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Benthic foraminiferal species tolerance for hydrothermal activity: a case of study from the Lucky Strike vent field.

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Abstract

Hydrothermal vent fields represent dynamic environments hosting rich ecosystems. At the Mid-Atlantic Ridge, the Lucky Strike (LS) vent field has been the focus of multiple biological studies. While ecological studies have been focusing on microbial and macrofaunal communities, some groups still remained out of the scope. We present here the first ecological study of benthic foraminifera inhabiting soft sediments in the peripheries of hydrothermal edifices at LS. A total of fifteen blade cores were analyzed. We combine microhabitat environmental descriptors with faunal density and diversity of benthic foraminifera (living & fossil) to investigate the impact of hydrothermal activity on their ecology. The far periphery, ~150 m away from vents, harbors a community of diverse foraminifera feeding on pre-degraded organic matter characterized by a phytoplankton detrital signal. Communities located at intermediate distance (~ 50 m) from venting showed the presence of opportunistic species likely feeding on chemosynthetic microorganisms. Finally, environments closer to active sites (few

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meters) showed very low abundance of living individuals, as the presence of harsh environmental conditions may limit foraminiferal growth. Unexpectedly, the presence of widespread iron-oxidizer bacterial biofilms was associated to the dissolution of all biogenic carbonate content raising questions on their impact on regional carbon budget.

Key words: Benthic foraminifera, hydrothermal activity, Lucky Strike vent filed, microbial biofilm.

1. Introduction

Benthic foraminifera are marine micro-organisms that represent more than 50% of the eukaryotic biomass in many deep-sea habitats and influence the structure and dynamics of marine biological communities, with benthic organisms as predators and microorganisms as preys (Gooday et al., 1994). These organisms have been widely studied as fossils in marine systems for more than a century and as living individuals for ecological purpose over the last decades. However, very few studies have been conducted on benthic foraminifera from deep-sea hydrothermal vents (Molina-Cruz and Ayala-Lopez, 1988; Jonasson et al., 1995; Burkett et al., 2018; Krüger et al., 2025) because of complex sampling techniques (hard substrates) and the usual focus on microbes and macrofauna in these environments.

Benthic foraminiferal distribution in the marine sediment is mainly controlled by the spatially opposed contents of organic matter and oxygen (Jorissen et al., 1995), but also by organic matter quality and source (e.g., Dessandier et al., 2016). In deep-sea environments, the food source for benthic foraminifera is often limited to degraded detrital material and microbial organic matter (Gooday et al., 1992). In extreme environments, where fluids enhance microbial activities, benthic foraminifera can thrive feeding on certain groups of bacteria, where the conditions allow them to survive (Dessandier et al., 2019).

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Extreme environments thus offer a nutrient-rich microbial food source for benthic foraminifera, yet they also represent a potentially harsh environment due to their challenging physical and chemical conditions. Hydrothermal vents are dynamic systems where cold seawater penetrate through cracks in the ocean crust and is heated and enriched in dissolved metals and sulfur in contact with rocks overlying the magma chamber. This process results in the emergence of hot, slightly acidic and chemically reduced fluids. Most of the metals dissolved in the ascending vent fluids precipitate when they mix with the surrounding cold seawater, resulting in black- and white smoker chimneys, large sulfide edifices and later, extensive mounds of accumulated massive sulfide. Hydrothermal vent fields are commonly referred as to "oases of life", harboring luxuriant endemic chemosynthetic faunal communities (Fisher et al., 2007). Associated food webs are mainly based on local microbial chemosynthesis (Childress and Fisher, 1992), performed by free-living and symbiotic chemoautotrophic microorganisms that utilize the chemical energy released by the oxidation of reduced chemicals species (H_2, H_2S, CH_4, Fe) present in the hydrothermal fluids (Childress and Fisher, 1992, Schmidt et al. 2008). In Juan de Fuca Ridge (North Pacific Ocean), the distribution of foraminifera was shown to be influenced by temperature, pH and substratum types, resulting in their absence at temperature higher than 20°C and on unstable surfaces such as friable anhydrite which prevents the attachment of agglutinated species (Jonasson et al., 1995). Among hydrothermal vent systems, the Lucky Strike vent field has been one of the most studied ecosystems since its discovery in 1992 and with more than 15 years of continuous multidisciplinary observations through the EMSO-Azores observatory deployed in 2010 (Matabos et al., 2025). Over these studies, it has been pointed out that regional distributions of macro- and meiofauna depend on abiotic parameters such as pH, temperature, sulfides and metals (e.g., Sarrazin et al., 2015, see Matabos et al., 2025 for a review). However, no studies yet filled the gaps about the role of the foraminiferal compartment in this system. Given its numerous active vent sites and well

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documented biotic and abiotic conditions, the Lucky Strike vent field provides an ideal setting for investigating benthic foraminiferal ecology in hydrothermal ecosystems and their role in influencing regional biodiversity. This study presents the first analysis of benthic foraminifera from the Lucky Strike vent field, integrating living and fossil foraminiferal individuals and environmental conditions across gradients of hydrothermal influence and associated microbial biofilms.

2. Study area

The Lucky Strike hydrothermal vent field on the Mid-Atlantic Ridge (MAR) at 37°17'N is one of the largest fields. It is located at ~1,700 m water depth and its ~25 active edifices are surrounding a 200 m diameter lava lake (Ondréas et al., 2009). Biological and geological evidence indicate a long venting history at Lucky Strike, with recent lava footprint analyses suggesting that modern volcanic activity has driven the resurgence of hydrothermal venting (Langmuir et al., 1997). Several active and inactive edifices have been identified since the first exploration of the field in 1993 (Fouquet et al., 1995). In addition to the sulfide structures, the seafloor is characterized by sulfide deposits and covered by hydrothermal slab corresponding to breccia of basaltic glass and plagioclase crystals indurated by silica and barite (Langmuir et al., 1997). The sediments surrounding the structures contain high concentration of metals such as Fe, Cu and Zn, particularly enriched at the Capelinhos vent site where the fault configuration enables hot fluid outflow (>300°C) (Fig. 1, Cotte et al., 2020).

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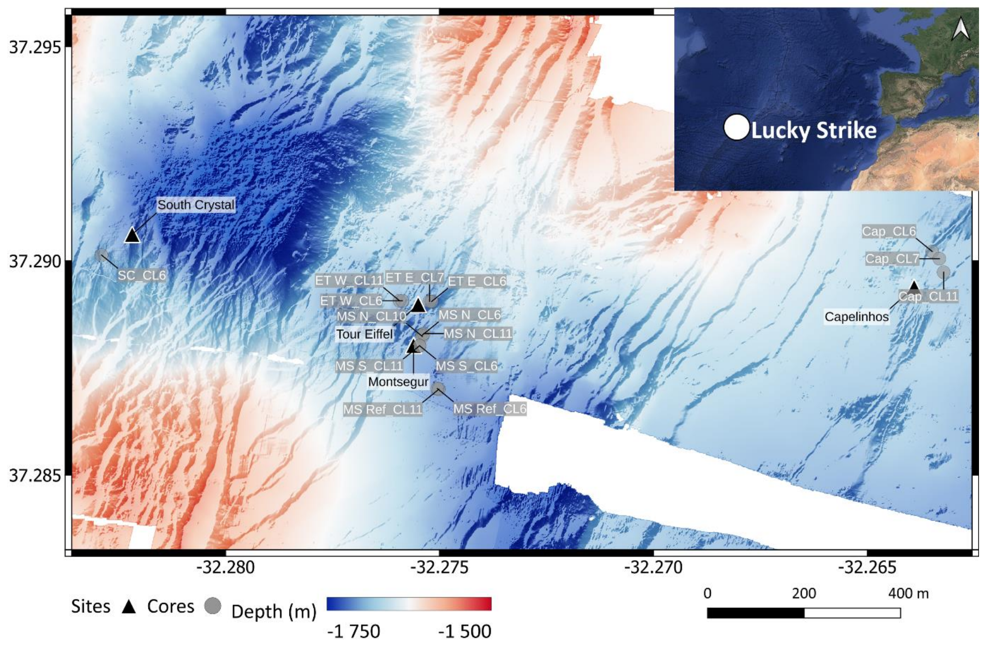

Fig. 1. Location of the Lucky Strike vent field on the Mid-Atlantic Ridge (inset) and of the sediment cores (grey circles) collected in 2020 near four active hydrothermal edifices (black triangle).

As observed in many different hydrothermal fields, the local biology is greatly enhanced by symbiosis with chemosynthetic microorganisms. That results at Lucky Strike in a strong dominance of *Bathymodiolus azoricus* mussel assemblages (Van Dover, 1995; Desbruyeres et al., 2001) that create habitats hosting at least 79 associated species, each occupying distinct ecological niches (Sarrazin et al., 2015; Husson et al., 2017; Sarrazin et al., 2020). Two other assemblages, dominated respectively by *Mirocaris fortunata* shrimp and by *Peltospira smaragdina* gastropods, dominate warmer areas (Sarrazin et al., 2022). The geochemistry of the plumes showed a strong dilution of the fluid a few meters (5 to 10 m) away from the venting locations, as suggested by measurements of temperature and pH gradients near one of the largest and most studied edifices (i.e., Eiffel Tower; Sarradin et al., 2009). The area of exported

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particles does not reach 500 m and the influence of the vent field on the open ocean remains restricted (Khripounoff et al., 2000). Even though the Lucky Strike vent field differs from the other Mid-Atlantic Ridge vent sites by the absence of well-developed peripheral macrofauna (Van Dover et al., 1996), the vent primary chemosynthetic production is exported at least as far as ~90 m in the field (Alfaro-Lucas et al., 2020). The peripheral fauna harbors unique species and functional entities that contribute to increase the biodiversity at the vent field scale (Alfaro-Lucas et al., 2020).

3. Material and methods

During the MoMARSAT cruise in September 2020, 15 sediment blade cores have been collected using the remotely operated vehicle *Victor6000* (Ifremer, Fig.1). Among them, 1 core was not analyzed due to missing sedimentary material, and 3 of them targeted microbial mats, visually attributed to iron-oxidizers biofilms, most likely zetaproteobacteria (Astorch-Cardona et al., 2023). Various venting locations were targeted (i.e., near Eiffel Tower, Montsegur, Capelinhos and South Crystal edifices) in addition to a more distal location ~100 m away from active venting (called Montsegur-Ref, Fig. 1). Each core has been sliced on board every centimeter and split in two equivalent volumes for each horizon, one preserved at -20°C for geochemical analyses and one preserved in a solution of Rose Bengale 2 g L^{-1} in 96% ethanol for living benthic foraminiferal identification (Table 1). The taxonomy of benthic foraminiferal species has been realized thanks to the Atlas of Benthic Foraminifera (Holbourn et al., 2013) and Loeblich and Tappan (1988). Scanning electronic microscope images of the most abundant species are represented in plate 1 (supplementary 1). Specimens were considered living when all chambers, except the last one, were stained. In case of doubt, notably for the miliolids, tests were broken to ensure that the staining came from internal cytoplasm.

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Table 1. List of collected samples. Note that Cap_CL11 was analyzed for geochemistry only and Cap_CL6 for foraminifera only.

Core name	Site	Station code	Day	Lat. N	Long. W	Water depth (m)	Geoch.	Foram.	Indiv.	S	H'	E
755-3_CL6	Montsegur N	MS N_CL6	15.09.2020	37 17.296	32 16.524	1703	0-5 cm	0-1 cm	16	8	1,808	0,7623
755-3_CL10	Montsegur N	MS N_CL10	15.09.2020	37 17.294	32 16.524	1703	0-8 cm	0-5 cm	33	14	2,317	0,7249
755-3_CL11	Montsegur N	MS N_CL11	15.09.2020	37 17.298	32 16.522	1703	0-6 cm	0-5 cm	34	7	1,582	0,695
757-5_CL6	Capelinhos	Cap_CL6	17.09.2020	37 17.413	32 15.809	1684	NA	0-1 cm	1	1	0	1
757-5_CL11	Capelinhos	Cap_CL11	17.09.2020	37 17.384	32 15.793	1684	0-6 cm	NA	NA	NA	NA	NA
757-5_CL7	Capelinhos	Cap_CL7	17.09.2020	37 17.403	32 15.799	1684	5-7 cm	0-5 cm	3	2	0,6365	0,9449
759-7_CL11	Eiffel Tower W	ET W_CL11	21.09.2020	37 17.344	32 16.556	1697	0-5 cm	0-5 cm	NA	NA	NA	NA
759-7_CL6	Eiffel Tower W	ET W_CL6	21.09.2020	37 17.344	32 16.552	1697	0-5 cm	0-5 cm	81	20	2,525	0,6245
760-8_CL7	Eiffel Tower E	ET E_CL7	22.09.2020	37 17.343	32 16.514	1701	0-7 cm	0-5 cm	7	5	1,475	0,8743
760-8_CL6	Eiffel Tower E	ET E_CL6	22.09.2020	37 17.343	32 16.511	1701	0-5 cm	0-5 cm	83	14	2,205	0,6476
761-9_CL6	South Crystal	SC_CL6	22.09.2020	37 17.408	32 16.974	1719	0-9 cm	0-5 cm	38	11	2,025	0,6886
762-10_CL6	Montsegur	MS_CL6	24.09.2020	37 17.281	32 16.528	1702	0-4 cm	0-4 cm	1	1	0	1
762-10_CL11	Montsegur	MS_CL11	24.09.2020	37 17.281	32 16.528	1702	0-4 cm	0-4 cm	NA	NA	NA	NA
763-11_CL11	Montsegur Ref	MS Ref_CL11	24.09.2020	37 17.220	32 16.501	1712	0-8 cm	0-5 cm	58	16	2,497	0,7592
763-11_CL6	Montsegur Ref	MS Ref_CL6	24.09.2020	37 17.221	32 16.503	1712	0-8 cm	0-5 cm	101	22	2,333	0,4684

Bulk chemical composition of each surface sediment (0-1 cm) sample was determined using a wavelength dispersive X-ray fluorescence spectrometer (BRUCKER AXS S8 Tiger) at Ifremer. Samples were ground to a powder (90% of particles < 80 µm) using an agate pestle and mortar. Major elements and selected trace elements were analyzed on pressed pellets and fused beads (with a specific preparation for S analysis of sulfide-rich sediment; supplementary 2). After acquisition, the measured net peak intensities, corrected for inter-element effects, were converted into concentrations using calibration curves generated from analysis of certified geochemical standard powders (measured under identical analytical conditions).

Total organic carbon and its isotopic signature (TOC, $\delta^{13}C_{TOC}$) have been measured using a LECO TruMac, after carbonate dissolution (HCl 1N) at Ifremer. Accelerator Mass Spectrometry ^{14}C dating has been performed on 7 samples from two blade cores, in order to estimate sedimentation rates near the active Eiffel Tower edifice (ET E_CL7) and at the periphery of the vent field (MS Ref_CL6). Radiocarbon dating was carried out at the Beta

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Analytic Radiocarbon Dating facilities in Miami, US. The age was converted into calendar years using the calibration program Calib 7.1 (Stuiver et al., 2014) with a marine reservoir age of -400 years that was incorporated within the Marine13 calibration curve (Reimer et al., 2013).

Faunal and environmental statistics have been performed using the software Primer v6.0 (Clarke and Warwick, 1994), for diversity indices (specific richness, Shannon and Evenness indices), principal component analysis (PCA) and matrices calculations (BioEnv). A PCA has been performed including standardized (minus average, divided by standard deviation) environmental parameters (Fe_2O_3, S, Cu, Ba, MnO, SiO_2, CaO, TC, TOC, $\delta^{13}C$ and grain size) and standardized living faunal descriptors (individuals, specific richness and Shannon Index values) in order to investigate the control factors of the faunal distribution. A redundancy analysis (RDA) was performed to investigate the influence of environmental variables on the distribution of dead and living most abundant taxa in the 0-1 cm layer. Dead and living organisms were pooled together in order to restrain taphonomical impacts, such as disappearance of soft-bodied foraminifera and seasonal effects and to ensure robust interpretations as rarefaction curves tend to show underestimation through living fauna (supplementary 3). Six species and two taxonomic groups were kept for the RDA analysis: *Quinqueloculina auberiana*, *Cibicides wuellerstorfi*, *Cibicides pachyderma*, *Cruciloculina triangulis*, *Epistominella exigua*, *Gavelinopsis translucens*, pooled *Fissurina* species and pooled non calcareous species. RDA was performed with the R software (R core team, 2025) and the vegan package (Oksanen et al., 2001). A forward selection was implemented to select the environmental variables significantly explaining the species distribution (function ordistep of the vegan package).

A correlation of environmental (Euclidean distance) and faunal (Bray-Curtis dissimilarity) matrices has been performed through the test BEST (BioEnv) to determine the main elements impacting the distribution of both fossil and living fauna on the study area (2 tests on total

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abundances). Environmental parameters considered in the calculation were grain size, SiO_2, Fe_2O_3, MnO, CaO, S, Ba, Cu, $\delta^{13}C_{TOC}$, TOC and TC.

4. Results

4.1. Microhabitat characterization

Sediment microhabitats have been studied through their particulate element composition, the main elements measured in each core surface (0-1 cm) have been represented as bar charts of relative abundance (Fig. 2) and secondary elements as superposed curves.

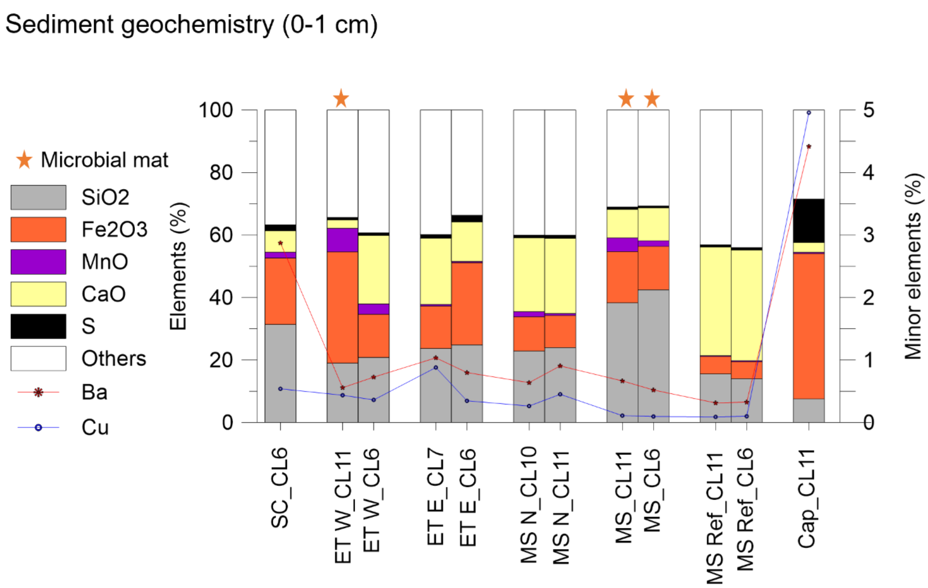

Fig. 2. XRF analyses of top layers (0-1 cm) of the 12 sediment cores sampled in 2020 on the Lucky Strike vent field (Mid-Atlantic Ridge). Ba and Cu are plotted as minor elements (right scale).

CaO represented the main component of stations MS N and MS Ref ranging from 24 to 35%. SiO_2 values ranged from 8% (station Cap_CL6) to 42% (station MS_CL6). Fe_2O_3 and S were

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the most abundant elements in station Cap_CL6, reaching 46% and 14%, respectively. This station also showed peaks of Ba (4.4%) and Cu (4.9%). Fe_2O_3 (36%) and MnO (8%) were high in station ET W_CL6. Finally, relatively high Fe_2O_3 (21%) and Ba (2.8%) have been measured in station SC_CL6. Major elements signature of surface sediments is related to mixing of particles form three different origin (Fig. 3): (1) pure pelagic sediments (carbonate), (2) pure metalliferous sediments (sulfides and/or oxides) and (3) mafic rocks (i.e., basalt) from the oceanic crust.

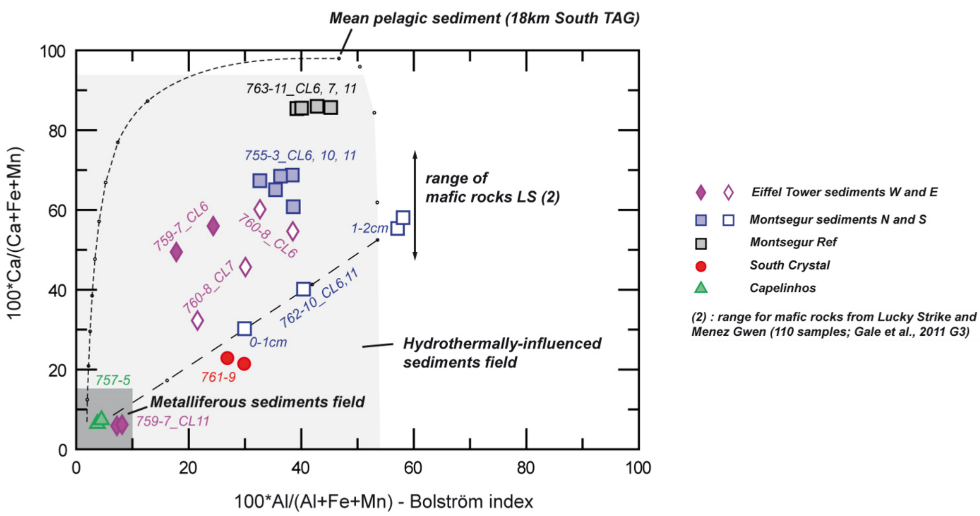

Fig. 3. Bolström diagram representing the geochemical analyses of the top sediment layers (0-1 cm) in the peripheries of four active edifices on the Lucky Strike vent field (Mid-Atlantic Ridge).

Sediments from Montsegur_Ref shows only little hydrothermal particles contribution and plot close to the mean pelagic sediment composition. Sediments from Capelinhos and two from Eiffel Tower W plot inside the metalliferous sediment field (Fig. 3) indicating a strong hydrothermal influence. Sediments from Montsegur S and South Crystal plot on a mixing line between metalliferous sediments and mafic rocks. Distribution of other sediments in Figure 3 indicate a variable mixture of pelagic sediments, mafic rocks fragments and metalliferous sediments.

Sedimentation rates have been calculated from two different sites (supplementary 4), one in the vicinity of the Eiffel Tower edifice (ET E_CL7) and one in the south periphery of Lucky Strike (MS Ref_CL6). These sedimentation rates showed relatively stable trends, especially for the station MS Ref_CL6, indicating a mean value of 2.3 cm.kyr^{-1}. At the basis of the Eiffel Tower edifice, the sedimentation rate was 4.3 cm.kyr^{-1}.

Inorganic and organic carbon as well as δ^{13}C of organic carbon have been measured on surface sediment samples (0-1 cm) and summarized in Table 2. Total carbon (TC) data showed maximal values in MS Ref stations, exceeding 7.5%. Minimum values (<1%) were obtained in the three cores targeting microbial mats (ET W_CL11, MS_CL6 and MS_CL11) and in the SC_CL6 core. Maximal total organic carbon (TOC) values were obtained in station MS N_CL11, Cap_CL6 and MS Ref. $\delta^{13}C_{TOC}$ ranged from -25.4‰ (ET W_CL11) to -22.3‰ (MS Ref_CL11).

Table 2. Organic and inorganic carbon data.

Core	TC (%)	TOC (%)	TOC st. dev.	$\delta^{13}C_{TOC}$	$\delta^{13}C_{TOC}$ st. dev.
MS N_CL6	2.19	0.17	0.002	-23.40	0.01
MS N_CL10	4.68	0.22	0.012	-22.63	0.35
MS N_CL11	4.90	0.32	0.033	-23.13	0.11
Cap_CL11	1.21	0.30	0.000	-23.58	0.00
ET W_CL11	0.80	0.18	0.012	-25.35	0.91
ET W_CL6	4.43	0.23	0.007	-23.35	0.11
ET E_CL7	1.99	0.19	0.010	-25.34	0.46
ET E_CL6	4.13	0.29	0.014	-23.87	0.15
SC_CL6	0.73	0.22	0.014	-25.11	0.35
MS_CL6	0.21	0.21	0.016	-24.35	0.53
MS_CL11	0.39	0.17	0.013	-24.66	0.41
MS Ref_CL11	7.66	0.26	0.004	-22.30	0.10
MS Ref_CL6	8.02	0.27	0.002	-22.34	0.11

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4.2. Foraminiferal distribution

In total, 54 species have been identified on the whole study area. Living individuals showed contrasted densities and diversities (Table 1) with the highest number of individuals (101) and specific richness (22) in station MS Ref_CL6 and a minimum of 1 individual in station Cap_CL6. Relatively high diversity characterized stations MS Ref_CL6 and ET E_CL6 with Shannon indexes of 2.5. The rest of the stations displayed Shannon index values ranging from 0.6 to 2.3.

When combining both living and dead individuals, the relationship between the specific richness and the number of identified individuals showed similar trends for most of the stations indicating that more than 90% of the species are identified within the first 300 individuals of the total assemblages. Stations ET E_CL6 and MS Ref_CL6 showed the highest diversity with 30 and 28 species for 300 individuals, respectively. A minimum of 13 species for 300 individuals was observed in MS N stations. Three cores revealed the absence (or only one individual) of benthic foraminifera (MS_CL6 and CL11 and ET W_CL11) where microbial mats have been targeted for the sampling.

A PCA was conducted to investigate the environmental factors influencing living benthic foraminiferal communities (Fig. 4).

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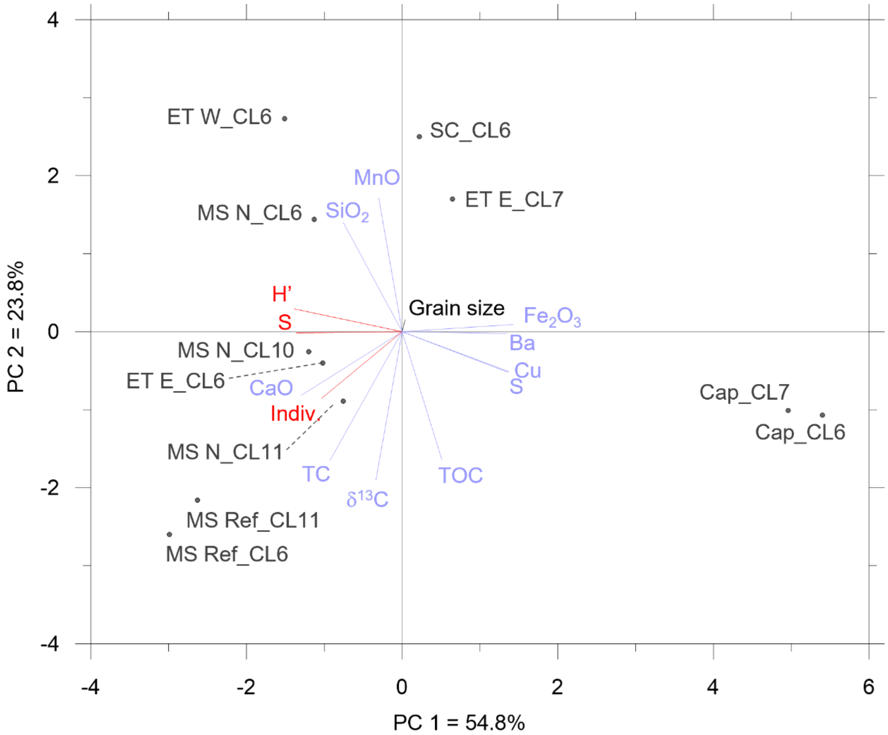

Fig. 4. Principal Component Analysis with environmental parameters in blue and biological metrics in red. H' = shannon index, S = specific richness, Indiv. = number of individuals.

The first two axes account for 78.6% of the total data variability, with PC1 explaining 54.8% and PC2 explaining 23.8% of the variance. PC1 seemed to correspond to hydrothermal inputs with positive loadings for the elements Fe_2O_3, S, Cu and Ba and slightly positive loading for TOC, while CaO displayed the most negative loading. Hence, the hydrothermal-derived elements on the PC1 particularly isolated the cores Cap_CL7 and Cap_CL6, representing the hydrothermal domain. SC_CL6 and ET E_CL7 also showed positive loading on PC1, suggesting a significant hydrothermal signal. The second axis suggested a control of the organic matter source with negative loadings of TC and $\delta^{13}C$ and CaO. Positive loadings on the PC2 were characterized by MnO and SiO_2. All cores showing negative loadings for both PC1 and

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PC2 were characterized by a pelagic sedimentation dominated by phytodetrital organic matter ($\delta^{13}C$ ~ -20 ‰ and high CaO content), representing the reference domain with cores MS Ref_CL11 and MS Ref_CL6. The last domain visible on the PCA was intermediate, showing a lower contribution of elements from the pelagic sedimentation (CaO) or from hydrothermal input (Fe_2O_3, S, Cu and Ba), resulting in higher contribution of SiO_2. MnO content suggested a slight influence of hydrothermal-derived particles, probably originating from low temperature Mn-oxides precipitation. The abundance of living benthic foraminifera was well correlated with the reference domain while faunal diversity better corresponded to the intermediate domain, suggesting an influence of the source of organic matter. BioEnv statistical tests (BEST, Primer v.06) was performed on both dead and living faunal communities with environmental data (Table 3). Both tests highlighted the control of Fe_2O_3 alone for the living communities and Fe_2O_3 with Ba for the dead ones as main control of faunal variability (Table 3), confirming the impact of hydrothermal-derived microhabitats at a regional scale.

Table 3. Statistical test BioEnv (matrices correlation).

BioEnv (living fauna). significance: 4%

Variables number	R^2	Variables
1	0.664	Fe_2O_3
2	0.659	Fe_2O_3. Ba
2	0.652	Fe_2O_3. Cu
3	0.651	Fe_2O_3. Ba. Cu

BioEnv (dead fauna). significance: 2%

Variables number	R^2	Variables
2	0.796	Fe_2O_3. Ba
3	0.796	Fe_2O_3. S. Ba
3	0.795	Fe_2O_3. Ba. Cu
4	0.795	Fe_2O_3. S. Ba. Cu

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The whole study area was dominated by *Quinqueloculina auberiana* and *Fissurina orbignyana* (the most abundant species among the *Fissurina* genus) (Fig. 5). In the southern most station, the Miliolid order was well represented with *Q. auberiana*, *Pyrgo informata*, *Cribromiliolinella subvalvularis*, *Cruciloculina triangularis* and *Triloculina oblonga* as well as other calcareous species *Cibicides wuellerstorfi* and *Fissurina orbignyana*. Non-calcareous species (agglutinated and allogromids) were mainly present in intermediate stations (MS N; ET W and ET E) such as *Martinottiella cylindrica*, *Karreriella bradyi* and *Vanhoeffenella* sp. Among the most abundant species, *Gavelinopsis translucens* had its highest relative contribution in stations ET E_CL6 and SC_CL6, in the latter associated with *Epistominella exigua* and *Cibicides pachyderma*. Stations Cap_CL6 and Cap_CL7 were characterized by a strong dominance of *Fissurina* spp, (~50%) including all identified species from this genus (*F. orbignyana*, *F. annectens*, *F. foliformis*, *F. laevigata*).

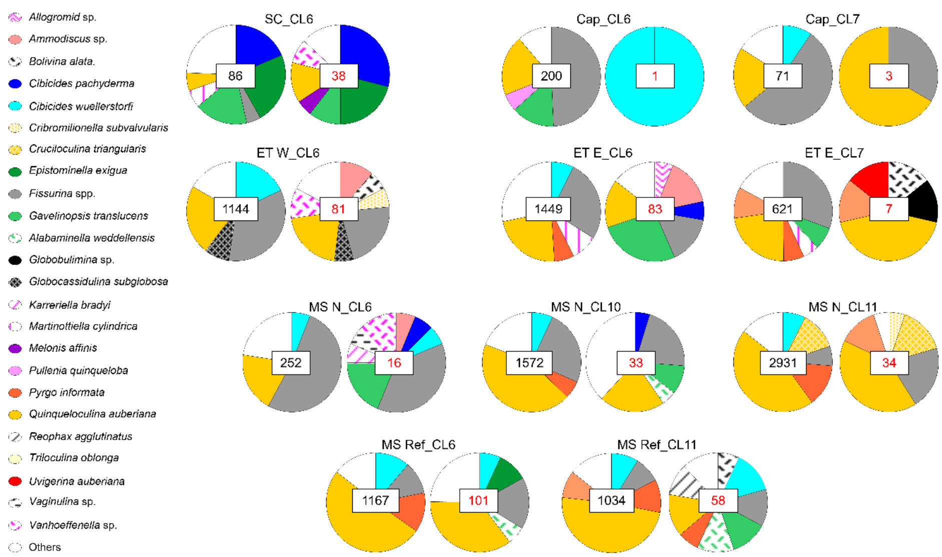

Fig. 5. Relative abundance (pie charts) and absolute number of individuals of the main benthic foraminiferal species (e.g., representing >5%) of the total abundance with dead communities represented on the left (black numbers) and living communities on the right (red numbers).

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The RDA performed on the main species distribution selected only CaO and Fe_2O_3 ($p < 0.05$) when implementing the forward selection on environmental variables (Fig. 6).

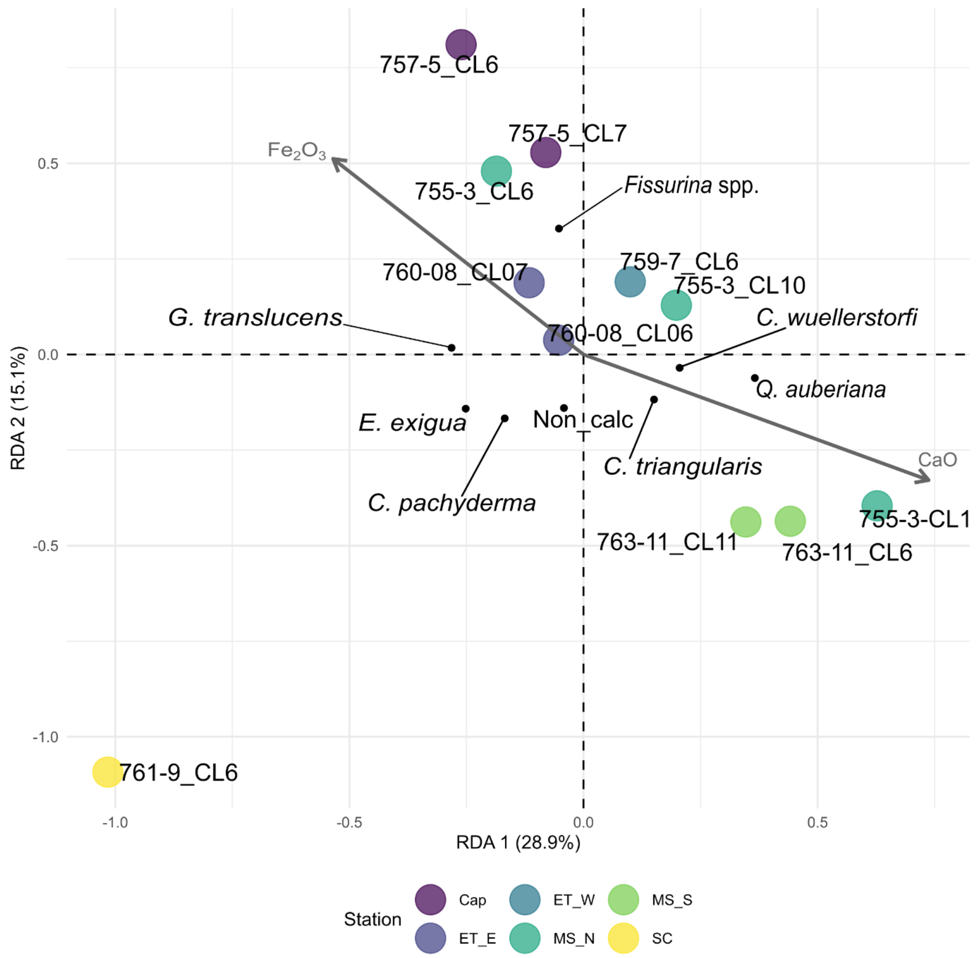

Fig. 6. Redundancy Analysis of the main benthic foraminiferal species (>5% of the total abundance) of the Lucky Strike vent field based on dead + living communities and environmental parameters of the top sediment layers (0-1 cm).

The first two axes represent together 44% of the data variability. Main distinctions are visible along the pelagic to hydrothermal gradient with *Q. auberiana* dominant in the reference cores on the bottom right quadrant of the RDA, associated with pelagic sedimentation (correlated to

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CaO) while *Fissurina* spp. were dominant in cores Cap_CL6 and Cap_CL7, in the most intense hydrothermal domain in the top left quadrant (correlated to Fe_2O_3). Cores in other venting locations are intermediate, with an exception with the South Crystal's core, showing a distinct pattern with the dominance of *E. exigua* and *C. pachyderma* species.

5. Discussion

5.1. Environmental control on faunal distribution

The Lucky Strike vent field developed on the summit of a large volcano (Ondréas et al., 2009) mainly composed of enriched mid-ocean ridge basalt (EMORB) characterized by high barium contents compared to normal MORB. This geological context allowed the enrichment in Fe and H_2S in the area as well as Cu, S, Zn and Ba in the close vicinity of the black smokers (Cotte et al., 2020). Our results confirm a sedimentary content enriched in these elements at close periphery of active edifices, while further periphery mainly represents phytodetritic influence. The contribution of hydrothermal-derived material close to Eiffel Tower edifice hence represents about 2.0 cm kyr^{-1} that corresponds to half of the sediment material. The elements measured in Capelinhos and South Crystal suggest an important geochemical maturation originating from the hydrothermally-derived metalliferous sediments, or more likely in Capelinhos from vestiges of inactive chimneys covering the sediment, as suggested by the pore water dissolved metals profiles (supplementary 5) thus implying a different potential impact on faunal distribution.

Inorganic carbon data appeared correlated with CaO content, mainly derived from the presence of planktonic foraminifera that were the most abundant in MS Ref stations according to visual stereoscopic microscope observations. Stable isotopic signature of carbon in these stations demonstrated a classical marine signal of phytodetritic material (Meyers, 1994). More depleted

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$\delta^{13}C$ of the sedimentary organic carbon measured in the vicinity of hydrothermal edifices Eiffel Tower, Capelinhos and South Crystal and within microbial mats suggested a microbial ^{13}C depletion. Hence, the benthic foraminiferal food source varied from exclusive phytodetritic material in the MS Ref stations to mixed pelagic and microbial carbon sources in periphery stations, and exclusive microbial source in mats.

Even though statistical tests on environmental control on fauna indicate a first variance explanation based on sedimentary content (i.e., Fe, Ba and CaO), these parameters showed significant autocorrelations with TOC and $\delta^{13}C$ of the organic carbon, suggesting that hydrothermal-derived material is strongly linked with the quantity and source of organic matter available for foraminiferal communities and should be considered for faunal interpretation. Additionally, microbial biofilms were not included in statistical tests because of the absence of fauna, being nevertheless key for distribution understanding.

5.2. A toxic microbial biofilm for foraminifera?

The abundance of both living and fossil benthic foraminifera suggested a main control by organic carbon content in the sediment that was not directly connected to the influence of venting activity. In particular, the cores collected on the zetaproteobacteria microbial mats (MS_CL11, MS_CL6 and ET W_CL11) revealed the absence of foraminifera. The visual observations of sediment samples pointed out the absence of all carbonated material, such as planktonic foraminifera, resulting in a very low total carbon and carbonate content (Table 2). These stalk-forming iron-oxidizing bacteria are known to produce flocculent iron oxide mats, which can be meters thick and cover hundreds of square meters (Emerson and Moyer, 2002). While oxidizing iron, they use Fe(II) and oxygen producing Fe(III) (eq. 1), that also occurs through abiotic reaction that almost directly results in the production of iron oxyhydroxides at circumneutral pH through the reaction (eq. 2) (Emerson et al., 2010).

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(1) $Fe^{2+} + 0.25\ O_2 + H^+ \rightarrow Fe^{3+} + 0.5\ H_2O$

(2) $Fe^{2+} + 0.25\ O_2 + 2.5\ H_2O \rightarrow Fe(OH)_3 + 2\ H^+$

In order to limit the precipitation of Fe(III); as well as produced by the abiotic iron oxidation in iron oxyhydroxides; they excrete acidic polysaccharids that acidify (to pH = 6) their microhabitat outside their cells in order to bind the Fe(III) and prevent its precipitation in minerals (Cohen, 2020). Hence, zetaproteobacteria biofilms may significantly decrease the microenvironmental pH in their mats, resulting in the dissolution of fossil planktonic foraminifera and preventing benthic foraminiferal colonization in surrounding sediments. These microbial communities are abundant on basaltic-rich substrates at the Lucky Strike vent field where they use the structural Fe(II) from the basaltic glass (Henri et al., 2016). Whether the absence of benthic foraminifera is explained by the presence of the microbial mats themselves (competition or lack of sediment substratum) or by the pH of the biofilm is unclear. However, the absence of all carbonated tests (planktonic foraminifera, ostracods, bivalves, gastropods) in these cores, combined with a very low inorganic carbon content in the three "microbial mat" cores further support the hypothesis of a dissolution of all carbonates in the mat. The organic carbon source there, might be limited to the microbial community itself, without pelagic contribution. Considering the sedimentation rate (2.3 cm $kyr.^{-1}$) and the carbonate content in the pelagic end-member, this dissolution would result in a rate of 0.5 $mg(CaCO_3).cm^{-3}.yr^{-1}$, that might have a significant impact on regional carbon budget considering the area covered by these mats.

5.3. The pelagic end-member

In the control stations (MS Ref), the organic carbon content showed its higher values in the study area, though it remained low compared to classical deep-sea environments (e.g., Dessandier et al., 2016; 2019; Krüger et al., 2025). Notably, these stations were characterized by the most abundant and diverse communities of both fossil and living benthic foraminifera.

The presence of miliolid species and *C. wuellerstorfi*, characterizing these stations, suggests a pre-degraded organic matter, which might correspond to phytodetritic deposits from the last spring. The main difference in the assemblages of benthic foraminifera between the reference and intermediate stations corresponds to the decrease of miliolid relative abundance with increasing proximity to the vents. This may be explained by the calcification strategy of this order that precipitate a shell with high Mg/Ca carbonate, hence necessitating an elevated pH in comparison with that of the surrounding water (de Nooijer et al., 2009). Since the pH in sediments and water at Lucky Strike drastically decreases from the periphery to the edifices (Sarradin et al., 1999), the energetic effort to precipitate these shells may be limiting. These results are in contradiction with a recent study conducted at the Rainbow vent field (Krüger et al., 2025) where miliolids have been observed in the closest relationship with hydrothermal plume. This could be explained by both a different geochemical context in Rainbow vent field and a different sampling strategy, with cores collected between 200 m and 41 km of distance to vents in Krüger et al. (2025) while all cores were distant from less than 50 m to chimneys in the present study (except for MS_Ref stations). Some *C. wuellerstorfi* individuals observed in the present study morphologically resembles *Cibicides lobatulus* taxon, conforming the shape of their test to the substrate where they are attached. Recently, it has been demonstrated that genetically identified *C. wuellerstorfi* flourishing on hard substrata present different morphologies from "classical" *C. wuellerstorfi* to ecophenotype *C. wuellerstorfi* var. *lobatulus* (Burkett et al., 2020). These authors proposed that both the substratum and microbial colonization influence the distribution of *Cibicides* species. *Cibicides pachyderma* is a facultative epifaunal species that preferentially lives as an infaunal dweller in moderate carbon flux areas, able to cover parts of its test by aggregates or algae in low pH environments (Wollenburg et al., 2018). Hence, this species may replace *C. wuellerstorfi* in environments characterized by harsher environmental conditions, such as slightly lower pH.

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5.4. Intermediate habitats, a pool of diversity

The stations in the vicinity of hydrothermal edifices Eiffel Tower and Montsegur harbored abundant and diverse fossil fauna while the living community remained less developed. Interestingly, the faunal diversity of the living community around Eiffel Tower appeared relatively high, showing abundant non-calcareous species (e.g., *Vanhoeffela* sp., *Reophax agglutinatus, Martinorinella cylindrica* and allogromid sp.) and *Globocassidulina subglobosa* that were rare in the rest of the stations. Monothalamids may be present in a greater extent due to harder substrata where they can attach their test, preferentially to most of the calcareous taxa. Their occurrence at Lucky Strike was however limited, in comparison with other deep-sea environments (e.g., Koho et al., 2007) potentially because of low pH microenvironments. As observed for agglutinated species in cold seeps (e.g., Dessandier et al., 2019), these species might not easily tolerate the environmental conditions derived from hydrothermal venting. Nevertheless, several of these species represent pioneer recolonizers following the end of venting or sediment disturbance (Kitazato, 1995; Panieri et al., 2005) and may flourish on inactive chimneys. The cores collected in sediments enriched in iron and sulfur (Capelinhos) displayed generally lower dead faunal abundances than those from the intermediate stations. Interestingly, South Crystal site, that is more a mix of basalt and metalliferous sediment, is characterized by a substantial living individuals' density and a slightly different faunal distribution, with *G. translucens*, *E. exigua* and *C. pachyderma* as the most abundant species. This assemblage highlights a potential fresher organic material than in the other stations that may be linked to a higher microbial productivity, triggered by the high content in iron and sulfur. Sen Gupta and Aharon (1994) observed *G. translucens* as a dominant taxon in a bathyal vent community of the Gulf of Mexico, associated with bacterial (*Beggiatoa*) mats and tolerant to anoxic conditions and high H_2S concentrations in sediments. Most of the deep-sea species may experience dormancy phases during periods of starvation and are likely able to switch to a

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biologically active phase when phytodetritus pulses reach the seafloor (Gooday and Rathburn, 1999), with a response that differs at daily to seasonal scales. In bathyal north Atlantic environment, *Quinqueloculina* sp. has been observed as dominant in late summer, after the degradation of fresh phytodetritic material, replacing opportunistic species (e.g., *Alabaminella weddellensis*, *E. exigua*) at the sediment water interface, after a probable migration up from a shallow infaunal microhabitat (Gooday and Rathburn, 1999). This phenomenon could explain the dominance of *Q. auberiana* in our study area sampled in September while opportunistic species (*G. translucens* and *E. exigua* and *A. weddellensis*) are restricted to sediments harboring additional food sources represented by microbial communities. *Epistominella exigua* and *A. weddellensis* represent the most common species in the deep-sea Atlantic Ocean in the >63 µm size fraction (Sun et al., 2006). These opportunistic species flourish whenever suitable food sources -such as phytoplankton or microorganisms (Turley et al., 1993)- become available (Gooday, 1988).

5.5. Capelinhos, the sulfide-rich metalliferous microhabitat

This living community was absent in Capelinhos where the very high content in hydrothermal-derived elements have probably directly or indirectly restrained foraminiferal growth. However, considering the elevated number of fossils in these two stations, it is clear that the microenvironment is not preventing colonization by benthic foraminifera as observed in the zetaproteobacterial mats. An equilibrium between the source of energy that promotes microbial communities and the more classical marine conditions represented in the reference stations seems to be necessary for the development of these opportunistic species that can thrive in sediments slightly impacted by venting. Surprisingly, a strong dominance of *Fissurina orbignyana* has been observed in the two Capelinhos stations as well as in one of the intermediate stations around Montsegur edifice. Very little is known about the ecology of the genus *Fissurina*, often observed in deep-sea environments, but never abundant enough to

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decipher its ecology. Its occurrence in both the intermediate and extreme environments (i.e., rich in Fe, S and Cu) suggest a wide range of tolerance for these single chambered specimens. Even though Capelinhos edifice lies in a different chemical domain than other edifices of the Lucky Strike vent field (Chavagnac et al. 2018), with the most enriched metal content (Cotte et al., 2020), we cannot exclude that the fossils observed of *Fissurina* species come from a period of a less intense vent activity. Alternatively, the more intense hydrothermal impact observed in this particular core may reflect a different source of particles that could originate from dismantled past chimneys, hence representing harsher environment than diffusion of metal from particles deposited through the hydrothermal plume. Further investigations on the tolerance of these species for high metallic content may be of interest in the future to better understand the ecology of this group.

6. Conclusions

Extensive symbiotic relationships between microorganisms and macrofauna lead to a bypass of meiofauna as major contributors in the vent trophic network. This limited role in energy transfer may explain why meiofauna -especially foraminifera- has received relatively little attention in these ecosystems. However, benthic foraminifera represent an essential chain of the deep-sea food web, making a link between phytoplanktonic and microbial communities on which they feed and a substantial number of predators from the metazoans feeding on foraminifera. In hydrothermal systems, the environmental conditions represent a challenge for these organisms to thrive (e.g., low pH, high H_2S content, hard substrates and in particular low organic carbon content), hence leading to a crucial role of microbial communities as an additional food source but also by the role they have in changing the environment (e.g., consuming H_2S).

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Our results demonstrated that the microbial food source allowed benthic foraminiferal opportunistic species to flourish in the direct vicinity to active chimneys where the elements present in the sediment (Fe, S) originated high microbial content. In the reference cores, the foraminiferal community showed adaptation for more refractory organic matter, which is partially explained by the period of sampling. Directly opposed to this trend, the establishment of biofilm from Zetaproteobacteria seems to trigger the dissolution of all carbonated shells. The absence of agglutinated or organic-walled specimens in these mats even revealed a toxic environment for all benthic foraminifera. This observation questions the role of these extended microbial mats in the carbon fluxes in hydrothermal vent systems, with the dissolution of foraminiferal tests that might export carbon from the sediment to the water column. The reasons for the establishment of mats of Zetaproteobacteria remains uncertain (Emerson et al., 2010), and no direct link can be made when focusing on the iron content in the sediment. This observation points out the extreme heterogeneity of the hydrothermal-derived microhabitats that affects the regional biodiversity where benthic foraminifera represent a powerful bio-indicator.

In the absence of symbiosis between microbes and macrofauna that occurs only in active hydrothermal vents, benthic foraminifera may represent a key trophic chain for the inactive systems. The intermediate stations observed in this study represent good analogues for inactive hydrothermal chimneys inhabiting microbial communities that use reduced elements accumulated in the sediments. There, benthic foraminiferal communities showed their highest diversities. These systems are nowadays under the scope of the society for economic interests in metalliferous sediment associated to sulfides deposits. There, the local biodiversity may be clearly impacted by removal the life conditions of benthic foraminifera. Hence, a good knowledge on benthic foraminiferal ecology from these environments, close to active vents, in the periphery and on inactive chimneys appears essential to prevent any damage in the deep-sea biodiversity.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data have been provided as supplementary material

Authors contribution

PAD designed the experiments, identified benthic foraminifera and analyzed the data. GP and JS supervised the project. RL contributed to statistical analyses and figures. EP, AB and SC analyzed and interpreted the geological data. AB and SF contributed to biological sampling and samples processing. All authors revised the manuscript.