribution des valeurs prédites de température estimées à partir d'une régression polynomiale. La taille des bulles est proportionnelle aux valeurs prévues.

Temperature spatio-temporal dynamics

Spatial heterogeneity of temperature data is observed. Results from the analysis of variance showed a significant difference between the three groups (ANOVA $F_{2,1749} = 283.88$, $p < 0.001$). The first group (mussel assemblage) displayed a higher mean temperature ($4.12 \pm 1.85^\circ\text{C}$) than the cirriped assemblage ($2.40 \pm 0.14^\circ\text{C}$) and the bare substratum ($2.20 \pm 0.23^\circ\text{C}$). However, no difference was observed between the last two groups. Analysis of the temperature periodic variability in the mussel assemblage displayed similar periodicities across the eight probes (Fig. 3). Significant periods varying between $T = 20.5$ hours and $T = 31.5$ hours were identified in all the contingency periodograms, with the exception of the VB probe for which no significant period was found. Six of the eight periodograms displayed a significant peak of amplitude at $T \approx 24$ hours (MA, VA, HA, MB, VC, and MD) and five of them

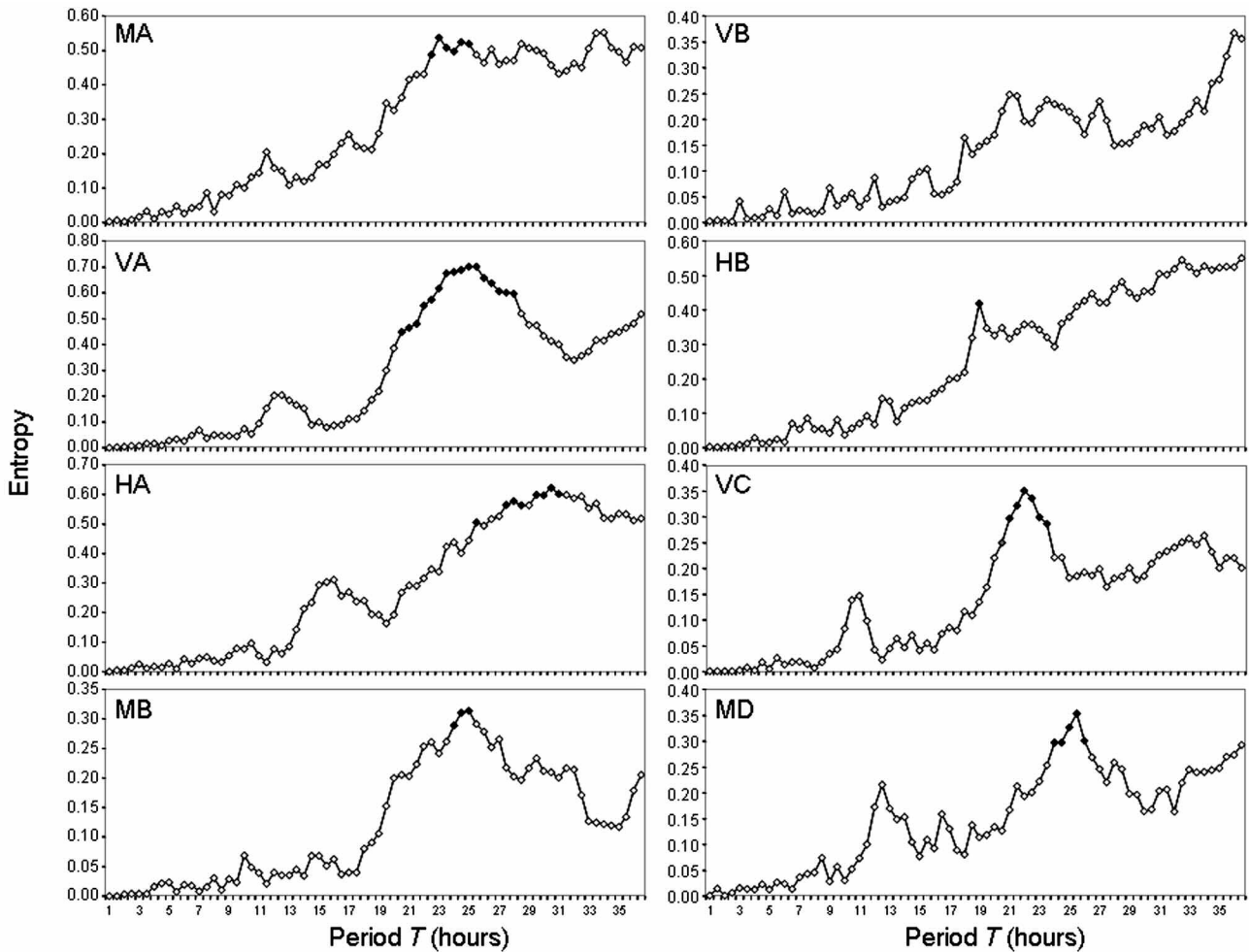


Figure 3. Periodic variability of the temperature data estimated from the eight temperature probes deployed in the mussel assemblage (see text for code details). Measures of the entropy are explained in the text. Filled symbols indicate significant temperature periods.

Figure 3. Variabilité périodique de la température estimée à partir de huit capteurs de température déployés dans l'assemblage de moules (se référer au texte pour les abréviations). Les mesures d'entropie sont expliquées dans le texte. Les symboles "pleins" indiquent les périodes de variations de température significatives.

displayed a second peak, although not significant, at $T \approx 12$ hours (MA, VA, HA, VC, and MD).

Mussel assemblage characteristics

Minimum of 38 species were identified in the assemblage. The associated fauna was dominated, in terms of abundance, by nematodes representing 32.7% of the associated epifauna, followed by amphipods (22.3%), two species of gastropods (15.1%, *Rhynchopelta concentrica* McLean, 1989 and *Lepetodrilus elevatus* McLean, 1988) and two species of polychaetes (13%, *Amphisamytha galapagensis* Zottoli, 1983 and *Ophryotrocha akessoni* Blake, 1985). The nematodes were the most diverse metazoan taxon with at

least 8 families and 12 genera identified. One nematode genus of the Monhysteridae family was dominant, representing 50 to 86% of the nematodes. Overall 9 taxa formed more than 96% of the abundance of this epifaunal assemblage. The faunal density reached 35886 individuals.m⁻² for mega- and macrofauna for a total density of 54229 individuals.m⁻², when the meiofauna is included (Table 1). The biomass of the mussels (without shells) in the assemblage is 43.4 kg.m⁻² (wet weight) and 6.6 kg.m⁻² (dry weight; Table 1). Despite a high biomass, the percentage of abundance of the mussels within the assemblage remains low (8%). The different diversity indices measured in comparisons with those of other chemosynthetic habitats are presented in Table 2.

Table 1. Comparisons of faunal density and biomass in different chemosynthetic assemblages from both deep-sea vent and cold seep habitats. All the macrofaunal species were included in the Endeavour biomass estimates whereas at the other sites, only the habitat builders were considered.

Tableau 1. Comparaison de la densité et de la biomasse de la faune de différents assemblages chimiosynthétiques (sources hydrothermales et suintements froids). Toutes les espèces de macrofaune ont été prises en compte dans l'estimation de la biomasse du site Endeavour alors que seules les espèces édificatrices ont été prises en compte pour les autres sites.

Site	Total density (ind.m ⁻²) without shell/tubes	Wet weight (kg.m ⁻²) without shell/tubes	Dry weight (kg.m ⁻²)	Type of assemblage	References
VENTS					
Oasis vent, SEPR	54 914	43.4	6.6	Mussel	This study
Endeavour segment, NEPR	941-250 000	0.052-16.62	0.011-4.68	Six faunal assemblages	Sarrazin & Juniper, 1999
Galapagos		10.1		Mussel	Hessler & Smithey, 1983
Edison Seamount	64	5.9-14.9		Bivalve	Stecher et al., 2003
SEEPS					
Peruvian margin	256-1670	30-50		Bivalve	Olu et al., 1996

Discussion

Bathymodiolus assemblages were located near visible diffuse flow emissions on broken pillow lavas. The sampled assemblage contained at least 38 species, including meiofauna. The biomass was dominated by *Bathymodiolus thermophilus* mussels that only accounted for 8% of the total species abundance. The dominance of a limited number of taxa is a pattern that is also seen in other vent mussel assemblages. Therefore, 8 taxa dominated almost 98% of the abundance on the NEPR (Van Dover, 2003) while on the SEPR, 11 taxa dominated about 94% of the assemblage (Van Dover, 2002). Four of these dominant taxa (*Amphisamytha galapagensis*, *Lepetodrilus elevatus*, amphipods and copepods) also dominated the other mussel assemblages (Van Dover, 2002 & 2003). A total of nine species of gastropods shared the mussel bed habitat. A better definition of their trophic regimes and spatial microdistribution would give insights into how they share the available resources in a such limited space.

At our taxonomic resolution, meiofaunal diversity was three times lower than what is usually observed in deep-sea environments (Vanreusel et al., 1997). The meiofauna was largely dominated by nematodes (~ 92 %) with the dominance of a single genus (probably *Thalasso-* or *Geomonhystra*) belonging to the family Monhystridae. *Thalassomonhystra* is a common deep-sea genus and is also found in high abundance in other vent and seep habitats (Vanreusel et al., 1997; Bright et al., 2005; Limen et al., 2005). Recently one dominant *Geomonhystra* sp.

was found thriving in seep environments (Van Gaever et al., 2006). The nematode densities (16.8 ind.10 cm⁻²) were lower than those reported from other deep-sea sediments at similar water depth (200 ind.10 cm⁻² in east Atlantic; Vanaverbeke et al., 1997) but within the range reported by Bright et al. (2005) in EPR vent communities (< 1 to 61 ind.10 cm⁻²). The meiofaunal results are concordant with other studies from deep-sea chemosynthetic habitats that document a relatively low diversity at higher taxonomic levels with a high dominance of nematodes and the presence of one dominant group. The role of the meiofauna in vent communities need to be examined as it may represent a crucial link between bacteria and higher trophic levels (Limen et al., 2005).

Our density data are much higher than what it is observed in other mussel beds from vents and seeps but lower than that obtained in *Ridgeia piscesae* Jones, 1985 assemblage from northern EPR (Table 1). In terms of biomass, our wet weight data are comparable to those obtained in seep mussel beds from the Peruvian margin but much higher than biomass from Edison seamount mussel bed or even from Endeavour *Ridgeia* communities (Table 1). In terms of diversity indices, it is interesting to note that among the vent sites, the SEPR harbours the highest diversity, followed by NEPR and MAR vents. This could relate to differences in fluid compositions between the different ridges, the age of the vent sites, to productivity levels or habitat stability (Van Dover, 2002). Closely-spaced hydrothermal systems may not only favour species survival but also species diversity. Nevertheless, our diversity data

Table 2. Comparisons of different diversity indices within mussel assemblages from both hydrothermal and intertidal habitats. Table modified from Van Dover (2002).

Tableau 2. Comparaison de différents indices de diversité entre des assemblages de moules provenant de divers sites hydrothermaux et aussi d'un habitat intertidal. Tableau modifié de Van Dover (2002).

Sites	S	Fisher's α	Shannon H'	References
Southern East Pacific Rise	57		2.25	Van Dover, 2003
Oasis	38	5.26	2.22	This study
Oasis	52	7.33	2.13	Van Dover, 2003
Animal Farm		7.21	2.47	Van Dover, 2002
Rehu Marka	48	6.94	2.42	Van Dover, 2002
Northern East Pacific Rise	61		1.61	Van Dover, 2003
Train Station	34	No data	1.50	Van Dover, 2003
East Walla	44		1.67	Van Dover, 2003
Biovent	46		1.66	Van Dover, 2003
Mid-Atlantic Ridge Lucky Strike	28	2.57	1.47	Van Dover, 2002
Intertidal Alaska	64	8.53	2.13	Van Dover, 2002

fall within the lowest observed on SEPR (Table 2). Whether this is due to a temporal change, to differences in sampling tools or in species identification or to a sampling bias is not known. We suspect that our sampling method was not ideal to collect small associated fauna. Sampling methods and tools used for quantitative collection at vents and seeps should be standardized to allow systematic ecosystem comparisons.

A temperature gradient, decreasing with increasing distance from the point source, is seen in the mussel assemblage (Fig. 2). The highest temperature (8.7°C) was measured on source margins located under the broken pillow lava. Temperature data varied both at a broad scale (linear gradient: X) and at a finer scale (three bump-shaped curve: Y³). Whether this Y³ variation is linked to a small temporal lag between each measurement or to local hydrodynamic processes is not known. Micro-scale analyses of currents, fluid flow velocity and temperature through time would allow the precise monitoring of small-scale hydrothermal plume as well as to assess the conditions experienced by the organisms. The next step is to link these spatial patterns of temperature with other measured environmental factors using multiscale statistical analyses (PCNM, Borcard & Legendre, 2002).

The analysis of temporal variability in temperature data showed significant periodic modulations near T = 24h. Although not significant, a second trend is also observed around T = 12h. Our results are partly in agreement with those obtained by Tivey et al. (2002) on the Juan de Fuca ridge. These authors found a significant 12.4 h periodicity in 82% of their time-series and a 24 h periodicity in half of the records that displayed the 12.4 h peak. Tivey et al. (2002) correlated their 12.4 h period to the semi-diurnal

tidal periodicity and showed that temperature variations were modulated by changes in horizontal currents. Whether our observations are linked to tidal variations or to factors that may be influenced by the tidal signal has to be evaluated.

The mussel habitat is significantly different from the two other habitats studied. Standard deviations of temperatures were higher in areas exhibiting higher mean temperatures (mussel assemblage) supporting the hypothesis that animals living in higher temperature habitats experience higher fluctuations of their environmental conditions (Sarrazin et al., 1999 & 2002) and can be periodically exposed to high chemical concentrations. Since temperature is a useful semi-conservative tracer of the hydrothermal fluid by seawater (Johnson et al., 1988), it can be a good indicator of fluid inputs. A linear model of dilution between the hydrothermal fluid (340°C) and the seawater (1.8°C) allowed us to estimate that the fluid input in the mussel habitat varied from 0.06 to 2%. Therefore, the mussel assemblage studied thrived in an environment bathed by a low percentage of hydrothermal fluids (~approximately 0.7% hydrothermal fluids at 4°C). According to the high biomass and densities observed, the corresponding chemical conditions appear to be sufficient to sustain symbiotic processes. The absence of cirripeds, which are extremely dense in the studied area (> 1620 ind.m⁻²), in the mussel habitat is however intriguing. Whether they are out-competed by the mussels, unable to thrive in harsher conditions or affected by other biotic or abiotic factors is unknown. In the vent habitat, even small temperature changes can reflect significant chemical variations. For example, a rough comparison with the chemical conditions encountered at 13°N (EPR) showed

that at 4°C, the sulfide concentrations were approximately 10 µM whereas at 2°C, the concentrations dropped to 1-3 µM (Le Bris et al., 2003). On the other hand, the cirriped habitat, characterized by lower environmental conditions, may be unable to sustain symbiotic processes. The cirripeds would colonize these unexploited vent habitats where concentrations of organic matter, emitted from the neighbour mussel assemblage and present within the fluids through microbial production, are elevated. A quantitative description of organic matter composition and origin should help assessing the transfer of energy between adjacent faunal assemblages. Finally, the absence of cirripeds on the bare substratum is also surprising since no significant temperature difference is seen between the two habitats. Long-term temperature monitoring of these assemblages, in relation with the environmental factors characterizing their habitats, will help defining the dynamics of these assemblages and supporting (or not) a succession hypothesis.

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