Table 7
Quantitative data expressed as total number of individuals (N), specimens of Agglutinated (Aggl.), Porcelaneous (Por) and Hyaline (Hyal) taxa, counted on the *P. oceanica* samples. Foraminiferal density is expressed as number of individuals recorded on rhizomes and leaves analyzed (F/P ratio). Foraminiferal diversity expressed as number of taxa (S), Shannon (H).

Sites	Samples	Leaves						Rhizomes						F/P	Sediments						
		N	S	H	Aggl	Por	Hyal	N	S	H	Aggl	Por	Hyal		Samples	N	S	H	Aggl	Por	Hyal
M2	P2	298	24	2.78	0	4	294	78	12	1.37	0	22	56	309	S8	39	11	1.67	0	26	13
M2	P3	94	9	1.91	0	0	94	40	7	1.07	0	1	39	99	S9	7	6	1.75	0	3	4
M1	P1	178	16	2.33	0	5	173	65	13	1.64	0	10	55	187	S2	14	8	1.97	0	6	8
Edge Intermatte	P4	178	42	2.93	1	5	173	302	10	1.65	5	88	214	327	G4	56	23	2.71	13	5	38

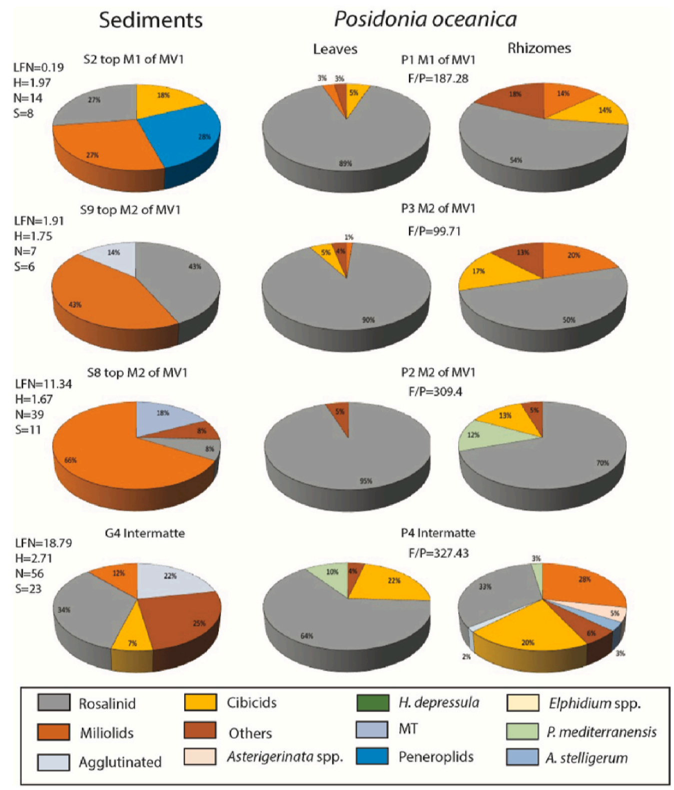

Fig. 8. Pie diagrams showing living foraminiferal assemblage recorded within sediments, leaves and rhizomes at the different study sites. The most abundant taxa are reported in the legend. Sediment samples collected at or as close as possible to the *Posidonia* samples are reported. (FN = density expressed as Foraminiferal Number in the sediment samples; H= Shannon index; N = number of total specimens; S = number of taxa; F/P = density expressed as total number of specimens recorded in leaves and rhizomes).

respectively. Among these, *G. praegeri* (mean abundance 13.82%) prevails in the former, occurring in most samples except for G13, S10 and S11 where it is replaced by *Rosalina* spp. *Posidonia* assemblages (P1-P3) are dominated by rosalinids too (Fig. 8). It should be noted that these typical shallow water taxa are associated with high percentages of *Bolivina* spp. These taxa are most common in the muddy sediments at the top of M2 (MV1: S8, S10-S13), with values ranging from 14.92% up to 37.88% (Fig. 10) and at the edge of M1 (18.22%, MV1: G9). Sometimes (G9, S12, S13) they are associated with frequent *Haynesina depressula* and very small specimens of *G. praegeri*. Shannon index (H) values range from 1.67 to 3.22, however it should be highlighted that the low values (<2) are recorded where the number of living specimens is minimum (Table 6).

(iv) Intermatte areas or morphological highs on the EPR flank (G3, G4, G5, G6, P4) - The samples retrieved from the intermatte zones and on the EPR flank (G3-G6) have faunal density (FN) values ranging from 0.50 to 19.13 ind/g for the living assemblage and between 0.26 and 68.79 ind/g for the dead one (Fig. 11). Except for G3, the dead assemblage clearly prevails over the living one in all samples. The H-index in both assemblages are very similar, with mean values of about 2. In the dead assemblage, the agglutinated taxa are characterized by carbonate cement (Textularia bocki) and a random occurrence, with maximum levels in sample G6 (4%). The porcelaneous group is well represented with values ranging from 20.20 to 33.33% (Table 5). Hyaline taxa show abundance percentages from 66.67 to 78.33%. Rosalinids and Lobatula lobatula are the dominant species followed by

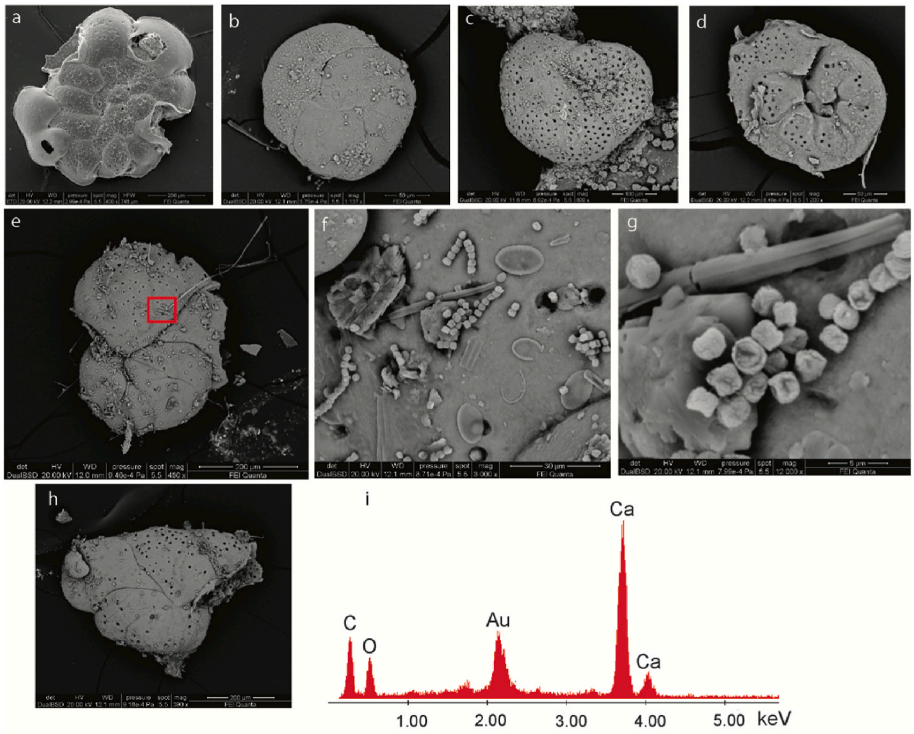

Fig. 9. SEM images of some species from *P. oceanica* samples. a) *Planorbulina mediterranensis* (P3 sample); b) *Neoconorbina posidonicola* (P1 sample); c) *Rosalina bradyi* surface view (P3 sample); d) *R. bradyi* apertural view (P3 sample); e-i) *Lobatula lobatula* (P3 sample): e) the red square shows calcite minerals; f-g) details of calcite minerals developed on the test surface; i) spectrum resulted from EDS analysis of the calcite minerals. All specimens show morphological variations, mainly in pore size and distribution; cracks and fractures affecting the chambers are also visible.

Asterigerinata spp., Planorbulina mediterranensis and Elphidium spp.

The living assemblage is characterized by more frequent and diversified agglutinated taxa (23.21–60%) with respect to the dead one, however they are totally absent in G6 (Table 6). The most representative species, like *Ammodiscus planorbis*, *L. ochracea* and *Ammoglobigerina globigeriniformis,* lack carbonate cement (Fig. 12). The porcelaneous taxa are scarcely represented with levels ranging from 8.93 to 15.38%, except for sample G3 where they are totally absent. *Quinqueloculina* and *Triloculina* are the most representative genera. The hyaline taxa are the most abundant (40–84.62%) (Table 6). Among these, rosalinids (*Rosalina* spp. and *G. praegeri*) is the only dominant group.

The *Posidonia* sample (P4) records the highest values in F/P ratio and biodiversity (H-index, Table 7).

5. Discussion

5.1. Response of foraminiferal assemblages to CH4 emissions

The analysis conducted at sites exposed to different degrees of CH_4 emissions around Scoglio d'Affrica allows us to make some considerations regarding the impact of this gas on the distribution, faunal density and biodiversity of foraminiferal assemblages. It is worth noting that while in deep-sea venting settings the environmental conditions are typically more homogeneous and support assemblages that are poorly diversified and mainly constituted by infaunal low-oxygen taxa (Rathburn et al., 2000; Panieri, 2003; Yanko et al., 2023), in shallow waters the higher partitioning of the microhabitats makes it more difficult to define a pattern of biota response and to identify seep-specialist taxa. Moreover, different from deep water seeps, shallow-water venting environments are also influenced by the input of photosynthetic carbon due to the presence of vegetal cover (Levin, 2005), leading to assemblages that are formed by the mixing of typical oxic, sandy, shallow-waters taxa with muddy, low-oxygen-tolerant taxa (MT).

Other aspects to be considered are the time of exposure of the benthic microfauna to the emissions and the seep intensity, factors linked to the temporal variability of the venting activity (Geistdoerfer et al., 1995; Shank et al., 1998). The resilience and recolonization capability of each species following environmental changes, however, can significantly determine the observed microfaunal distribution. In our case, the presence of methane emissions in the area has been known for at least 60 years, suggesting a relatively long-lasting impact on the seabed, although the intensity of emissions and their spatial distribution can vary over short time scales (annually or monthly). This may explain the wide variability of assemblages (composition, density and diversity) highlighted in this study. Moreover, the presence of typical morphological (mud volcanoes, pockmarks, gryphons and mud flows) and sedimentological (muddy sediments) fluid seepage indicators, along with widespread bacterial mattes and authigenic Mg-rich carbonate crusts, testifies to a consolidated, long-term venting activity.

Our data show that the processes linked to the methane emissions exert a strong influence on the characteristics of foraminiferal assemblages. Indeed, the emission of mud breccia mainly associated with mud eruptions (mudflows or violent gas outbursts like the 2017 event), as well as the formation of small gryphons produced by sustained emissions, represent very anomalous conditions for shallow-water benthic foraminiferal communities that are mainly adapted to a sandy substrate with an epifaunal style of life. It is possible that the mud leakage represents an additional stressor in addition to that due to methane emissions. However, our data do not allow us to distinguish whether the effect of CH_4 seepage is more or less influential than the mud emplacement. The impacts of these two stressing factors are highly variable at a small spatial scale, resulting in a complex interplay between local abiotic and biotic factors.

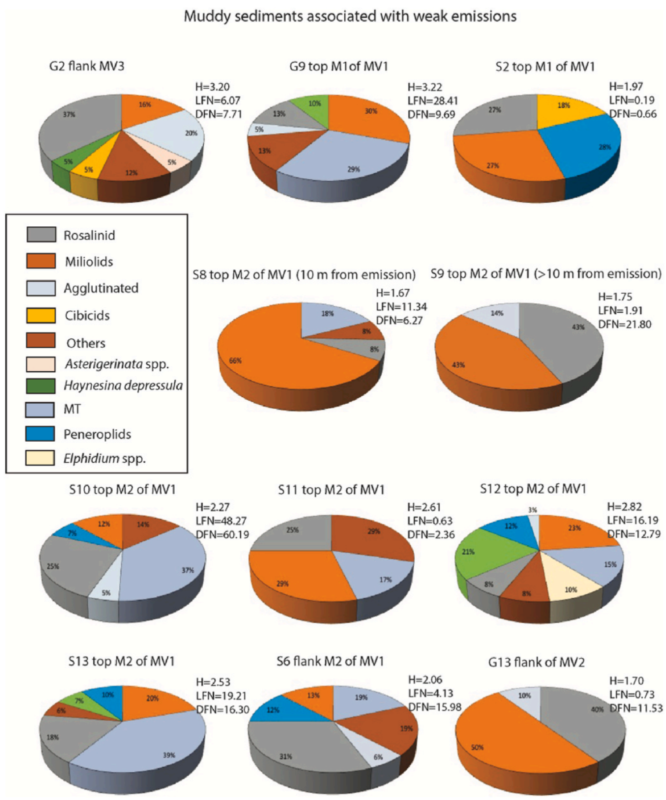

Fig. 10. Pie diagrams showing the living foraminiferal compositions in muddy sediment samples collected near weak emissions (Living foraminiferal density = LFN; Dead foraminiferal density = DFN; H= Shannon index; MT = muddy preference taxa).

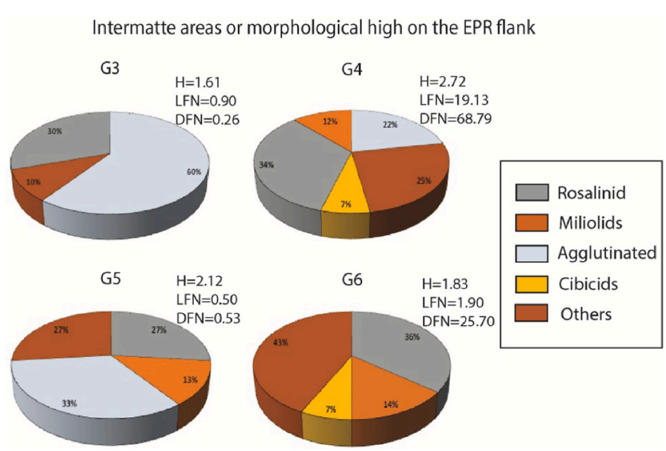

Fig. 11. Pie diagrams showing the living foraminiferal compositions in the sediment samples collected in the intermatte areas (Living foraminiferal density = LFN; Dead foraminiferal density = DFN; H= Shannon index).

Considering the morphological characteristics of the seafloor, linked to different degrees of venting activity, we can detect 5 different distribution patterns on and off the mud volcanoes.

(i) *Areas with strong emission activity at the top of the MV, locally associated with gryphons and mud flows* – These are commonly characterized by fluffy muddy sediments on which the development of foraminiferal communities is strongly inhibited. Similar to other organisms (Levin, 2005), the direct exposition to methane and/or mud leakage may not be conducive for colonization by propagules (very small individuals <32 μm, in a resting stage), thus hindering the start of biomineralization and/or agglutination processes (Alve and Goldstein, 2010) both on and inside the seafloor. Moreover, the presence of abundant fragments of authigenic carbonate crusts suggest probable hostile conditions for foraminiferal life. Indeed, the precipitation of authigenic carbonates observed in these areas is favored by methane oxidation presumably coupled to sulphate reduction at the water/sediment interface. This process can potentially result in extremely high concentrations of hydrogen sulphide, release of CO_2, decrease of pH and severe depletion or absence of O_2 immediately below and at the sediment/water interface (Gupta et al., 1997; Levin, 2005; Kravchishina et al., 2021).

(ii) *Mud flows along the mud volcano flanks* – The anomalous absence of foraminiferal content along the flank of MV1, where emissions are not actually recorded, should be highlighted. A possible explanation for this observation is that overlapping mudflows may create strong anoxic microhabitats that inhibit foraminiferal colonization and development. In this case, the absence of life is probably due to the impact of the mudflows on the sea bottom rather than the methane emissions.

(iii) *Muddy sediments associated with weak emissions* – In some locations, weak emissions are recorded on sandy muddy sediments or among sparse blocks, with intermittent bubbling not associated with any particular morphological structure.

In this environmental setting, microfauna presents different living/dead ratios depending on the time of colonization by each species. In more detail, the samples characterized by a greater living than dead assemblage (G9, S8, S12, S13) indicate a new phase of colonization, whereas where the dead content dominates the colonization was already under way thus reflecting more normal marine conditions (G13, S2, S6, S9-S11). In both cases, living and dead assemblages are characterized by the presence of infaunal muddy preference taxa, like bolivinids, that are well adapted to scarcely oxygenated bottoms (Gupta and Machain-Castillo, 1993; Bernhard et al., 1997; Bernhard and Sen Gupta, 1999). At the species level, *Bolivina variabilis* (probably corresponding to the Norvegian *B. pseudopunctata*, Alve and Goldstein, 2010) and *B. pseudoplicata* show a better adaptation to seep environments, similar to deep water conditions, thus confirming their opportunistic behavior (Armynot du Châtelet et al., 2011; Jorissen et al., 2018; Bouchet et al., 2021). These species have been observed in European oxygen-depleted bottom waters from the Mediterranean to the Norwegian Sea (Murray, 2006), like in deep Norwegian fjords (Kuhnt et al., 2007; Alve and Goldstein, 2010; Schmiedl et al., 2003). These species are the only ones we find in our study that also occur in a deep environment (Rathburn et al., 2000; Yanko et al., 2023). Their infaunal way of life (including their tolerance to low oxygen and organic-matter-rich environments) probably favors their adaptation to seep conditions. In samples S11, S12, S13 and G9, bolivinids are sometimes associated with high levels of *H. depressula,* infaunal taxon tolerant to high organic carbon concentrations and that likely feed on bacterial mats (Murray, 2006; Panieri, 2006; Armynot du Châtelet et al., 2011). Amongst the miliolids, *Quinqueloculina stelligera* seems to be the species that is most tolerant to the emissions, although experimental data show this species to be sensitive to long-lasting anoxia in the presence of hydrogen sulfide (Langlet et al., 2014). Its occurrence in fine sediments agrees with data coming from the Tyrrhenian Sea (Celia Magno et al., 2012; Mendes et al., 2012), while controversial behavior of this species is reported in the presence of environmental stressors like pollution, organic carbon or anoxia (Romano et al., 2009; Buosi et al., 2012; Langlet et al., 2014; Sreenivasulu et al., 2019). Amongst the rosalinids, *G. preageri* and *R. bradyi* are the species that are more tolerant to stressing conditions. They are two epifaunal taxa which can live on a wide range of sediment types and depths. In particular, the former may be recovered from inner shelf to deep basin waters (Sgarrella and Montcharmont-Zei, 1993; de Stigter

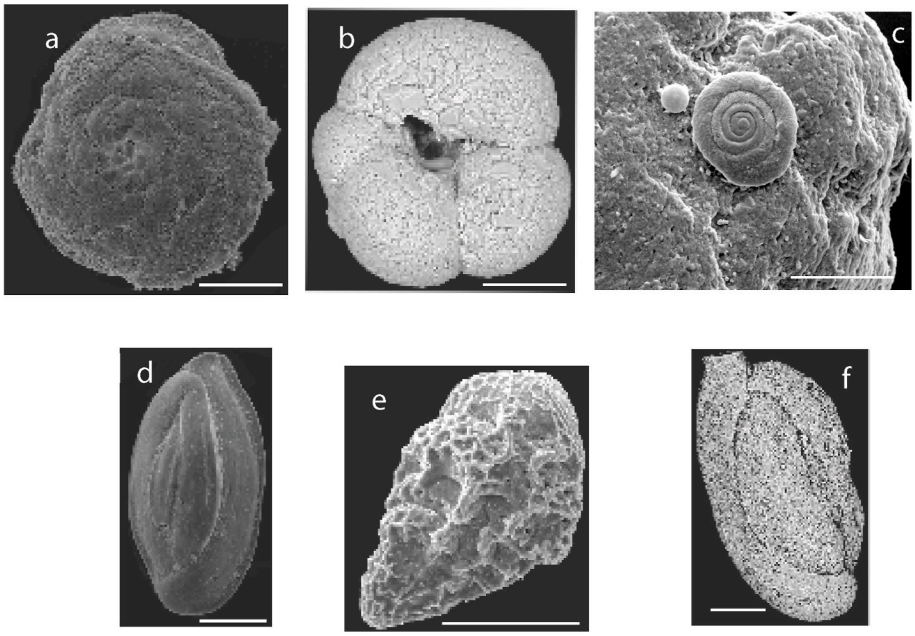

Fig. 12. *SEM images of some foraminiferal specimens recorded in the samples from the intermatte areas or morphological highs on the EPR flank*: a) *Lepidodeuterammina ochracea* side view (sample G3); b) *Ammoglobigerina globigeriniformis* apertural view (G4 sample); c) *Ammodiscus planorbis* side view (sample G4); d) *Quinqueloculina stelligera* side view (sample S8); e) *Bolivina pseudoplicata* side view (sample S10); f) *Siphonaperta aspera* side view (sample G9). The bar corresponds to100 μm.

et al.,1996; Murray, 2006; Bergamin et al., 2018) whereas *R. bradyi* has exhibited a high tolerance to natural and anthropogenic stressors (from in situ and laboratory experiments), showing a greater adaptability to future warming (Damak et al., 2020), high euthrophic environments (Romano et al., 2021), pH fluctuations (Ramajo et al., 2019) or other extreme environments (Lei et al., 2015).

(iv) *Intermatte zones associated with bioclastic sediments without emissions*– (G3-G6). These samples are located outside of the active MV and are not presently affected by methane emissions. The absence of muddy sediments suggests no recent leakage of mud and presumably no methane emissions. The ratio of dead and living assemblages reflect normal marine conditions with the dominance of dead taxa and the absence of muddy preference taxa. In this case, it is reasonable think that higher values of dead association are due to the sum of many generations while the living assemblage represents only the time of sampling (linked to patchiness and seasonality) (Murray, 1991). Only one sample (G3) shows microfaunal features that are more similar to that recorded in samples collected in the areas with weak emissions. From a compositional point of view, the assemblages of these samples (included G3) are characterized by typical shallow water taxa belonging to cibicids, rosalinids and miliolids, indicative of well-oxygenated conditions and high hydrodynamism.

(v) *Posidonia rhizomes and leaves* - The distinction between leaves and/or rhizomes microhabitats allows us to speculate not only on the microhabitat preference of foraminifers at the species level but to also highlight their functional aspect. The intermatte area and its edges (P4) can be considered as being representative of normal marine conditions, recording healthy leaves and high epiphytic diversity and density for the whole rhizomes and leaves, similar to that observed on the surrounding sediments (G4). However, it is to note that density and diversity recorded in intermatte area and its edges (P4) are lower than those recorded in other Mediterranean Posidonia meadows not affected by venting activity (Langer, 1993; Mateu-Vicens et al., 2014 and referein). This may be due to a possible indirect influence of the emissions. The decrease in density and diversity recorded in the rhizomes coming from the emission areas (P1-P3) indicate a negative impact probably due to the vicinity of fluid leakage. A comparison between leaves, rhizome and sediment assemblages show similar patterns (Table 7, Fig. 8). The leaf assemblages are more abundant and diversified, testifying that this elevated microhabitat provides better life conditions than the rhizomes and sediments. Different from other venting activity areas, where rhizomes can act as "refugia", in this case leaves can offer "elevated" substrates (e.g., Linke et al., 1993; Schönfeld, 1997; Schönfeld, 2002) on which suspension feeders can better exploit nutrients in the surrounding water mass, a greater degree of oxygenation and probably a better advantage of the *Posidonia* buffer effect (Langer, 1993; Baruffo et al., 2021; Buosi et al., 2012; Di Bella et al., 2022). Very little is known about the relationship between methane and its effect on *Posidonia* productivity. Although our results do not highlight a clear relationship between emissions and epiphytic assemblages, it is possible that *P. oceanica* meadows have an indirect buffer effect in the presence of CH_4 emissions, like that demonstrated for CO_2 emissions both in situ and during laboratory experiments (Vizzini et al., 2010; Ramajo et al., 2019; Di Bella et al., 2022; Capó-Baucà et al., 2023). The slightly more depleted isotope values obtained from the *P. oceanica* samples near the emissions may be due to its capability to sequester CO_2 by mean of photosynthesis. Although CO_2 concentrations in the gas bubbles are relatively low (Table 3), values may increase in the dissolved phase due to methane oxidization process favored by the well-oxygenated water characterizing the study site. Moreover, the methane stored inside the first centimeters of seafloor could be oxidized by the microbial activity, or enhanced respiration could take place in the nutrient-rich muds, thus increasing the CO_2 concentrations in the sediments where *Posidonia* have their roots (Knittel and Boetius, 2009; Herguera et al., 2014; Li et al., 2021). From a compositional point of view, the increase of rosalinids in both microhabitats (leaves and rhizomes) of *P. oceanica* samples near the emissions confirms their opportunistic behavior to the detriment of miliolids. Although in normal conditions miliolids are considered opportunistic taxa well-adapted to stressful conditions (Langer, 1993; Mateu-Vicens et al., 2014 and referein), the low frequencies recorded in this site can be due to the high Mg-calcite test composition that make them more susceptible to dissolution in acidic conditions (Dias et al., 2010; De Nooijer et al., 2009). This result appears to be confirmed by data obtained from other venting sites like Aeolian Archipelago (Di Bella et al., 2022).

Impact on biomineralization processes and morphological abnormalities - Evident morphological abnormalities with reduced biomineralization is observed in the foraminifer' tests, both in sediments and *P. oceanica* samples. This is very similar to the poor state of shell preservation recorded at sites with strong CO_2 emissions that lower the pH and acidify the waters. Studies from in situ observations and experimental data indicate critical threshold pH values around 7.8 and 7.6 that limit the building of carbonate tests (Dias et al., 2010; Pettit et al., 2013). Di Bella et al. (2022) report similar test fragility at pH values ranging between 7 and 8, in foraminifera from sites off Panarea Island (Eolian Archipelago). In our case-study, although the CO_2 content in the bubbling gas is low (Table 3) it may be sufficient to decrease pH values and inhibit test calcification. This mechanism may justify the poor preservation state of the tests. Moreover, some morphological abnormalities, like increased pore size and their inhomogeneous distribution on the dorsal surface observed on some recovered epifaunal specimens (*L. lobatula, P. mediterranensis, R. bradyi*), may represent additional evidence of stressed environmental conditions. The epifaunal taxa are generally adapted to well-oxygenated environments and usually exhibit pores on the dorsal surface of the tests for gas acquisition and respiration (Leutenegger and Hansen, 1979; Bernhard et al., 2010; Glock et al., 2012). Size and number of pores on benthic foraminifera from oxygen-poor environments tend to be higher than those of specimens from well-oxygenated habitats (Rathburn et al., 2018 and referein). Thus, variations of the dissolved oxygen content may cause morphological pore abnormalities. In our case, the increase of the pore sizes against a decrease in their number on the surface of the chambers may be linked (directly or indirectly) to the emissions, similar to morphological abnormalities observed in specimens living in other venting sites. However, their relationship with the dissolved oxygen content is still difficult to establish. For example, whereas pore abnormalities recorded in the infaunal taxa could be due to oxygen variations because they live inside the sediment where oxygen depletion is conceivable, it is more difficult to explain their occurrence on specimens from vegetal microhabitats where the intense hydrodynamics and photosynthetic activity should yield a well-oxygenated environment.

6. Conclusions

The analysis conducted at sites affected by CH_4 venting activity around the Scoglio d'Affrica allow us to make some considerations on benthic foraminiferal response to these gas (±mud) emissions in shallow water environments. Our data show that there is a strong influence of the sedimentary processes linked to the methane emissions on the foraminiferal assemblages, resulting in a very patchy spatial distribution of foraminiferal assemblages linked to complex abiotic and biotic interactions. On the basis of our observations, methane emissions and mud emplacement represent the two main stressor factors for the benthic foraminiferal assemblages. At present, it is not possible to define whether the effect of CH_4 is more or less influential than mud emplacement.

Considering the morphological characteristics of the seafloor linked to different degree of venting activity, 5 different settings on and off the mud volcanoes were detected, associated with distinct characteristics of the microfaunal assemblages.

1) Areas with strong emission activity at the top of MVs, locally associated with gryphons and mudflows, where the environmental conditions are clearly prohibitive for foraminiferal life.
2) Mud flows along the flanks of mud volcanoes, where overlapping mudflows probably have a negative impact on life development, leading to barren sediments.
3) Muddy sediments associated with weak emissions where the development of the foraminiferal community is favored, although with differences in terms of density, diversity and compositional features linked to time of colonization by each species. In this setting, infaunal taxa (bolivinids) are favored to rapidly colonize muddy, poorly oxygenated sediments linked to the emissions. Among miliolids, *Q. stelligera* seems to be the most tolerant together with rosalinids (mainly *R. bradyi* and *G. praegeri)* and the hyaline taxa *H. depressula*.
4) Intermatte zone under scarce or absent emissions, characterized by typical shallow water taxa belonging cibicids, rosalinids and miliolids and indicative of well-oxygenated conditions and high hydrodynamism.
5) *P. oceanica* substrates, characterized by higher foraminiferal content on leaves compared to the rhizomes and surrounding sediment samples. In venting zones, *P. oceanica* leaves potentially offer "refugia" to epifaunal taxa that generally live on the seafloor under normal marine conditions. Similar to the surrounding sediment samples, the epiphytic assemblages are dominated by rosalinids, showing them to be a highly resilient taxa with an opportunistic behavior.

Many questions still remain open concerning the relations and influences of methane on the benthonic associations in shallow water environments. Although it is difficult to define a pattern of biota response and to identify seep exclusive taxa, benthonic foraminifera can represent good environmental proxies for both monitoring the variability of recent venting activity and detecting stressed conditions occurring in the geological record. The seafloor around Scoglio d'Affrica may represent a very promising study site for multidisciplinary marine research regarding venting activity, geochemistry of cold seep fluids and their effects on benthic organisms.

CRediT authorship contribution statement

Letizia Di Bella: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Martina Pierdomenico:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Aida Maria Conte:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Irene Cornacchia:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Tania Ruspandini:** Writing – review & editing, Writing – original draft, Methodology, Data curation. **Daniele Spatola:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Stanley Eugene Beaubien:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Sabina Bigi:** Writing – review & editing, Conceptualization. **Alessia Conti:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation. **Giovanni Gaglianone:** Methodology, Data curation. **Michela Ingrassia:** Writing – review & editing, Methodology, Data curation. **Francesco Latino Chiocci:** Writing – review & editing, Supervision. **Daniele Casalbore:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Data curation, Conceptualization.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpetgeo.2024.107130.

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