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A threefold perspective on the role of a pockmark in benthic faunal communities and biodiversity patterns

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ABSTRACT

Pockmarks are circular-shaped depressions that increase seabed heterogeneity and are characterized by discontinuous fluid emissions. To understand how environmental conditions of pockmarks affect the structure of macro- and meiofauna, we investigated two sites in a pockmark field in the northwestern Madagascar margin. In a comparative approach, we explored the community structure of the dominant taxa (Polychaeta, Nematoda and hyaline foraminifera) in each component (macro-, metazoan meiofauna and foraminifera, respectively). The investigated active pockmark showed approximately two times higher meiofauna abundance compared to in a site away from another pockmark field, but macrofauna showed the opposite trend, with almost half density at the pockmark site. However, at both sites, macro- and meiofauna showed higher richness and abundance values in the top well-oxygenated layers of the sediment than in the underlaying ones. Polychaeta and Nematoda showed lower richness in the pockmark, opposed to hyaline foraminiferans, but lower evenness in the pockmark was found for the three groups. The detection of gas flares in the water column attests of the recent activity within the pockmark. High amount of sulfur-bearing minerals (mainly pyrite) evidences a production of dissolved free sulfides (not detected at the time of sampling) by sulfate reduction process driven by organic matter degradation and anaerobic oxidation of methane. Furthermore, recent increase in sedimentation rates in the past 70 years and organic matter inputs could have led to higher organic matter degradation rates resulting in reduced conditions and a high oxygen consumption. All this together seem to act as key factors in the determination of variation in richness, abundance and community composition of macrofauna and meiofauna. Additionally, some taxa seem to be more tolerant to these extreme conditions, such as species belonging to the Nematoda genus *Desmodora* and the phylum Kinorhyncha, which are highly abundant in the pockmark, and hence, may be considered as potential bioindicators of pockmark activity in this area. Further studies are required for a better assessment.

1. Introduction

Deep-sea floor exploration has revealed vast geological, chemical, and biological heterogeneity on continental margin ecosystems (Levin and Sibuet, 2012; Menot et al., 2010). Among them, pockmarks specifically refer to circular/ellipsoid depressions in the seabed which increase seafloor heterogeneity as they represent habitats with high structural complexity where fluid emission can vary in space and time (Dando et al., 1991; Hovland and Judd 1988). Organisms inhabiting in active pockmarks are able to cope with the conditions that can

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Table 1
Position of sampling: Site 1, active pockmark on the Mahavavy Sud slope; Site 2, outside another pockmark field on the Betsiboka slope.

Site	Location	Latitude (S)	Longitude (E)	Depth (m)	Cruise label	Gear	Date (dd/mm/yy)
Site 1	Inside the pockmark	15° 31,1748′	45° 42,93,384′	775	MOZ01-KGS03	USNEL box	07/10/2014
		15° 31,14,888′	45° 42,9309′	789	MOZ01-MTB06	Barnett-type multi-corer	07/10/2014
		15° 31,1559′	45° 31,1559′	776	MOZ01-MTB07	Barnett-type multi-corer	07/10/2014
Site 2	Ouside the pockmark field	15° 22,05054′	45° 22,05054′	528	MOZ01-KGS01	USNEL box	04/10/2014
		15° 22,04772′	45° 22,04772′	529	MOZ01-MTB01	Barnett-type multi-corer	04/10/2014

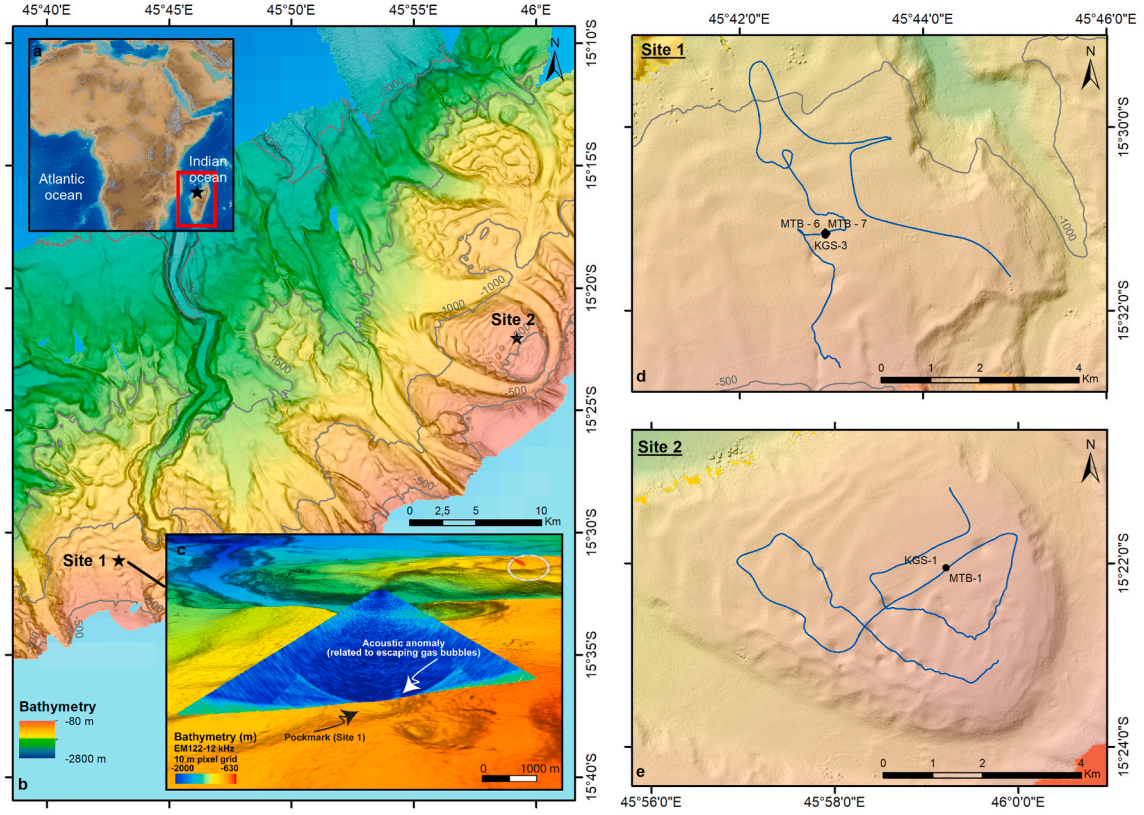

Fig. 1. a) Relief map (from Globe software © Ifremer) with location of the study sites offshore northwestern Madagascar margin in the Mozambique Channel. The Blue Marble data (2004) is courtesy of Reto Stockli (NASA/GSFC). b) Shaded bathymetry map offshore Majunga Basin (northwestern Madagascar margin) from the PTOLEMEE and PAMELA-MOZ01 oceanographic expeditions with locations of the two sampling sites. c) 2D water column polar echogram and seafloor shaded bathymetry in the pockmark area of Site 1. Acoustic anomaly in the water column is interpreted as gas bubbles escaping from the seafloor at this location. d) Detailed bathymetry of the active pockmark Site 1 showing the SCAMPI immersion path and location of the sampling sites. e) Detailed bathymetry of the Site 2, away from a pockmark field, showing the SCAMPI immersion path and location of the sampling sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

characterize this kind of environments, such as high concentrations of reduced chemical compounds, low oxygen levels, and high primary production based on chemoautotrophic bacteria (Levin, 2005; Sibuet and Olu, 1998; Zeppilli et al., 2018).

The presence of specific macrofaunal communities (organisms > 1 mm length) can serve as a valuable tool for identifying the various habitats created by gas emissions. In particular, some Polychaeta families, such as Ampharetidae, Hesionidae, Capitellidae or Dorvilleidae, are adapted to sulphide-rich and hypoxic sediments and therefore dominate such environments (Decker et al., 2012; Donnarumma et al., 2019; Guillon et al., 2017; Levin, 2005; Menot et al., 2010; Portail et al., 2015; Rouse and Fauchald, 1997; Rouse and Pleijel, 2001). In contrast, deep-sea meiofaunal communities, both metazoan and foraminifera (pluricellular and unicellular organisms < 1 mm length, respectively), have been historically less investigated in these habitats, although they can also be used as benthic indicators of changes in environmental conditions (Table 1 in Zeppilli et al., 2015) due to their rapid generation time and the lack of larval dispersion in the dominant groups (Giere, 2009). Moreover, several studies have shown that specific taxa, such as Draconematidae and Monhysteridae nematodes, Darcythompsoniidae and Dirivultidae copepods (Table 1 in Zeppilli et al., 2018 for detailed information), can tolerate or even thrive in extreme environmental conditions, such as high levels of hydrogen sulfide or hypoxia, where most species cannot survive (Baldrighi et al., 2020a; Gooday et al., 2009; Levin, 2003; Van Gaever et al., 2006).

To date, few studies assessed the response of both deep-sea macrofauna and metazoan meiofauna to cold fluid emission simultaneously, showing similar patterns for diversity in both communities, but opposite trends or little differences compared to background sediments for density (Ritt et al., 2010; Van Gaever et al., 2009a and references therein), and no comparative study includes foraminiferal fauna. In the present study, we investigated the distribution and diversity patterns of benthic fauna using an integrative ecological approach including macrofauna and meiofauna from the Majunga Basin in the northwestern Madagascar margin (Mozambique Channel) (Fig. 1a). In this area, pockmark clusters were recently discovered along the slope, front of two main Mahavavy

Sud and Betsiboka rivers, given rise to a serial of multidisciplinary sampling campaigns in the framework of PAMELA project (Dupré et al., 2019; Jorry, 2014; Olu, 2014). Foraminifera community structure and their paleoenvironmental application were previously investigated in the referred area (Fontanier et al., 2016, 2018), showing extremely elevated diversity in areas characterized by high concentrations of degraded organic matter and moderate oxygen penetration in the seafloor (15 and 30 mm), while areas of reduced oxygen penetration showed lower diversity (Fontanier et al., 2016). The foraminifera dataset of this paper will be used for the comparison between sites and with the other benthic components. Since our study is part of a large multidisciplinary project, more stations and samples were investigated for other purposes, but samples of the three benthic components were only collected at two sites. Therefore, a complete data set that allow the comparison among the three faunal components is only available from these two sites: one within an active pockmark and another one located away from pockmarks. The main goals of our study were to: 1) characterize and compare macrofauna, metazoan meiofauna and foraminifera benthic communities in the referred two sites; 2) discuss the effect of environmental constraints on the distribution and diversity of the three aforementioned benthic components; and 3) evaluate the reliability of key most dominant taxa (i.e. Polychaeta, Nematoda and Hyaline) at the upper most sediment layer (0–1 cm, which usually host vast majority of benthic organisms) as potential indicators of pockmark activity.

2. Materials and methods

2.1. Seepage exploration and study sites

The study area was selected based on previous samples of bivalves usually associated with cold seeps (Bathymodiolinae shells and living Vesicomyidae) and collected during the MIRIKI cruise (2009) (P. Bouchet, pers. comm.). Our sampling sites (Fig. 1b) were chosen based on geophysical data (seismics, bathymetry and seafloor backscatter data and acoustic imagery of the water column) of the Ptolemée and Pamela-Moz01 cruises (Jorry, 2014; Olu, 2014) and seabed inspection with the deep-towed camera Scampi to locate cold seeps (e.g. reduced sediment, bivalves, microbial mats) (Olu, 2014; Dupré et al., 2019). Multibeam echosounder surveys were conducted during these marine expeditions with the use of a EM122 ship-borne multibeam echosounder operated at 12 kHz. Seafloor bathymetry (Fig. 1b and c) and acoustic imagery of the water column (Fig. 1c) were acquired offshore northwestern Madagascar in the Majunga Basin. Given the impedance contrast between the ambient seawater and gas bubbles, water column echosounder data record acoustic anomalies caused by the presence of gas bubbles, providing thus crucial information on potential active seeping sites (Dupré et al., 2015). Two sites located on Betsiboka and Mahahavy Sud slopes (ca. 30 km apart) were chosen for faunal sampling with samples collected inside an active pockmark and away from another pockmark field. Nevertheless, all three faunal components were only analyzed at two sampling points (Table 1; Fig. 1). At Site 1 on the Mahavavy Sud slope, samples were specifically collected within an active pockmark (600 m of diameter), at c.a. 780 m water depth. At Site 2 on the Betsiboka slope, samples were taken outside another pockmark field, at c.a. 529 m water depth.

2.2. Regional settings

The large pockmark sampled at Site 1 (600 m diameter) presented a marked shift in sediment accumulation rates around the 1950s (Fontanier et al., 2018), with values similar to the rest of the continental slope before that (around 0.04–0.06 cm yr-1 - Pastor et al., 2020), and much higher values during the last 70 years (0.25 cm yr-1 - Fontanier et al., 2018) representing the 0–16 cm layer. This pulsed sedimentation was interpreted as two or three main input events over the last 70 years (Fontanier et al., 2018), favored by episodic reconnection of the Mahavavy Sud River with the canyon head during extreme climatic events (Pastor et al., 2020). These events brought high loads of relatively degraded organic matter as shown by low enzymatically to total hydrolysable amino acid ratios (EHAA/THAA ratio; Fontanier et al., 2018). This surficial layer is also characterized by a very high accumulation of total sulfur, most certainly *in situ* formed pyrite due to the pulsed high loads of organic matter, its degradation by sulfate reducers, and concomitant high concentration of iron oxides (Pastor et al., 2020). These pulsed episodes seemed to be also responsible for a shift in foraminifera communities (Fontanier et al., 2018).

Sampling in Site 2 occurred about 3.5 km away from the closest active pockmark field, at slightly shallower water depths. In this area, sediment accumulation rates reflected a very low input of particulate matter from the Betsiboka River (Pastor et al., 2020).

2.3. Sediment sampling and processing

Following the recommendations of Montagna et al. (2017), only one replicate sample per station with pseudoreplicated cores were collected. Macrofauna was sampled using USNEL box corers (KGS), subsampled three times with blade corers (surface = 0.018 m^2). MOZ01KGS03 was collected on the Mahavavy Sud slope (Site 1); and MOZ01KGS01 on the Betsiboka slope (Site 2). USNEL blade cores for macrofauna were sliced horizontally in five layers to 15 cm depth (0–1, 1–3, 3–5, 5–10, 10–15 cm). Each layer was sieved through 1 mm, 500 μm and 300 μm mesh size sieves. Samples for morphological studies were fixed onboard in 4% formalin for 24 h and then transferred to 90% ethanol. Macrofaunal animals were sorted and identified to major taxonomic levels (phylum/class/subclass/order/family) using a binocular stereomicroscope Leica M125. Only macrofauna *sensu stricto* (Hessler and Jumars, 1974) were included, and typical meiofaunal taxa such as Nematoda and Copepoda were excluded from these samples. Macrofaunal Polychaeta in the first sediment layer (0–1 cm) were identified to the family level using a binocular stereomicroscope Leica M125.

Metazoan meiofauna were sampled using a multi-corer (Barnett-type, MTB), with a total of three cores from the same deployment (62 mm of internal diameter) at each site. MOZ01MTB06 samples were collected at Site 1 near the center of the pockmark; and MOZ01MTB01 was collected at Site 2 (both deployments suffered of common minor variations from the GPS points of the macrofauna sampling due to sampling environmental conditions; see Table 1). Cores for metazoan meiofaunal studies were sliced on board horizontally in 5 layers (0–1, 1–2, 2–3, 3–4, 4–5 cm), and subsequently fixed in 4% formalin. The sediment of each slice was sieved on 1 mm and 32 μm mesh size sieve; animals were extracted from the sediment using Ludox centrifugation (Heip et al., 1985) and then sorted and identified using a binocular microscope Leica MZ 8 to the higher taxonomic levels typically used for meiofaunal studies (phylum/class/subclass/order/family) (Danovaro, 2010). Additionally, approximately 100 nematodes from the first sediment layer (0–1 cm) of each core were mounted on slides and identified to genus level using a microscope Leica DM2500 LED. The foraminifera community was sampled from two cores (62 mm of internal diameter) at each site, MOZ01MTB07 at Site 1 and MOZ01MTB01 at Site 2 (deployments were displaced a few meters away of the GPS points of the macrofaunal sampling, as already referred for the metazoan meiofauna samplings; see Table 1). In the present study, we used the identification dataset to species level generated by Fontanier et al. (2016) to cluster the specimens in the main foraminifera groups: hyaline, agglutinated, porcelaneous and soft-shell foraminifera (see the referred publication for detailed information on sampling procedure and identification of alive specimens).

Oxygen profiles were measured *ex situ* using Clark-type electrodes as described in Pastor et al. (2011). Organic Carbon (OC) was measured on freeze-dried and crushed sediment after removal of carbonates with 2 M HCl using an automatic ThermoFinnigan EA1112 Series Flash elemental

Table 2
Number of taxonomic groups (richness) and number of specimens (abundance) of macrofauna, meiofauna and foraminifera present in the pockmark (Site 1) and away from a pockmark field (Site 2). Data are given for each core and layer along the vertical profile. X gives the mean values ± standard deviation.

		Sediment layer	SITE 2 MOZ01 KGS01/MTB01				SITE 1 (pockmark) MOZ01 KGS03/MTB06/MTB07			
			A	B	C	X	A	B	C	X
MACROFAUNA	Richness	0–1	6	7	5	6 ± 1	5	5	6	5.33 ± 0.58
		1–3	6	6	4	5.53 ± 1.15	3	3	0	2 ± 1.73
		3–5	5	4	4	4.33 ± 0.58	1	2	1	1.33 ± 0.58
		5–10	3	3	2	2.66 ± 0.58	1	2	2	1.66 ± 0.58
		10–15	2	2	2	2 ± 0	0	1	2	1 ± 1
	Abundance	0–1	27	26	37	30 ± 6	40	74	21	45 ± 26.85
		1–3	22	52	23	32 ± 17	6	8	0	4.66 ± 4.16
		3–5	19	10	14	14 ± 5	1	5	1	2 ± 2.31
		5–10	33	11	15	20 ± 12	2	11	6	6.33 ± 4.51
		10–15	4	3	3	3 ± 0.6	0	1	4	1.66 ± 2.08
MEIOFAUNA	Richness	0–1	6	7	12	8.33 ± 3.21	–	12	7	9.5 ± 3.54
		1–2	8	7	9	8 ± 1.00	8	8	9	8.33 ± 0.58
		2–3	6	6	4	5.33 ± 1.15	6	8	10	8 ± 2.00
		3–4	3	4	4	3.66 ± 0.58	5	2	5	4 ± 1.73
		4–5	0	2	1	1 ± 1.00	2	3	7	4 ± 2.65
	Abundance	0–1	199	374	336	303 ± 92	–	3841	740	2291 ± 2193
		1–2	1030	940	1778	1249 ± 460	1225	737	6476	2813 ± 3182
		2–3	756	1078	521	785 ± 279	735	560	1686	994 ± 606
		3–4	222	323	281	275 ± 51	571	497	416	495 ± 77
		4–5	0	90	1	30 ± 52	267	224	147	212 ± 60
FORAMINIFERA	Richness	0–1	102	99		100 ± 2	67	121		94 ± 38
		1–2	38	49		43 ± 8	36	41		39 ± 4
		2–3	25	28		26.5 ± 2	15	18		17 ± 2
		3–4	17	15		16 ± 1	11	5		8 ± 4
		4–5	18	6		12 ± 8	6	2		4 ± 3
		5–6	13	1		7 ± 9	4	1		2.5 ± 2.12
		6–7	2	1		1.5 ± 0.7	3	0		1.5 ± 2.1
		7–8	2	1		1.5 ± 0.7	3	0		1.5 ± 2.1
		8–9	1	1		1 ± 0	4	0		2 ± 2.8
		9–10	1	0		0.5 ± 0.7	0	0		0
	Abundance	0–1	603	616		609 ± 9	626	2024		1325 ± 988
		1–2	129	96		113 ± 23	460	544		502 ± 59
		2–3	55	67		61 ± 9	78	83		80 ± 4
		3–4	30	22		26 ± 6	17	33		25 ± 11
		4–5	28	7		17.5 ± 14.8	12	19		15.5 ± 4.9
		5–6	13	1		7 ± 9	4	1		2.5 ± 2.1
		6–7	2	1		1.5 ± 0.7	3	0		1.5 ± 2.1
		7–8	3	1		2 ± 1.4	3	0		1.5 ± 2.1
		8–9	1	1		1 ± 0	4	0		2 ± 2.8
		9–10	1	0		0.5 ± 0 .7	0	0		0

analyzer. Total sulfur was measured on the same powdered samples using a LECO CNS-2000 auto-analyzer. On-board measurements of H_2S were based off the Cline method (Cline 1969; Grasshoff et al., 1999) and the absorbance was read at 670 nm (Pastor et al., 2020).

2.4. Faunal data and statistical analysis

Macrofauna, metazoan meiofauna and foraminifera community descriptors were: (1) richness, (2) abundance and (3) taxonomic composition. We used the same community descriptors for Polychaeta, Nematoda and hyaline foraminifera, considering only the uppermost 0–1 cm of the vertical profile because it is the single layer for which we obtained a complete dataset and which allows a comparable study among the three groups (cores for macrofauna were sliced at different depths than those for meiofauna). Richness was measured as the number of high-taxonomic-level taxa of the macrofaunal, metazoan meiofaunal and foraminifera communities. In addition, we used the number of families for Polychaeta, the number of genera for Nematoda, and the number of species for hyaline foraminifera. Abundance was measured as the number of individuals in a core sample and densities were calculated as the number of individuals per surface area (1 m^2 for macrofauna and Polychaeta, 10 cm^2 for metazoan meiofauna, foraminifera, Nematoda and hyaline foraminifera). Statistics were based on pseudoreplicates, which explain larger spatial variance of richness and abundance than true replicates do according to Montagna et al. (2017). Hence, analyses of each benthic component were performed using the faunistic data from all cores collected at each site, considering them as independent units.

Differences in taxa richness and abundance were described along the vertical profile within each site (intra-site study) for macrofauna (0–1, 1–3, 3–5, 5–10, 10–15 cm), metazoan meiofauna (0–1, 1–2, 2–3, 3–4, 4–5 cm) and foraminifera (0–1, 1–2, 2–3, 3–4, 4–5, 5–6, 6–7, 7–8, 8–9, 9–10 cm). Layer 0–1 of core MOZ01MTB6-A used for metazoan meiofauna studies was excluded due to processing problems that resulted in the loss of most animals. Then, we tested for the effect of the pockmark occurrence on the fauna (inter-site study). Generalized Linear Models (GLMs) and Generalized Linear Mixed-effect Models (GLMMs) were chosen to assess for faunal differences between the sites, instead of non-parametric analysis, because they allow to make assumptions about the distribution of our data. Therefore, after verifying data distribution of richness and abundance, models were implemented following Poisson and Gaussian (after logarithmic transformation of the abundance data) distributions, respectively (Crawley, 2012). GLMMs were conducted to test for differences in richness and abundance of macrofauna, metazoan meiofauna, and foraminifera between the two sites (1 and 2, Fig. 1b), using the site as a discrete explanatory variable (i.e. inter-site study), including the variables of “sediment depth” and “core” as random factors. Similarly, GLMs were performed considering only the 0–1 cm layer for the following taxa: family for Polychaeta, genera for Nematoda and species for hyaline foraminifera. GLMs and GLMMs were conducted using the ‘glm’, ‘lmer’ and ‘glmer’ functions implemented in R (Zuur

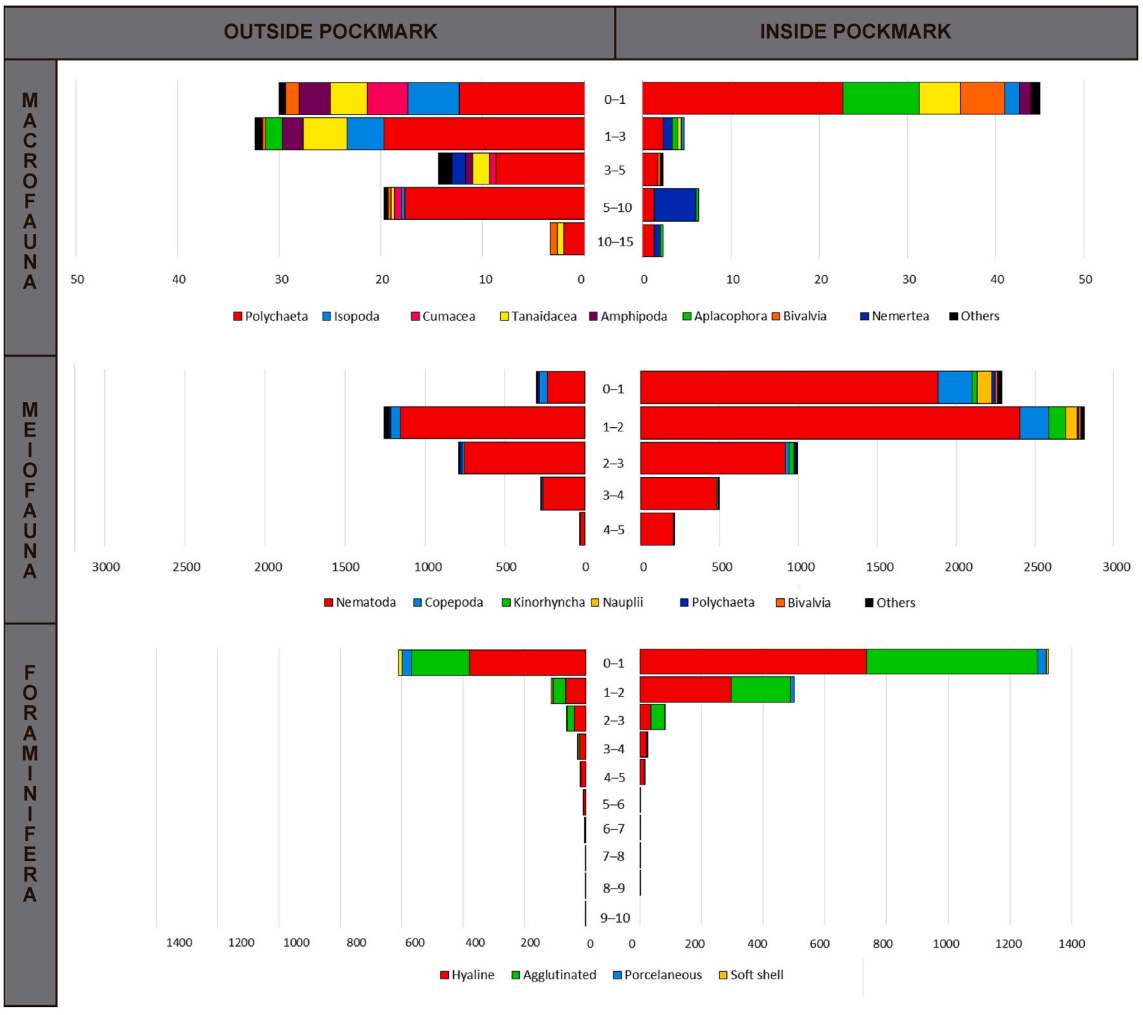

Fig. 2. Faunal community structure characterizing the study sites. Faunal composition of each site is given according to studied layers along the vertical profile of the sediment (Y axis). The contribution of the major taxa is expressed as mean of specimens observed in each layer (X axis). For macrofauna and metazoan meiofauna, the group 'others' includes all taxa representing less than 2% and 0.5%, respectively, of the community.

Table 3
Total macrofauna *sensu stricto* taxa collected at both sites. Abundance of each taxonomic group is given for each core. Total abundance shows number of specimens for each core. Total richness shows number of taxonomic groups for each core. X gives the mean values ± standard deviation. Cores A, B, C in Site 2 (away from a pockmark field) correspond to cores 1, 2, 3 respectively of the sampling campaign. Cores A, B, C in Site 1 (inside the pockmark) correspond to cores 9, 10, 11, respectively, of the sampling campaign.

MACROFAUNA TAXA	SITE 2 MOZ01KGS01				SITE 1 (pockmark) MOZ01KGS03			
	A	B	C	X	A	B	C	X
Amphipoda	9	3	5	5.67 ± 3.06	0	2	2	1.33 ± 1.15
Aplacophora	0	2	3	1.67 ± 1.53	15	13	2	10.00 ± 7.00
Astacidae	1	0	0	0.33 ± 0.58	0	0	0	0.00
Bivalvia	3	5	0	2.67 ± 2.52	5	9	2	5.33 ± 3.51
Cumacea	8	4	4	5.33 ± 2.31	0	0	0	0.00
Gastropoda	0	1	1	0.67 ± 0.58	0	0	2	0.67 ± 1.15
Halacarida	1	0	0	0.33 ± 0.58	0	0	0	0.00
Isopoda	7	15	5	9.00 ± 5.29	5	0	1	2.00 ± 2.65
Mysidacea	1	0	0	0.33 ± 0.58	0	0	0	0.00
Nemertea	0	4	0	1.33 ± 2.31	2	10	5	5.67 ± 4.04
Oligochaeta	0	0	0	0	0	1	0	0.33 ± 0.58
Polychaeta	64	53	64	60.33 ± 6.35	21	50	17	29.33 ± 18.01
Sipunculidae	0	4	0	1.33 ± 2.31	1	0	0	0.33 ± 0.58
Tanaidacea	11	11	10	10.67 ± 0.58	0	14	1	5.00 ± 7.81
Total abundance	105	102	92	99.67 ± 6.81	49	99	32	60.00 ± 34.83
Total density (ind/1 m^2)	5833	5667	5111	5537 ± 378	2722	5500	1778	3333 ± 1935
Total richness	9	10	7	8.7 ± 1.5	6	7	8	7 ± 1

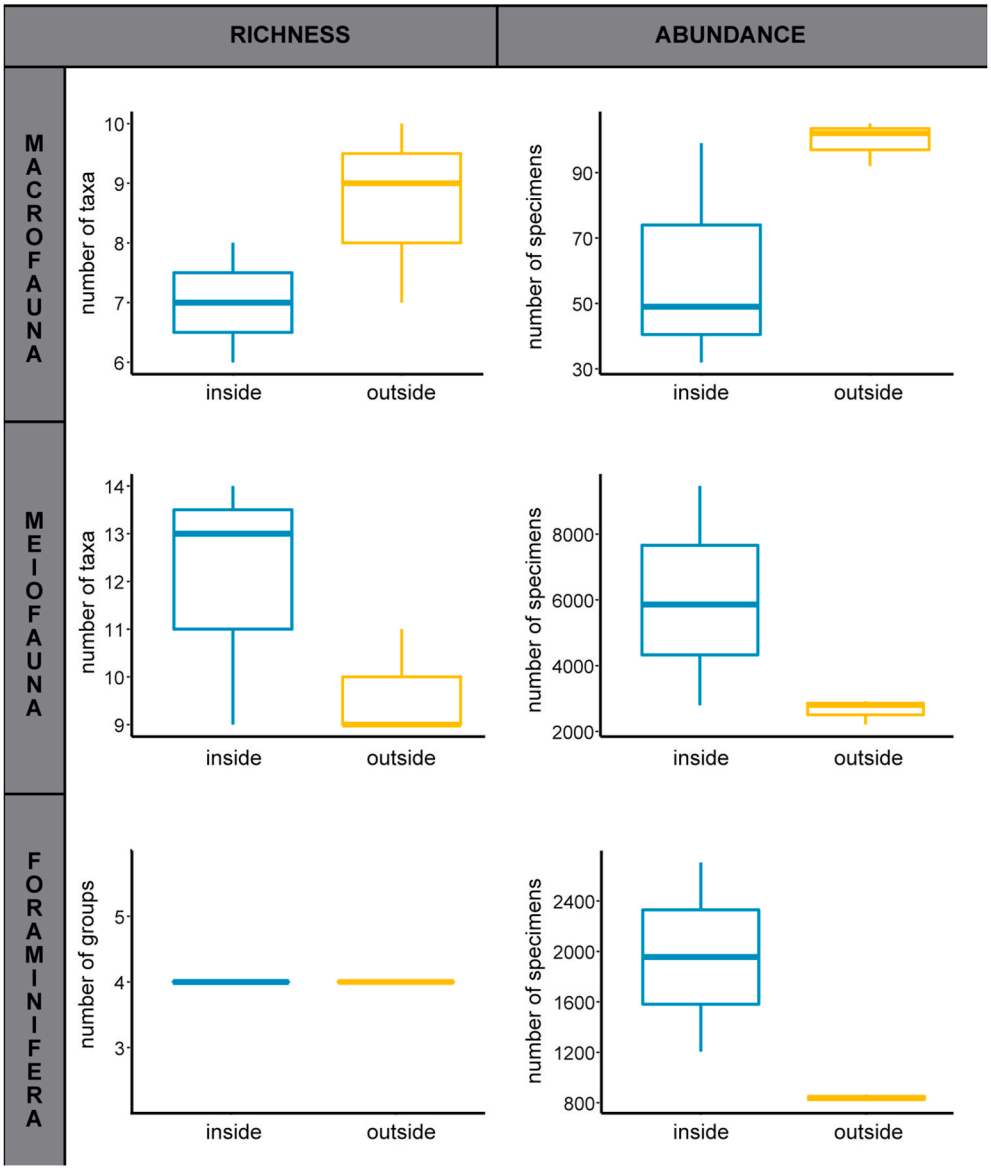

Fig. 3. Richness and abundance of macrofauna, metazoan meiofauna and foraminifera at the two studied sites, inside a pockmark (Site 1; blue) and away from a pockmark field (Site 2; yellow). Boxplots of macrofaunal, metazoan meiofaunal and foraminifera richness are based on the number of high-taxonomic-levels/groups. Y-axes indicate values of richness (high-taxonomic-levels/groups) and abundance (number of specimens) measures considering all the cores of each benthic component (sampling area for macrofauna: 0.018 m^2; sampling area for meiofauna: 30 cm^2). Boxplots depict the median value (horizontal line in the box), the distributions of 50% of the data (the box), and the highest and lowest values within 95% of the distribution (the whisker). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

et al., 2007). Polychaeta, Nematoda, and hyaline foraminifera diversities were measured using the Shannon–Wiener diversity index (H′, log-base *e*) with the Pielou index (J) for evenness, using the 'diversity' function included in the R package vegan v. 2.2-1 (Oksanen et al., 2015).

Differences in community composition were tested using Ružička matrix with a permutational analysis of variance models (PERMANOVA). Ružička index were calculated using the 'beta' function of the R package vegan v. 2.2-1 (Oksanen et al., 2015), and PERMANOVA was performed using the 'adonis' function included in the R package vegan v. 2.2-1 (Oksanen et al., 2015).

To visualize community structure variations between sites in macrofauna, metazoan meiofauna, and foraminifera as well as in Polychaeta, Nematoda, and hyaline foraminifera, we conducted a Principal Component Analysis (PCA) on abundance using the 'rda' function of the R package vegan v. 2.2-1 (Oksanen et al., 2015). Abundance data were transformed (Hellinger distance) using the 'decostand' function of vegan 2.5–5 package (Oksanen et al., 2018), because this distance gives a lower weight to dominant taxa and does not consider double absence as an indicator of similarity between samples (Legendre and Gallagher, 2001). A post hoc test of the PCA axes was performed by the function 'envfit' of the R package vegan 2.4–4 (Oksanen et al., 2018).

3. Results

3.1. Water column acoustic data

At the pockmark of Site 1, seepage activity, although of relatively low intensity, was evidenced based on acoustic water column data (Fig. 1c). At this area, some of the water column echoes identified in 2D polar echograms were rooted in the seabed and interpreted as escaping gas bubbles, most likely composed of methane. In contrast, Site 2 located away from another pockmark field was not characterized by methane seepage, at least at the time of the survey. No active pockmarks have been reported in the close vicinity of Site 2, the closest inactive pockmark being distant from more than 600 m.

3.2. Geochemical settings

In the recovered sediment at Site 1, dissolved oxygen was consumed within 17.5 mm, no dissolved free sulfide ($\sum H2S = S2- + HS- + H2S$) was detected and methane (CH4) was <1 μM, organic carbon concentrations were around 2.0% (Pastor et al., 2020; this study) (Annex I).

At Site 2, OC contents were lower than in Site 1 reaching 1.1%, and

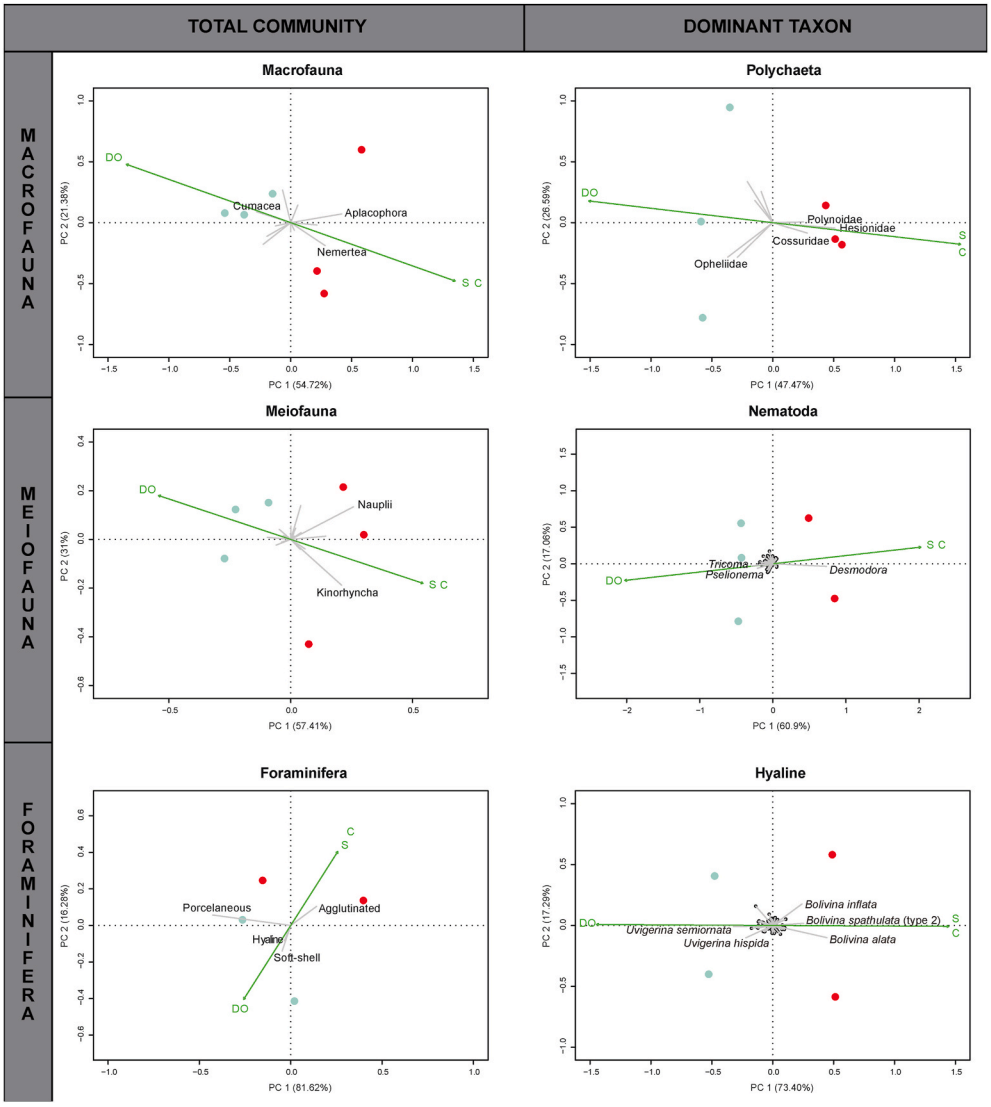

Fig. 4. Principal component analysis (scaling 2) biplots based on Hellinger-transformed data on taxon composition of each community (macrofauna, metazoan meiofauna and foraminifera) and their dominant taxa (Polychaeta, Nematoda, hyaline foraminifera) at the two study sites, inside a pockmark (Site 1; red) and away from another pockmark field (Site 2; blue). Passive (*post hoc*) explanations of axes using environmental variables (DO, dissolved oxygen; S, total sulfur; and C, organic carbon concentrations) were conducted to find factor averages of the studied environmental variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

even more degraded with EHAA/THAA lower than 10% (Fontanier et al., 2016). O_2 penetration depth was around 30 mm. No CH_4 was detected and a peak of $\sum H_2S$ of 34 μM at 11 cm depth was measured (Pastor et al., 2020; this study) (Annex I).

3.3. Macrofaunal community

3.3.1. Intra-site

Abundances at Site 2 (away from the pockmark field) showed similar high values at the two uppermost sediment layers but decreasing gradually with sediment depth (ca. 30% of the fauna in 0–1 cm; ca. 32% in 1–3 cm) (Table 2; Annex II). Most taxa showed a similar trend, except Polychaeta, whose abundance at Site 2 reached a peak at layers 1–3 and 5–10 cm (Fig. 2). At Site 1 (inside the active pockmark), total macrofaunal abundance was high in the first centimeter, with ca. 75% of the total abundance, and much lower in the deeper layers (Table 2; Fig. 2; Annex II); taxa abundance showed a similar pattern. At Site 2, richness was the highest in the surface layers down to 3 cm depth, decreasing only in the layers below 3 cm (from 6.0 ± 1.0 and 5.5 ± 1.2 in layers 0–1 and 1–3 cm, respectively, to 2 ± 0 at 10–15 cm) (see Table 2; Annex II). At Site 1, most of the richness was present in the uppermost sediment layer (0–1 cm, 5.3 ± 0.6), with a maximum of two taxonomic groups per layer below the surface (Table 2; Annex II). The community along the vertical profile at the two study sites was dominated by Polychaeta from the upper to the lower layers (Fig. 2), with one single exception: Nemertea was the dominant taxon in layer 5–10 cm at Site 1 (ca. 74% of the macrofauna community in this layer). Peracarid crustaceans (Isopoda, Tanaidacea, Cumacea, and Amphipoda) were relatively abundant (ca. 52%) in layer 0–1 cm at Site 2.

3.3.2. Inter-site

Overall macrofauna abundance was higher at Site 2, with 99 ± 7 specimens per core at Site 2 and 60 ± 35 at Site 1 (GLM, $P < 0.05$; Annex III) (Table 3). Polychaeta dominated both sites, accounting for ca. 61% and ca. 49% of the overall abundance at Sites 2 and 1, respectively. Aplacophora, Nemertea, and Bivalvia abundances reached higher values at Site 1 than at Site 2 (ca. 17% at Site 1 vs. 1.7% at Site 2; 10% at Site 1 vs. 1.3% at Site 2; 8% at Site 1 vs. 2.7% at Site 2, respectively), and Cumacea was only found at Site 2 (Table 3; Fig. 2). For the most abundant taxonomic groups (greater than 5% of the total community at one site), the analysis confirmed variation between sites in Polychaeta, Cumacea, Tanaidacea, and Amphipoda (see Annex III). Significant differences in richness between the two study sites were found as well, with 8.7 ± 1.5 taxa at Site 2 and 7.0 ± 1.0 at Site 1 (GLM, $P < 0.01$; Annex III) (Table 3; Fig. 3; Annex II).

According to the PERMANOVA analysis, the "site" factor significantly affected the shifts between the two study sites ($P = 0.005$; Annex III). PCA conducted on abundances discriminated faunal composition

Table 4
Polychaeta families collected in the 0–1 cm layer at both sites. Abundance of each family is given for each core. Total abundance shows the number of specimens for each core. Total richness shows the number of families for each core. X gives the mean values ± standard deviation. Cores A, B, C from Site 2 (away from a pockmark field) correspond to cores 1, 2, 3, respectively, of the sampling campaign. Cores A, B, C from Site 1 (inside the pockmark) correspond to cores 9, 10, 11, respectively, of the sampling campaign.

POLYCHAETA FAMILY	SITE 2 MOZ01KGS01				SITE 1 (pockmark) MOZ01KGS03			
	A	B	C	X	A	B	C	X
Sigalionidae	1	0	1	0.67 ± 0.58	0	0	0	0.00
Syllidae	3	0	4	2.33 ± 2.08	1	0	0	0.33 ± 0.58
Flabelligeridae	1	0	0	0.33 ± 0.58	0	0	0	0.00
Spionidae	4	1	9	4.67 ± 4.04	6	12	6	8.00 ± 3.46
Sphaerodoridae	2	0	0	0.67 ± 1.15	0	0	0	0.00
Opheliidae	0	1	4	1.67 ± 2.08	0	0	0	0.00
Pilargidae	0	0	0	0.00	0	0	1	0.33 ± 0.58
Cossuridae	0	0	0	0.00	0	11	1	4.00 ± 6.08
Serpulidae	0	1	1	0.67 ± 0.58	0	0	0	0.00
Hesionidae	0	0	0	0.00	6	5	6	5.67 ± 0.58
Onuphidae	0	0	1	0.33 ± 0.58	0	0	0	0.00
Trichobranchidae	0	0	1	0.33 ± 0.58	0	0	0	0.00
Maldanidae	0	0	1	0.33 ± 0.58	0	0	0	0.00
Capitellidae	0	0	0	0.00	0	5	0	1.67 ± 2.89
Polynoidae	0	0	0	0.00	4	4	0	2.67 ± 2.31
Total abundance	11	3	22	12.00 ± 9.54	17	37	14	22.67 ± 12.50
Total density (ind/1m^2)	611	167	1222	667 ± 530	944	2056	778	1259 ± 695
Total richness	5	3	8	5.33 ± 2.52	4	5	4	4.33 ± 0.58

between the two sites. PC1 explained 54.7% of the variance and was mainly affected by the high abundance of Cumacea at Site 2, and those of Aplacophora and Nemertea affected Site 1 (Fig. 4).

3.3.3. Polychaeta community

In the first sediment layer, differences in abundance between the two sites were not statistically significant, with 12 ± 10 specimens per core at Site 2 and 23 ± 12 at Site 1 (GLM, $P > 0.05$; Annex III; Table 4; Fig. 6). The dominant family at both sites was Spionidae representing ca. 39% and 35% of the community at Sites 1 and 2, respectively (Table 4; Fig. 5). At Site 1, inside the active pockmark, Hesionidae and Cossuridae were also abundant (ca. 25% and 18% of the Polychaeta fauna, respectively), followed by Polynoidae and Capitellidae (ca. 12% and 7%). At Site 2, away from the pockmark field, Syllidae was the second most dominant family after Spionidae (ca. 19%) and its presence in Site 1 was restricted to a singleton (Table 4; Fig. 5). Abundance of the remaining families was extremely low (Fig. 5). Opheliidae were only present at Site 2 (ca. 14%) (Table 4; Fig. 5). Hesionidae, Cossuridae, Polynoidae, and Capitellidae were only found at Site 1. Analyses performed for each family only found statistically significant changes for the Hesionidae (GLM, $P < 0.001$; Annex III). Richness and diversity also had similar values at both sites (5.3 ± 2.5 families at Site 2 and 4.3 ± 0.6 families at Site 1, GLM, $P > 0.05$; Annex III; H′ 1.8 and 1.6; J′ 0.8 and 0.8, respectively) (Table 4; Fig. 6). PCA conducted on abundance revealed a strong discrimination in family composition between sites. PC1 explained 47.5% of the variance and was mostly affected by the high densities at Site 1 of Cossuridae, Hesionidae, Polynoidae; whereas the high abundance of Opheliidae characterized Site 2 (Fig. 4).

3.4. Metazoan meiofauna community

3.4.1. Intra-site

Total abundance along the vertical profile was higher at the second layer of the sediment (ca. 47% at both sites) (Table 2; Annex II). Nematoda were the dominant taxa in each layer (>78% of the community in all layers at Site 2, and >82% in all layers at Site 1), followed by Copepoda (Fig. 2). At Site 2, abundances strongly decreased from the third layer, comprising ca. 30% of the community, about three times higher than in the uppermost centimeter (Table 2, Annex II). All taxa abundances followed this pattern except for Polychaeta, which showed similar abundances down to the fourth layer (Fig. 2). Similar patterns were observed at Site 1, inside the active pockmark, although the decrease in abundance in the third sediment layer (2–3 cm) was even more drastic, from ca. 47% down to 16% (Table 2, Annex II). Kinorhyncha increased in the second layer at Site 1, from 1.3% to 3.6% at 1–2 cm depth (Fig. 2). Gradual changes in richness along the vertical profile were observed at Site 2, with the highest values in the upper layers (8 ± 3 and 8 ± 1 taxa, respectively), and the lowest values in the bottom layers (5.3 ± 1.2 and 1 ± 1 taxa, respectively). At Site 1, most of the richness was in the uppermost sediment layers (10 ± 4 and 8 ± 2), decreasing down to 3–4 cm depth (Table 2, Annex II).

3.4.2. Inter-sites

Meiofauna were more abundant at Site 1, with 6041 ± 3337 versus 2643 ± 381 specimens per core at Site 2 (GLM, $P < 0.01$; Annex III), whereas both sites were similar in terms of richness, with 12.0 ± 2.7 taxa at Site 1 and 9.7 ± 1.2 at Site 2 (GLM, $P < 0.05$; Annex III; Table 5, Annex II). This pattern of general meiofaunal abundance was observed for most of the studied taxonomic groups, except for Polychaeta, Tantulocarida, Tardigrada, Platyhelminthes, and Isopoda. The main dominant taxa in each site was Nematoda (ca. 87% at Site 1, 92% at Site 2), followed by Copepoda (ca. 6% and 5%). Kinorhyncha, which were almost absent at Site 2, ranked third in abundance at Site 1, representing up to 2.7% of the meiofauna (Table 5; Fig. 2). Other taxa were recovered in one or the other site in low numbers: Tantulocarida, Platyhelminthes, and Isopoda at Site 2; Amphipoda, Aplacophora, Cnidaria, Gastropoda, and Halacarida at Site 1 (Table 5; Fig. 2). Analyses of the three most abundant groups (greater than 5% of the total community at any one site), revealed statistical differences between the two sites for Nematoda and Kinorhyncha (GLM, $P < 0.01$ and $P < 0.01$ respectively; Annex III).

According to the PERMANOVA results, the “site” parameter had a significant effect ($P < 0.05$; Annex III). PCA visualizing the trends of the meiofauna community composition in terms of abundance discriminated between the two study sites due to PC1, which explained 57.4% of the variance and was mainly affected by the high densities of Kinorhyncha, followed by Nauplii at Site 1. PC2 explained 31% of the variance and was mostly affected by Copepoda and Kinorhyncha (Fig. 4).

3.4.3. Nematoda community

The abundance in the 0–1 cm layer was higher at Site 1 than at Site 2,

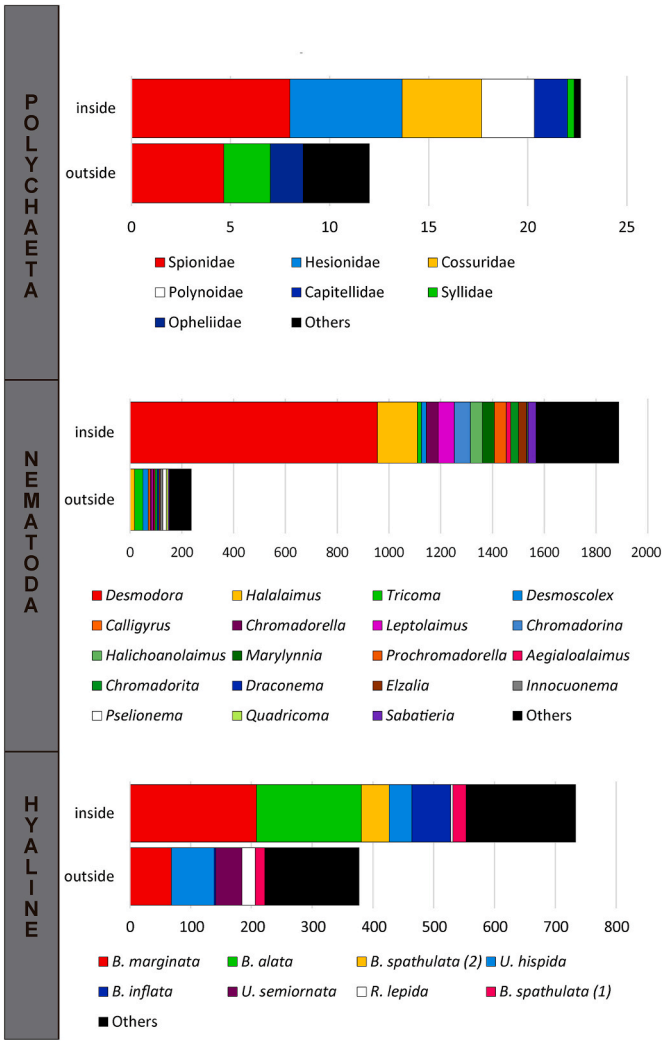

Fig. 5. Polychaeta, Nematoda and hyaline foraminifera community structure characterizing the uppermost sediment layer (0–1 cm) at the two study sites. Taxon contribution is expressed as mean of specimens (abundance of each Nematoda genus was estimated based on subsample data) (Y axis). The group 'others', in black, includes all taxa whose presence is limited to 1 or 2 Polychaeta specimens (Site 1: 1 family; Site 2: 7 families); less than 2% of total Nematoda community (Site 1: 23 genera; Site 2: 59 genera); and 4% of total foraminifera community (Site 1: 66 species; Site 2: 49 species).

with 1888 ± 1806 specimens per core and 236 ± 88 specimens per core, respectively, but the differences were only marginally significant (Table 6; Fig. 6). The most dominant taxa at Site 2 were *Tricoma* (ca. 14%), *Desmoscolex* (ca. 9%), *Halalaimus* (ca. 7%), and *Pselionema* (ca. 6%), whereas a single genus was dominant at Site 1, *Desmodora* (ca. 51% of the Nematoda community), followed by *Halalaimus* (ca. 8%) (Table 6; Fig. 5). The genera *Pselionema* and *Desmodora* were restricted to just one site, away from a pockmark field and inside an active pockmark, respectively. The remaining genera represented together ca. 74% and 41% of the Nematoda community at Site 2 and Site 1, respectively, but the contribution of each genus to total abundance was always less than 5%. Analysis on the most abundant genera (above 5% of the total community at any one site), only found statistically significant changes between the two sites for *Desmodora* and *Pselionema* (GLM, $P < 0.001$ and $P < 0.01$ respectively; Annex III). Moreover, Site 2 showed significantly higher genus richness and higher diversity than Site 1, with 40 ± 11 and 19 ± 17 genera, respectively (GLM, $P < 0.001$; Annex III; H′ 3.6 and 1.7; J′ 0.8 and 0.5, respectively) (Fig. 6; Table 6).

PCA conducted on abundance revealed a strong difference in Nematoda composition between the sites due to the abundance of *Tricoma* and *Pselionema* at Site 2 and the exclusive presence and high abundance of *Desmodora* at Site 1. *Desmodora* abundance strongly affected PC1, which explained 60.9% of the variance (Fig. 4).

3.5. Foraminifera community

3.5.1. Intra-sites

At both sites, the highest abundance along the vertical profile was found at the uppermost sediment layer, with 609 ± 9 specimens per core at Site 2, and 1325 ± 989 specimens at Site 1 (Table 2; Annex II, Fig. 2). At Site 2, the decrease in abundance from the surface to the deeper layers was steeper than at Site 1 (Table 2, Annex II). Similar patterns were observed for main foraminifera groups and hyaline and agglutinated foraminifera dominated in each layer regardless of site (Table 7).

3.5.2. Inter-sites

Changes in foraminifera abundance between sites were not significant, with means of 1956 ± 1059 and 839 ± 37 specimens per core at Site 1 and Site 2, respectively (Table 7; Annex II and III). Hyaline foraminifera were dominant at both sites, followed by agglutinated, porcelaneous and soft-shell foraminifera (Table 7, Fig. 2). The four main foraminifera groups were present at both sites and no significant changes were detected. Considering each group, richness was mostly due to the presence of hyaline foraminifera (42 ± 2.8 species at Site 2 vs. 50 ± 14.8 at Site 1) and agglutinated foraminifera (50.5 ± 4.9 vs. 37 ± 12.7), and the contributions were marginal for porcelaneous (ca. 13 ± 0.0 vs. 5.5 ± 2.1) and soft-shell taxa (ca. 3.0 ± 1.4 vs. 1.0 ± 0.0). At Site 1, the hyaline foraminifera dominated along with agglutinated foraminifera. Analysis performed on groups showed significant changes only in soft-shell foraminifera abundance between sites (Annex III).

PERMANOVA performed on the four foraminifera groups did not reveal any significant differences in the community structure of the two sites (Annex III). PCA did neither discriminate between the two sites (Fig. 4).

3.5.3. Hyaline community

Variations in abundance and richness in layer 0–1 cm were not significant between sites, with means of 736 ± 429 vs. 379 ± 44.5 specimens per core, and 49.5 ± 14.8 vs. 42 ± 2.8 species at Site 1 and Site 2 respectively (see Annex III; Fig. 6 and Table 8 for details). Site 1 showed slightly lower diversity than Site 2 (H′ 2.6 and 2.9; J′ 0.6 and 0.7, respectively). The species *Bulimina marginata* and *Uvigerina hispida* were abundant at both sites, but the dominance of *B. marginata* at Site 1 was not comparable to that of *U. hispida*: *B. marginata* ca. 28% of the community followed by *Bolivina alata* ca. 24%, *Bulimina inflata* ca. 9%, and *U. hispida* ca. 5% (208 ± 144, 173 ± 165, 63.5 ± 37.5, 37.5 ± 39, respectively) (see Table 8 and Fig. 5). Some species were relatively abundant at Site 1, but absent at Site 2, such as *B. alata* (ca. 24%), *Bolivina spathulata* (type 2) (ca. 6%) (173 ± 165 and 45.5 ± 19.1, respectively), and *B. inflata* ranking third in abundance at Site 1 (ca. 9%, 63.5 ± 37.5) and mostly absent at Site 2; *Uvigerina semiornata* was present as a singleton at Site 1 and in relatively high abundance at Site 2 (ca. 11%, 43.5 ± 0.7) (see Table 8 and Fig. 5). At the species level (above 5% of the total community at any one site), only changes in *U. semiornata*, *B. alata*, *B. spathulata* (type 2), and *B. inflata* were significant (see Annex III).

PCA conducted on abundances discriminated between the species composition of both sites due to PC1 (73.4% of the variance), which was strongly affected by the high abundances of *B. alata*, *B. spathulata* (type 2) and *B. inflata*, characterizing Site 1; *U. semiornata* and *U. hispida* characterized Site 2 (Fig. 4).

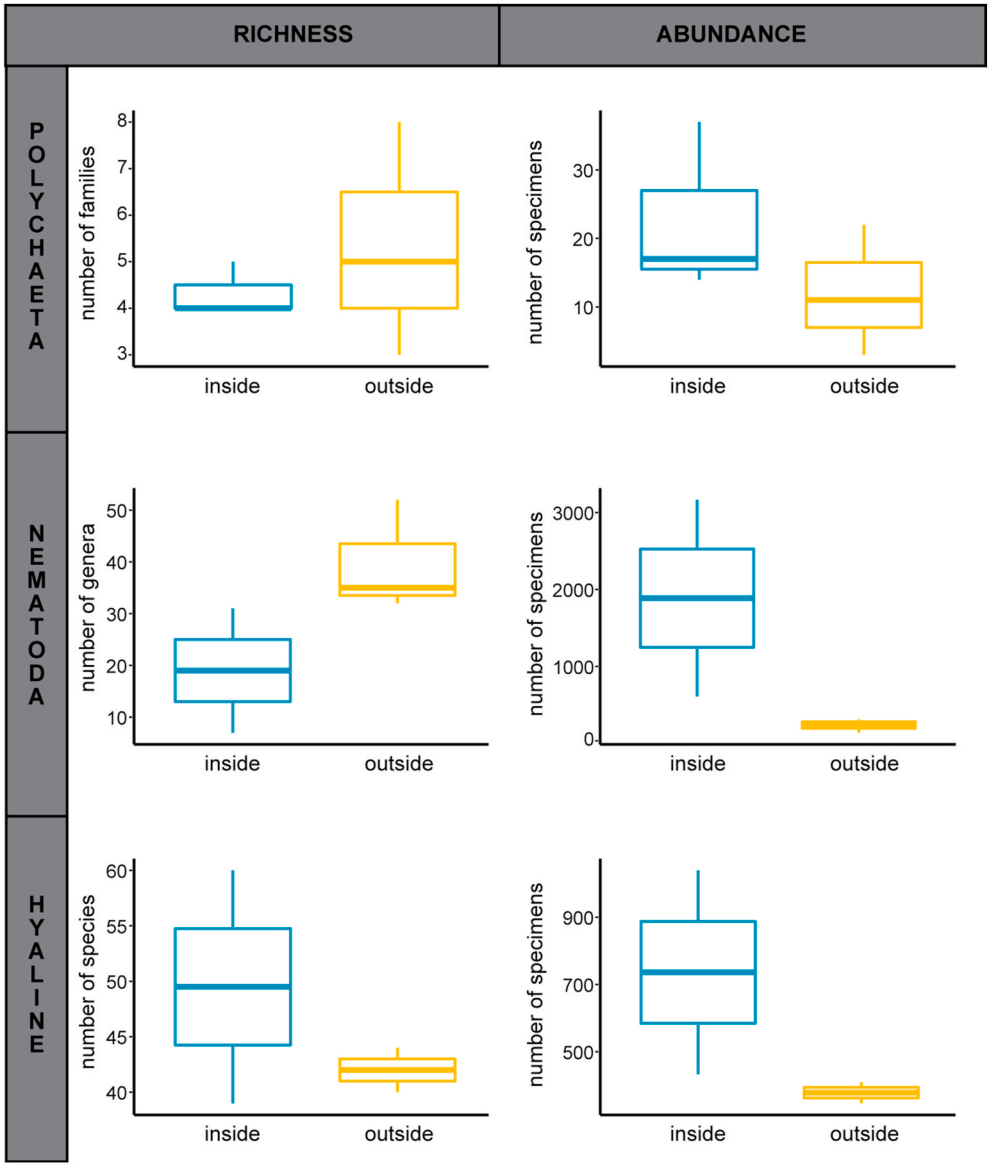

Fig. 6. Richness and abundance of Polychaeta, Nematoda and hyaline foraminifera at the two study sites, inside a pockmark (Site 1; blue) and away from a pockmark field (Site 2; yellow). Y-axes indicate values of richness (families, genera and species, respectively) and abundance (number of specimens) measures considering all the cores of each benthic component (sampling area for macrofauna: 0.018 m^2; sampling area for meiofauna: 30 cm^2). Boxplots represent the median value (horizontal line in the box), the distributions of 50% of the data (the box), and the highest and lowest values within 95% of the distribution (the whisker). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

4.1. Are macrofaunal, metazoan meiofaunal and foraminifera communities similarly affected by pockmark occurrence?

Our results pointed that the three benthic communities were influenced by the environmental conditions, namely low oxygen availability and reduced conditions mainly due to high organic matter contents. Derived biological and geochemical processes linked to the presence of methane in the subseafloor as inferred from gas escapes within the pockmark (visible in acoustic water column data) could also influence the repartition of communities. Nevertheless, macro- and meiofauna were affected in different ways.

In our study, macrofauna abundance was significantly lower at the active pockmark (Site 1) compared to the site out of seep influence, in contrast to the meiofauna and foraminifera. Although high macrofaunal densities have been reported in some pockmarks (Decker et al., 2012; Guillon et al., 2017; Levin et al., 1991, 2003, 2010; Menot et al., 2010; Ritt et al., 2010; Sahling et al., 2002), opposite density patterns between meiofauna and macrofauna have been already observed in cold-seep environments, attributed to the sulfide gradient and biotic interactions between these two faunal compartments (see section 4.3) (Van Gaever et al., 2009a). The low macrofauna abundances can be explained by the reduced oxygen availability, usually concomitant to high H_2S levels (Decker et al., 2012; Guillon et al., 2017; Levin et al., 1991, 2003, 2010; Menot et al., 2010; Ritt et al., 2010; Sahling et al., 2002). Also, the vertical profile of fauna abundance was affected by the low oxygen penetration, following general fauna distribution patterns also shown in other pockmarks (Jensen, 1986; Montagna et al., 1989; Powell et al., 1983; Ritt et al., 2011), where organisms were concentrated in the upper centimeters within the pockmark but were more equally distributed along the vertical profile at site out of seep influence. According to Pastor et al. (2020), Site 2 was never impacted by any methane outflow, while sediment at Site 1 present clear geochemical imprints of methane circulation. The meter-scale spatial heterogeneity of these particular areas, also evidenced by the Scampi video near-bottom surveys, most likely explain the very low CH_4 and the absence of H_2S in our samples within the pockmark. It is worth noting that the sampling, although in the close vicinity of gas emissions, are distant from them (i.e. c.a. 10 m for MOZ01MTB07, 30 m for MOZ01KGS03 and 50 m for MOZ01MTB06). The oxidation of methane through migration towards surficial sediment layers, eventually forms sulfur-bearing minerals such

Table 5
Total meiofauna taxa collected at both sites. Abundance of each taxonomic group is given for each core. Total abundance shows the number of specimens for each core. Total richness shows the number of taxonomic groups for each core. X gives the mean values ± standard deviation. Cores A, B, C from Site 2 (away from a pockmark field) and Site 1 (inside) the pockmark correspond to cores 1, 2, 3 of both sites, respectively, of the sampling campaign.

MEIOFAUNA TAXA	SITE 2 MOZ01MTB01				SITE 1 (pockmark) MOZ01MTB06			
	A	B	C	X	A	B	C	X
Amphipoda	0	0	0	0.00	4	3	1	2.7 ± 1.5
Aplacophora	0	0	0	0.00	4	3	8	5 ± 3
Bivalvia	0	0	1	0.3 ± 0.6	4	31	55	30 ± 26
Cnidaria	0	0	0	0.00	0	2	0	0.7 ± 1.2
Copepoda	122	127	162	137 ± 22	71	368	642	360 ± 286
Cumacea	0	0	2	0.7 ± 1.6	0	1	1	0.7 ± 0.6
Gastropoda	0	0	0	0.00	0	7	2	3.0 ± 3.6
Halacarida	0	0	0	0.00	0	0	1	0.3 ± 0.6
Isopoda	3	0	0	1.0 ± 1.7	0	0	0	0.00
Kinorhyncha	4	14	12	10.0 ± 5.3	115	64	315	165 ± 132
Nauplii	4	0	27	10 ± 14	9	188	228	142 ± 117
Nematoda	2028	2611	2668	2436 ± 354	2568	5116	8124	5269 ± 2781
Ostracoda	10	8	3	7.0 ± 3.6	2	24	53	26 ± 26
Platyhelminthes	0	4	0	1.3 ± 2.3	0	0	0	0
Polychaeta	31	38	27	32.0 ± 5.6	21	44	26	30 ± 12
Tanaidacea	4	1	1	2.0 ± 1.7	0	8	8	5.3 ± 4.6
Tantulocarida	0	1	1	0.7 ± 0.6	0	0	0	0
Tardigrada	1	1	13	5.0 ± 6.9	0	0	1	0.3 ± 0.6
Total abundance	2207	2805	2917	2643 ± 382	2798	5859	9465	6041 ± 3337
Total density (ind/10 cm^2)	731	929	966	875 ± 126	927	1941	3135	2001 ± 1105
Total richness	9	9	11	9.7 ± 1.2	9	13	14	12.0 ± 2.7

as pyrite (large amount of this sulfur-bearing minerals were detected at Site 1 according to Pastor et al., 2020) and the process is partially or totally mediated by anaerobic methanotrophic and sulfate-reducing bacteria (Boetius et al., 2000; Orphan et al., 2001). Bacterial communities form a major food source for meiofauna which in turn could explain their sizable densities in subsurface layers (Van Gaever et al., 2009a). On the other hand, the high input in labile organic matter in the uppermost sediment layer (Fontanier et al., 2016) could induce higher bacterial densities as well, which may explain the enhancement of meiofauna population at the surface layer. Moreover, the significant higher abundances of metazoan meiofauna in the pockmark indicated that at some sites, this benthic component could better cope with more extreme conditions (Ritt et al., 2010), likely through replacement with opportunistic specialized taxa that flourish in these environments (Vanreusel et al., 2010). The relatively high heterogeneity found in meiofauna abundance among cores at Site 1 can be a result of diffusive methane taking multiple exit pathways through the pockmark sediment even at the meter- scale corresponding to the area sampled by the multi-corer.

Richness of the three benthic components followed different patterns, and only macrofauna showed lower richness in the active pockmark, as usually reported for seep communities (Levin, 2005). Along the vertical profile, richness of the three components decreased more gradually away from the pockmark due to greater dissolved oxygen penetration and availability, whereas the decrease was more abrupt at Site 1 within the pockmark. Acoustic evidences of present-day methane outflows reported at this site may also explain the differences in richness patterns between the two sites. This idea comes from the fact that the hydrogen sulfide produced in methane oxidation is toxic for most metazoans (Bagarinao, 1992; Somero et al., 1989), and only well-adapted taxa can tolerate the presence of sulfide compounds, which is usually reflected in low richness (Dando et al., 1991; Diaz and Rosenberg, 1995; Levin, 2005; Levin et al., 2010; Menot et al., 2010; Pearson and Rosenberg, 1978; Sahling et al., 2002; Shirayama and Ohta, 1990; Vanreusel et al., 2010).

Regarding macrofauna, Site 1 was characterized by the presence of more tolerant taxa to the pockmark conditions, such as Nemertea, Aplacophora, and Bivalvia, as observed in several cold seeps in northern California, Gulf of Mexico, and New Zealand (Bergquist et al., 2003; Levin, 2000; Levin et al., 2003; Thurber et al., 2013). Other groups, such as Cumacea, Amphipoda, and Isopoda less tolerant to low oxygen availability disappeared inside the pockmark, as observed in other cold-seep sites (Guillon et al., 2017; Levin, 2003; Levin et al., 2010; Menot et al., 2010; Sandulli et al., 2015). The metazoan meiofauna at both sites followed common patterns of communities largely dominated by Nematoda and Copepoda (Giere, 2009; Higgins and Thiel, 1988; Lampadariou et al., 2013; Levin, 2005; Van Gaever et al., 2009a; Zeppilli et al., 2011, 2012, 2018), with Kinorhyncha ranking third in dominance inside the active pockmark (ca. 55 ind/10 cm^2), reaching densities never reported so far from any other deep-sea environment (Neuhaus, 2013). Hyaline and agglutinated foraminifera showed higher abundances inside the pockmark, likely indicating their preference for sediments rich in organic matter content (Fontanier et al., 2018). The picture emerging from these results agrees with the general idea of meiofauna in seepage environment well-adapted to live under these conditions (Bernhard and Sen Gupta, 1999; Duchemin et al., 2007; Duros et al., 2011; Eberwein and Mackensen, 2006; Fontanier et al., 2002, 2008, 2013, 2016; Langezaal et al., 2006; Licari et al., 2003; Vanreusel et al., 2010; Zeppilli et al., 2012).

Our results could also indicate past changes or disturbance events in the pockmark that may have altered the original community (Fontanier et al., 2018). Meiofaunal animals are indeed among the first and the main colonizers of ephemeral and unstable habitats due to their tiny size, rapid generation times, and fast metabolic rates that make them less vulnerable to disturbance than the macrofauna (Giere, 2009; Schratzberger and Ingels, 2018; Woodward, 2010). The presence of Kinorhyncha in high abundance (Cepeda et al., 2020) is another unusual feature to support this idea, because they are considered potential colonizers at other sulfidic settings, specifically at deep-sea vents after catastrophic eruptions (Mullineaux et al., 2012); or opportunists in mangrove forests (Ostmann et al., 2012).

4.2. Can the dominant taxa function as useful indicators of present and/or past seepage?

In deep-sea seeps, Polychaeta and Nematoda are generally the dominant macrofauna and metazoan meiofauna groups, respectively (Lampadariou et al., 2013; Levin, 2005; Menot et al., 2010; Van Gaever

Table 6
Nematoda genera collected in the 0–1 cm layer at both sites. Nematodes from subsamples were first identified and the final contribution of each genus to the total nematode abundance was then estimated (estimated values are shown as "ca."). Abundance of each genus is given for each core. Total abundance shows the number of specimens for each core. Total richness shows the number of genera for each core. X gives the mean values ± standard deviation. Cores A, B, C from Site 2 (away from a pockmark field) and Site 1 (inside) the pockmark correspond to cores 1, 2, 3 of both sites, respectively, of the sampling campaign.

NEMATODA GENUS	SITE 2 MOZ01MTB01				SITE 1 (pockmark) MOZ01MTB06		
	A	B	C	X	B	C	X
Actinonema	0	4	7	3.7 ± 3.5	0	0	0
Aegialoalaimus	4	11	0	5.00 ± 5.6	31	0	16 ± 22
Ammotheristus	0	2	3	1.7 ± 1.5	0	0	0
Araeolaimus	1	0	0	0.3 ± 0.6	31	0	16 ± 22
Amphimonhystrella	1	0	0	0.3 ± 0.6	31	0	16 ± 22
Calligyrus	10	9	7	8.7 ± 1.5	0	0	0
Chromadorella	10	2	0	4.0 ± 5.3	93	0	47 ± 66
Chromadorita	3	15	7	8.3 ± 6.1	62	0	31 ± 44
Chromadorina	0	2	0	0.7 ± 1.2	124	0	62 ± 88
Cyartonema	1	2	0	1.0 ± 1.0	0	6	3 ± 4
Cyatholaimus	0	0	3	1.0 ± 1.7	31	0	16 ± 22
Comesomoides	0	0	0	0	62	0	31 ± 44
Daptonema	1	6	0	2.3 ± 3.2	0	0	0
Desmodora	0	0	0	0	1334	576	955 ± 536
Desmodorella	6	2	3	3.7 ± 2.1	0	0	0
Desmoscolex	19	15	27	20 ± 6	31	6	19 ± 18
Diplopeltoides	0	4	3	2.3 ± 2.1	0	0	0
Diplopeltula	3	0	0	1.0 ± 1.7	0	0	0
Draconema	3	13	7	8 ± 5	0	0	0
Eleutherolaimus	1	2	0	1.0 ± 1.0	0	0	0
Elzalia	4	9	3	5.3 ± 3.2	62	0	31 ± 44
Endeolophos	0	4	0	1.3 ± 2.3	0	0	0
Gnomoxyala	0	2	0	0.7 ± 1.2	31	0	16 ± 22
Halalaimus	9	24	17	17 ± 8	310	0	155 ± 219
Halichoanolaimus	0	0	0	0.00	93	0	47 ± 66
Innocuonema	0	17	10	9.0 ± 8.5	0	6	3 ± 4
Linhystera	1	4	3	2.7 ± 1.5	0	0	0
Leptolaimus	3	9	7	6.3 ± 3.1	124	0	62 ± 88
Longicyatholaimus	1	4	0	1.7 ± 2.1	31	0	16 ± 22
Marylynnia	1	4	0	1.7 ± 2.1	93	0	47 ± 66
Metasphaerolaimus	0	0	3	1.0 ± 1.7	31	6	19 ± 18
Oxystomina	0	2	7	3.0 ± 3.6	0	0	0
Paracomesoma	1	4	3	2.7 ± 1.5	31	0	16 ± 22
Paracyatholaimus	0	2	3	1.7 ± 1.5	0	0	0
Paralongicyatholaimus	0	2	7	3.0 ± 3.6	0	0	0
Parachromadorita	0	6	0	2.0 ± 3.5	31	0	16 ± 22
Paramonohystera	0	2	0	0.7 ± 1.1	31	0	16 ± 22
Parodontophora	0	4	0	1.3 ± 2.3	0	0	0
Pierrickia	1	11	0	4 ± 6	62	0	31 ± 44
Prochromadorella	0	0	0	0.00	93	0	47 ± 66
Pseudodesmodora	4	2	3	3 ± 1	0	0	0
Pselionema	7	11	24	14 ± 9	0	0	0
Quadricoma	0	15	7	7 ± 8	0	6	3 ± 4
Richtersia	0	0	7	2 ± 4	0	0	0
Sabatieria	7	0	7	5 ± 4	62	0	31 ± 44
Spilophorella	1	2	0	1 ± 1	0	0	0
Thalassomonhystera	0	11	0	4 ± 6	62	0	31 ± 44
Terschellingia	1	2	0	1 ± 1	31	0	16 ± 22
Tricoma	16	37	45	33 ± 15	31	0	16 ± 22
Wieseria	0	2	3	1.7 ± 1.5	0	0	0
Undeterminated	0	0	7	2 ± 4	0	0	0
Total id. specimens	95	145	74	105 ± 36	102	104	103 ± 1
Total abundance	141	314	254	236 ± 88	3165	611	1888 ± 1806
Total density (ind/10cm^2)	47	104	84	78 ± 29	1048	202	625 ± 598
Total richness	35	52	32	39.67 ± 10.79	31	7	19 ± 16.97

Remaining taxa were recovered at one of the sites as singletons before estimations of the contribution of each genus to the total community. Singletons at Site 1: *Anoplostoma*, *Cobbia*, *Paralinhomoeus* and *Prochromadora*. Singletons at Site 2: *Achantolaimus*, *Antomicron*, *Apenodraconema*, *Amphimonhystera*, *Anticyathus*, *Bathyeurystomina*, *Belbolla*, *Bolbonema*, *Calyptronema*, *Campylaimus*, *Dasynemoides*, *Dichromadora*, *Graphonema*, *Greeffiella*, *Halomonhystera*, *Linhomoeus*, *Metadesmolaimus*, *Metalinhomoeus*, *Promonhystera*, *Retrotheristus*, *Southerniella*, *Scaptrella*, *Spiliphera*, *Synodontium* and *Theristus*.

Table 7
Total foraminifera taxa collected at both sites. Abundance of each main group and dominant species is given for each core. Total abundance shows the number of specimens for each core. Total richness shows the number of species for each core. X gives the mean values ± standard deviation. Cores A, B from Site 2 (away from a pockmark field) and site 1 (inside) the pockmark correspond to cores 1, 2 at both sites, respectively, of the sampling campaign.

FORAMINFERA TAXA	SITE 2 MOZ01MTB01			SITE 1 (pockmark) MOZ01MTB07		
	A	B	X	A	B	X
Hyaline	524	527	526 ± 2	758	1459	1109 ± 496
B. marginata	80	93	86 ± 9	139	371	255 ± 164
B. alata	0	0	0	252	520	386 ± 190
G. barbata	19	10	14 ± 6	1	1	1 ± 0
U. semiornata	51	54	53 ± 2	2	1	1.5 ± 0.71
Agglutinated	286	237	262 ± 35	434	1161	798 ± 514
H. bradyi	0	0	0	94	221	158 ± 90
N. compressa	0	0	0	157	372	265 ± 152
Porcelaneous	41	30	36 ± 8	11	72	42 ± 43
Soft shell	14	18	16 ± 3	4	12	8 ± 6
Total abundance	865	812	839 ± 37	1207	2704	1956 ± 1058
Total density (ind/10cm^2)	123.83	114.37	118 ± 5	170.00	380.85	275 ± 149
Total richness	80	114	97 ± 24	124	123	123.5 ± 0.7

et al., 2009a; Zeppilli et al., 2011, 2012, 2018). In this study, only Polychaeta and Nematoda in the uppermost sediment layer followed the general biodiversity patterns found at hypoxic, organically enriched environments, harboring low richness but high abundance (Diaz and Rosenberg, 1995; Pearson and Rosenberg, 1978). Nevertheless only the Nematoda trends proved to be significant and hence effects of the studied pockmark conditions were more evident in this community in the first centimeter of sediment, as considered for this comparison. Considering the whole core, differences in community composition are also significant for Polychaeta (K. Olu, unpubl. data).

According to our results, the conditions found in the pockmark likely prevented the survival of some macro- and meiofauna taxa. Within Polychaeta, only Opheliidae were absent in the studied active pockmark, although present in relatively high abundance at Site 2. This family does not seem to tolerate the environmental conditions that characterized the active pockmark area, as inferred from other studies at cold seeps (Guillon et al., 2017; Menot et al., 2010). Similarly, the Nematoda *Pselionema*, *Tricoma,* and *Desmoscolex* usually avoid reduced sediment (Portnova et al., 2014; Zeppilli et al., 2011). This can explain their relatively high densities only at the site away from pockmarks (Site 2), and their presence inside the studied active pockmark as singletons (Site 1). Regarding hyaline foraminifera, *U. semiornata* was the only-most abundant species in Site 2, but mostly absent in the pockmark, likely reflecting low tolerance to the environmental constraints.

Interestingly, at both studied sites there were several groups known as tolerant of sulfide and hypoxia, such as Spionidae and Syllidae Polychaeta, although not known to dominate polychaete communities at seeps (Gamenick et al., 1998; Guillon et al., 2017; Levin, 2005; Levin et al., 2003, 2006, Levin et al., 2013). Also, other taxa frequently associated with oxygen stress and sediment disturbance, such as the Nematoda genus *Sabatieria* (Garcia et al., 2007; Leduc et al., 2014; Schratzberger et al., 2009), were observed at both sites in low numbers. This fauna, together with the detection of sulfur-bearing minerals at deep layers (black sediment with high amount of pyrite in the pockmark, and detection of free H_2S in very low concentration away from another pockmark field), underline past and present sulfate reduction at both sites. This sulfide production is due to methane diffusion in the pockmark but also because of organoclastic organic matter mineralization without link to fluid or gas emission which is known to have never happened at Site 2 (Pastor et al., 2020).

Among the taxa well-adapted to hypoxia and the presence of sulfides (Fauchald and Jumars, 1979), four Polychaeta families were exclusive and relatively abundant in the active pockmark: Hesionidae (ca. 25%), Cossuridae (ca. 18%), Polynoidae (ca. 12%), and Capitellidae (ca. 7%). However, only the distribution of Hesionidae was statistically different between the two sites. These four families were often found in sediments enriched in H_2S, methane, organic matter, as well as in oxygen minimum zones, likely indicating tolerance to these hostile conditions (Grassle and Morse-Porteous, 1987; Levin et al., 2003; Menot et al., 2009, 2010; Sahling et al., 2002; Thurber et al., 2013). For instance, Cossuridae are usually abundant at seeps because they appear to feed on anaerobic methane-oxidizing microbes or sulfate-reducing bacteria (Levin et al., 2003; Menot et al., 2010); while Hesionidae, Capitellidae, and Polynoidae are considered opportunist taxa with specific adaptations to hypoxic conditions (Decker et al., 2012; Levin, 2003; Menot et al., 2009, 2010; Ritt et al., 2010). Among the hyaline foraminifera, only one species was absent in Site 2 but relatively abundant in the active pockmark site, *B. alata* (ca. 24%) (reported as well by Fontanier et al., 2016). Regarding the Nematoda community within the studied pockmark, the low genus diversity was attributed to the dominance of a single taxon, *Desmodora*. In fact, this genus was recovered only at this site, accounting for up to 51% of the Nematoda abundance. Comparable Nematoda community composition was reported by Van Gaever et al. (2009b) in cold seeps at the Gulf of Guinea, with low Nematoda richness in the area of seepage influence and with 70% of the abundance belonging to *Sabatieria mortenseni* and *Desmodora* sp. Conversely, surveys on the Mediterranean Sea have revealed higher values of Nematoda richness at pockmarks than at a reference station (Zeppilli et al., 2011), and without dominant taxa in sediments affected by strong gas emissions. Overall only the foraminifer *B. alata*, Hesionidae Polychaeta, and the Nematoda *Desmodora* are typically present in high numbers inside our investigated active pockmark but only *Desmodora* was the best representative of its community at this site.

Some *Desmodora* species were likely not only able to survive under such extreme conditions, but it benefited from pockmark habitat features. In fact, the general Nematoda body shape, long and thin, seems to be an advantage for living in these conditions (Lampadariou et al., 2013). Interestingly, there were epifaunal protists present on several, female specimens of *Desmodora* (16% of the genus abundance; see Annex IV). These protists were loricate ciliates attached along the body surface appearing with no more than four specimens per Nematoda individual. Curiously, similar, attached loricate ciliates were observed on a high number of Kinorhyncha from mangroves (Ostmann et al., 2012), another extreme environment characterized by the presence of dissolved free sulfides in which Kinorhyncha are relatively abundant, as in our study. The conditions generated by sulfides in pockmark and mangrove environments may reduce host fitness and promote epifaunal growth (Hauton et al., 2000; Wang and Chen, 2005). Alternatively, both organisms may draw a mutual advantage from this kind of association in extreme conditions (Baldrighi et al., 2020b).

Table 8
Hyaline foraminifer species collected in the 0–1 cm layer at both sites. See Fontanier et al. (2016) for detailed information on the reported data. Abundance of each species is given for each core. Total abundance shows the number of specimens for each core. Total richness shows the number of species for each core. X gives the mean values ± standard deviation. Cores A, B from Site 2 (away from a pockmark field) and Site 1 (inside) the pockmark correspond to cores 1, 2 at both sites, respectively, of the sampling campaign.

HYALINESPECIES	SITE 2 MOZ01MTB01			SITE 1 (pockmark) MOZ01MTB07		
	A	B	X	A	B	X
Bolivina alata	0	0	0	56	290	173 ± 165
Bolivina spathulata (type 1)	11	21	16 ± 7	18	25	22 ± 5
Bolivina spathulata (type 2)	0	0	0	32	59	46 ± 19
Bolivinita quadrilatera	1	1	1 ± 0	18	14	16 ± 3
Bulimina inflata	4	1	2.5 ± 2.1	90	37	64 ± 38
Bulimina marginata	62	75	69 ± 9	106	310	208 ± 144
Cassidulina laevigata var. carinata	5	5	5 ± 0	8	14	11 ± 4.24
Cibicides bradyi	8	5	6.5 ± 2.1	1	3	2 ± 1
Cibicidoides kullenbergi	8	0	4 ± 6	4	8	6 ± 3
Cibicidoides pachydermus/kullenbergi	4	9	6.5 ± 3.5	0	0	0
Cibicidoides ungerianus	3	9	6 ± 4.2	0	0	0
Hoeglundina elegans	9	16	13 ± 5	8	20	14 ± 8
Lenticulina sp.1	3	7	5 ± 3	1	1	1 ± 0
Lenticulina peregrina	0	1	0.5 ± 0.7	7	16	12 ± 6
Nuttallides rugosus	12	8	10 ± 3	3	5	4 ± 1
Pullenia sp.2	0	0	0	0	16	8 ± 11
Pullenia bulloides	2	1	1.5 ± 0.7	18	19	18.5 ± 0.7
Rotorbinella lepida	18	25	22 ± 5	1	6	3.5 ± 3.5
Siphogenerina columellaris subs. costulata	10	15	13 ± 4	4	1	2.5 ± 2.1
Siphonina reticulata	9	2	6 ± 5	0	0	0
Trifarina bradyi	7	12	9.5 ± 3.5	1	1	1 ± 0
Uvigerina hispida	46	94	70 ± 34	10	65	38 ± 39
Uvigerina semiornata	44	43	43.5 ± 0.7	0	1	0.5 ± 0.7
Total abundance*	347	410	379 ± 45	433	1039	736 ± 429
Total density (ind/10 cm^2)*	48.87	57.75	53 ± 6	60.99	146.34	104 ± 60
Total richness*	40	44	42 ± 3	39	60	50 ± 15

Remaining taxa represent less than 1% of the total hyaline community at both sites. Total abundance, total density, and total richness include all the taxa observed in the samples.

4.3. Inter-community comparison: spatial segregation of benthic components

Different benthic size components, such as meiofauna and macrofauna, are usually investigated independently even though they are part of the same system in which each component is interconnected. Macro- and meiofauna are biologically linked because several individuals found in the metazoan meiofauna realm are macrofaunal juveniles, the so-called “temporary meiofauna” (Giere, 2009; Higgins and Thiel, 1988). Definitions of macro- and metazoan meiofauna are based on size, specifically on sieve mesh size (Giere, 2009; Higgins and Thiel, 1988; Somerfield and Warwick, 2013), ignoring important ecological traits, as the fact that metazoan meiofauna links macro- and microbenthos. The current definition for separating both communities, albeit short, is supported by recent studies that found macro- and metazoan meiofauna as discrete ecological entities (Somerfield et al., 2018).

Our results showed opposite macro- and meiofauna abundance patterns. The study of the benthic fauna along the vertical profiles showed the macrofauna mostly inhabited the uppermost sediment layer (0–1 cm depth) and the metazoan meiofauna was more concentrated at the subsurface layer (1–2 cm depth). Competition for food and other biological interactions (predation) could explain this spatial separation (Van Gaever et al., 2009a). An alternative explanation is that meiofauna, or at least some taxa, are better adapted than macrofauna to the environmental conditions at the subsurface layers, such as high reduced compound concentrations and lower oxygen availability. For instance, as already observed by Fontanier et al. (2016), the high number of foraminifera inside the pockmark was mainly due to *Haplophragmoides bradyi*, *Nouria compressa,* and buliminids, well-adapted taxa to eutrophic environments (Bernhard and Sen Gupta, 1999; Duchemin et al., 2007; Duros et al., 2011, 2013; 2013; Eberwein and Mackensen, 2006; Fontanier et al., 2002, 2008, 2013; Langezaal et al., 2006; Licari et al., 2003). Hence, under the stressful conditions of the pockmark area, macrofauna are less common and restricted to the well-oxygenated surface sediment layer, whereas metazoan meiofauna and foraminifera exploit this niche, increasing recruitment. Moreover and regarding the low methane emissions in the pockmark, the meiofaunal organisms inhabiting there might be able to survive in the pockmark for a while, preserving the community until the next fluid emission occurs.

Finally, the original meiofauna community may also have been affected by disturbance events in the pockmark, i.e. an increase of sedimentation from terrestrial origin (Fontanier et al., 2018), altering density and composition. Meiofaunal animals are among the first and the main colonizers of ephemeral and unstable habitats, because their biological features make them less vulnerable to disturbance than macrofauna (Giere, 2009; Schratzberger and Ingels, 2018; Woodward, 2010). Accordingly, we observed elevated Kinorhyncha density (discussed above, see section 5.1) and the presence of some Nematoda genera, such as *Sabatieria*, often recovered at disturbed sediments (Garcia et al., 2007; Leduc et al., 2014; Schratzberger et al., 2009). Similarly, the relatively higher abundance inside the pockmark of the foram *B. marginata* suggested a recent disturbance event, because it generally appeared in unstable and ephemeral cold seeps acting as pioneer species (Fontanier et al., 2014a, 2014b, 2016; Hess et al., 2005; Hess and Jorissen, 2009).

5. Conclusions

The present study investigated the distribution and diversity of benthic communities from a pockmark environment by using a threefold approach and the effect of environmental conditions on different infauna components. Despite the reduced number of sampling sites, we could make the following conclusions with caution in data interpretation:

1) At the studied active pockmark, macro-, metazoan meiofauna and foraminiferans showed differences in their taxonomic composition compared to fauna found at a site located away from another pockmark field. Macrofauna showed lower abundance and lower diversity with dominance of well-adapted taxa, while the higher meiofaunal abundances reflected the presence of taxa able to take advantage of the environmental constraints. Environmental features that characterized the two study sites likely played a key role in determining the variation of infauna at both sites and along the vertical profile in terms of number of taxa, abundance and community composition, possibly due to geochemical and biological conditions induced by organic matter degradation and oxidation of methane process along with lower oxygen availability in the pockmark.

2) Macrofauna were more abundant in layers harboring low metazoan meiofaunal densities (0–1 cm depth), that corresponded to well-oxygenated layers. Differently, specific meiofaunal taxa can tolerate low oxygen levels and seems more competitive under these conditions.

3) Considering the dominant taxa, Polychaeta and Nematoda followed the general trends usually reported in extreme environments, with low diversity and high abundance. In the active pockmark, Polychaeta were characterized by a dominance of families adapted to sulfide-rich and oxygen-depleted environments. High abundance of the foraminifer *Bulimina marginata* was also indicative of a disturbance event, associated with either methane flux or organic matter inputs. Similarly, most of the Nematoda abundance was due to *Desmodora*. Thus, the *Desmodora* genus could then be a potential benthic candidate indicator of stressed environmental conditions related to fluid emissions, but further studies at the area testing this are needed.

4) The detection of dissolved free sulfide in low concentrations away from the pockmark area, along with the presence of some organisms able to tolerate sulfide-rich and/or hypoxic conditions indicate that this off-site may be an ecotone in which the sulfide concentrations are not selective for most of the heterotrophic organisms, allowing their co-occurrence with fauna associated with reduced environments.

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Author contribution

KO and SD conceived and designed the sampling strategy; NS wrote the first draft of the manuscript, analyzed the data; KO, AV and DZ conceived the analytical methods for macrofauna and meiofauna respectively; EB identified the Nematoda specimens; MGL processed the macrofauna data; LM processed meiofauna on board; CB and LP provided geochemical data; SD was involved in the water column acoustic data acquisition, processing and interpretation; GG helped with the data analyses; all authors helped revise the manuscript, and read and approved the revised version.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2020.103425.

ANNEXES

Annex I. Depth profiles of oxygen (O_2), methane (CH_4), organic carbon (OC), total sulfur (S) and hydrogen sulfide (H_2S) content at the two study sites.

Annex II. Richness and abundance values of macrofaunal, metazoan meiofaunal and foraminifera communities along the vertical profile at both sites (Site 1 and Site 2, inside a pockmark and away from a pockmark field, respectively). Columns represent median values and whiskers illustrate the highest and lowest values within 95% of the distribution. Changes in total sulfur and dissolved oxygen concentrations along the vertical profile are illustrated in red and green, respectively. Concentrations of total sulfur and dissolved oxygen are expressed in μmol/L.

Annex III. Results of the inter-site statistical analyses for the macrofaunal, meiofaunal and foraminifera communities. P-value < 0.05 in the GLMs indicates that the factor "site" has effect on the response variables (richness and abundance of macro-, meiofauna, and foraminifera, abundance of taxonomic groups, as well as for their dominant taxa, Polychaeta, Nematoda, and hyaline foraminifers) (P, p-value; S, t-value and z-value reported by the 'glm', 'lmer' and 'glmer' functions; E, estimate). PERMANOVA shows differences in community composition inside and away from a pockmark field (Site 1 and Site 2) when p-value < 0.05 (differences are analyzed in terms of abundance of macro-, meiofauna and foraminifera, as well as for their dominant taxa, Polychaeta, Nematoda, and hyaline foraminifers) (P, p-value; F, F-model; R^2, explained variance). Results statistically significant are highlighted in bold.

Annex IV. Differential interference contrast photograph of epifaunal protists on a Desmodora specimen (Nematoda).

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