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Comunità meiobentoniche caratterizzanti le sorgenti idrotermali costiere delle Isole Eolie

Meiofaunal assemblages inhabiting shallow water hydrothermal vents from the Aeolian Islands

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Sommario

ABSTRACT

Le sorgenti idrotermali costiere sono state studiate in diverse aree marine in tutto il mondo compreso il Mar Mediterraneo, specialmente il Mar Tirreno. Tuttavia, la meiofauna in questi ambienti ha ricevuto meno attenzioni in passato rispetto alla sua corrispondente di vent profondi. In particolare, nell'arcipelago delle Eolie è stata studiata solo la comunità della meiofauna dell'isola di Panarea. In questo studio, sono stati investigati due siti idrotermali delle isole di Vulcano e Salina. È stato seguito un transetto composto di tre stazioni in entrambi i siti. La stazione uno si trovava nell'area di attività, la stazione due in un'area ancora influenzata dall'attività idrotermale e la stazione tre in un'area inalterata o quanto più possibile non influenzata. Le abbondanze totali hanno mostrato variazioni all'interno di un ampio range, con differenze significative tra stazioni. PL2 ha mostrato le abbondanze più basse, mentre PL3 le più alte. Le stazioni di PO e PL3 hanno mostrato un aumento delle abbondanze totali scendendo dalla superficie verso gli strati intermedi, mentre PL1 e PL2 hanno presentato abbondanze più elevate negli strati superficiali. In totale sono stati trovati 21 taxa e PL2 si è mostrata essere la stazione più ricca (17). Il numero di taxa e le abbondanze totali sono apparse per lo più indipendenti, in particolare alla stazione PL2. Le abbondanze dei Copepoda con i loro *nauplii*, tra i taxa più rappresentati,

hanno mostrato una tendenza all’aumento allontanandosi dai vent, mentre i Nematoda non hanno mostrato particolari trend, ma hanno fatto registrare in entrambi i casi le loro abbondanze minori nelle stazioni intermedie. I taxa più rappresentativi si sono dimostrati essere Nematoda, Copepoda con i *nauplii*, Ciliata e Foraminifera, con alcuni contributi rilevanti di taxa minori a seconda della stazione considerata. Le comunità totali della meiofauna hanno mostrato differenze significative tra siti, stazioni e layer dovute a Nematoda, Copepoda e i loro *nauplii* e Foraminifera e ad altri taxa meno rappresentati, come Ciliata, Polychaeta, Cladocera, Cnidara, Sipuncula, Rotifera e Ostracoda. Questo studio ha confermato alcuni trend della meiofauna relativa ai vent costieri, come una generale migrazione di organismi meiobentonici verso strati sub-superficiali e una distribuzione eterogenea, associata a un’eterogeneità ambientale su piccola scala tipica degli ambienti di vent. Per contro, sono stati registrati alti valori di abbondanza e diversità di taxa in contrasto con i risultati ottenuti precedentemente e presenti nella letteratura relativa ai vent. Fattori come la presenza di biofilm, l’aumento di temperatura, la diminuzione del pH, l’alta temperatura del sedimento, l’emissione di fluidi di vent, la presenza di depositi di zolfo e la dimensione delle particelle di sedimento sono state indicati come possibili driver della distribuzione e diversità della meiofauna.

1. INTRODUCTION

1.1 Hydrothermal vents: an overview

Hydrothermal vents, also called hot springs, are areas where geothermally heated water discharges through a planet's crust onto the surface, either subaqueously or subaerially (Price and Giovannelli, 2017). These environments present extreme conditions that strongly select or drive living components of the area, alter communities' structure, ecological pathways, such as the transfer of matter and energy along the food webs, and force organisms to find alternative solutions to cope with the hostile conditions found (Zeppilli and Danovaro, 2009).

Hydrothermal vents generate from water coupled with an adequate heat source capable to drive hydrothermal circulation (Price and Giovannelli, 2017). On Earth, this heat usually comes from tectonic activity near plate boundaries. Although magma can generate at all the plate boundaries type (divergent, convergent and transform), hydrothermal venting usually occurs at divergent boundaries on mid-ocean ridge systems, and at convergent boundaries in the case of seamounts and island arc volcanoes (Figure 1).

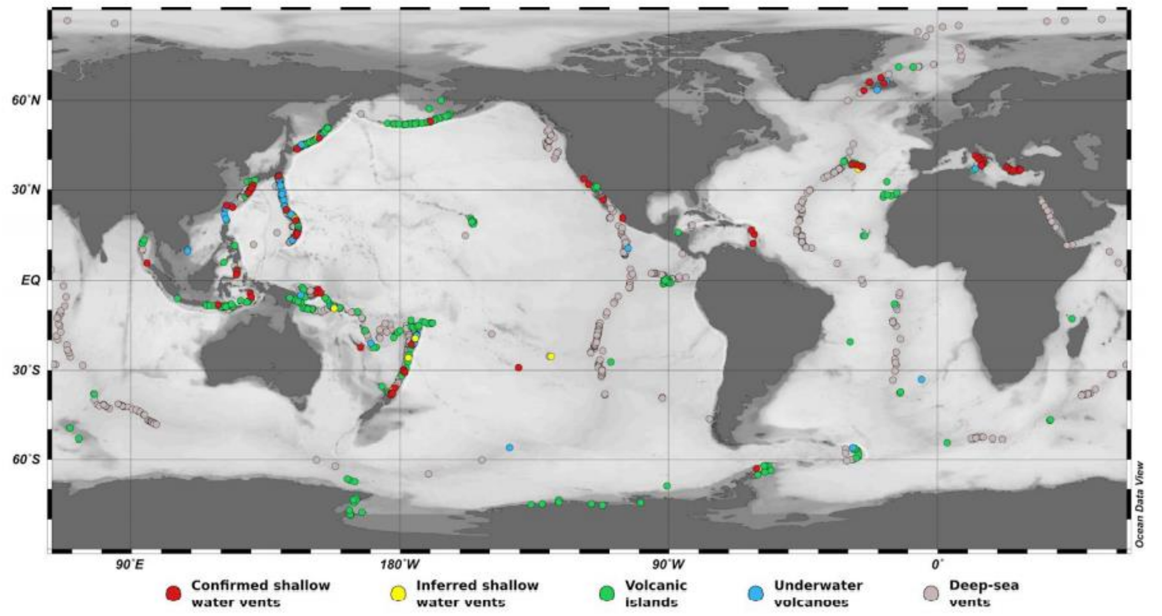

Figure 1 - Map showing the location of confirmed and inferred shallow-water hydrothermal vents, volcanic islands, underwater volcanoes, and deep-sea hydrothermal vents (from Price and Giovannelli, 2017)

Hydrothermal vents can occur from the intertidal to the abyss, covering a wide depth range (Tarasov *et al.*, 2005). Shallow vents are often related to active plate boundaries, and littoral and sub-littoral venting is linked with sites where volcanic and seismic activities are present (Dando *et al.*, 1999). Fluid formation usually takes place from relatively shallow sources (1-2 km depth) (Di Bella *et al.*, 2016).

Shallow-water vent conditions can strongly differ from those of surrounding seafloor due to an increased temperature. The natural emitted fluids can be enriched in some elements (i.e., manganese, iron and arsenic, Prol-Ledesma *et al.*, 2004; Melwani & Kim, 2008), but also depleted in others (i.e., chlorine, sodium and strontium; Sedwinck and Stuben, 1996; Fitzsimons *et al.*, 1997;

Melwani & Kim, 2008); additionally, they can show low salinity and pH. Under these environmental conditions, hydrothermal vents can be considered biologically-stressful environments (Melwani & Kim, 2008).

Shallow-water vents have been studied in different coastal areas, such as Sulawesi, Indonesia (Zeppilli & Danovaro, 2009), Papua, New Guinea (Tarasov *et al.*, 1999), New Zealand (Kamenev *et al.*, 1993), but also in the Mediterranean Sea, including the Tyrrhenian Sea (Di Bella *et al.*, 2016; Colangelo *et al.*, 2001; Maugeri *et al.*, 2010; Baldrighi *et al.*, 2020) and the Aegean Sea (Dando *et al.*, 1995; Thiermann *et al.*, 1997). They have been documented on the summit of seamounts, on the flanks of volcanic islands and in other near-shore environments characterized by high heat flow (Italiano and Nuccio, 1991; Pichler, 2005; Price *et al.*, 2013; Tarasov *et al.*, 2005).

Shallow-water vents manifestation can vary from focused vents, areas of seemingly pure free gas discharges with little fluid, and areas of diffuse venting through sediments (Price and Giovannelli, 2017).

1.2 Shallow-water vs. deep-sea hydrothermal vents

A primary classification can be done by depth: the accepted definition to date says that shallow-water vents occur at <200m depth (Tarasov *et al.*, 2005). This depth was chosen since it roughly coincides with the maximum depth light penetration into the ocean (Price and Giovannelli, 2017). Consequently, shallow vents can count on the presence of light, so that both photosynthetic and chemosynthetic production are present, making these shallow vents high-energy systems, while in the deep-sea production can rely exclusively on geothermal fluids, thus allowing solely chemosynthetic primary production (Sorokin, Sorokin and Zakuskina, 1998). This condition promotes symbiotrophic forms in deep-sea communities, while they are not usually present at shallow vents. In addition, at deep-sea vents the distribution of biomass and symbiotrophic species shows a concentric pattern, while in shallow-water systems this feature is lacking (Tarasov *et al.*, 2005). This is due to the fact that venting is the key variable in deep environments to the distribution of both mats and organisms harbouring symbiotic bacteria, that rely on chemosynthesis to survive, while in shallow waters the presence of light can sustain algal mats without regarding to their position and symbiotrophy is absent, so biomass distribution is influenced only by mats allocation.

Moreover, deep-sea vents are generally characterized by vent-specific taxa, that are usually absent in shallow-water systems (Tarasov *et al.*, 2005).

Often, shallow-water hydrothermal vents present streams of gas bubbles (Figure 2), issuing from the vents themselves, contrary to deep-sea ones (Dando *et al.*, 1995), thus they are commonly called gas hydrothermal vents after Tarasov *et al.* (1990).

Figure 2 - Sampled site in Porto Levante Bay, Vulcano Island (Sicily). Credits: G. Bernardi

When related to island volcanic arcs, the gasses are usually dominated by CO_2, with trace amount of sulphide and methane (Price and Giovannelli, 2017). Because of the enhanced gas exsolution, fluid chemistry is significantly altered by mass transfer from gas to aqueous phase (Price and Giovannelli, 2019).

Evidence suggests that most of the subsurface processes taking place at deep-sea vents are also present in shallow-water systems, to some extent; nevertheless, shallow-water vents show unique near-surface processes, that differentiate them from their deep-sea counterparts (Price and Giovannelli, 2017). Shallow-water vents are exposed to the activity of waves, tidal cycles, and storms, that are more dynamic than the processes to which deep-sea vents are exposed to and that can determine temperature fluctuations (Price and Giovannelli, 2017).

Due to their proximity to land masses, shallow-water vents show a significant amount of terrigenous organic carbon and phytodetritus, evidently much larger than the one seen at the deep-sea ones. This input can have considerable impact on carbon cycling and primary productivity in these environments (Price and Giovannelli, 2017). Dissolved organic matter is co-precipitated with iron close by shallow-water vents, thus removing aromatic compounds and considerably modifying the molecular composition of the remaining dissolved organic matter pool (Gomez-Saez *et al.*, 2015). Ultimately, this process can potentially alter the availability of more labile fraction to microbial consumers (Price and Giovannelli, 2017).

1.3 Shallow vent communities

In shallow-water vent environments, the nutrient-enriched hydrothermal fluids can promote phytoplankton populations' development; on the other hand, the same fluids have low salinity and contain toxic heavy metals and reduced sulphur compounds; thus, when spreading in the surface water layer, they have an influence on the composition of phytoplankton communities because of these contrasting effects. Moreover, the volcanic emissions and hydrothermal water rich in methane, hydrogen and reduced sulphur compounds stimulate microbial chemosynthesis, therefore enhancing the production of particulate food for the planktonic and benthic filtering fauna (Sorokin, Sorokin & Zakuskina, 1998).

In regions where volcanic activity is present, bacterioplankton can reach a high biomass together with phytoplankton, creating a large trophic potential for both benthic and planktonic filtering fauna (Sorokin, Sorokin & Zakuskina, 1998).

Prokaryotes, represented by both *Bacteria* and *Archaea*, are usually the main biological component of these environments (Di Bella *et al.*, 2016). The investigations conducted show that they mostly belong to mesophilic, thermophilic and hyperthermophilic *Archaea* and *Bacteria* (Dando *et al.*, 1999).

At shallow-water vents, bacterial mats can reach a thickness of 30 cm and they usually are more complex than those present in deep waters. It is possible to separate three different types of mats, dominated by: 1) diatom, 2) algae-bacterial and 3) bacterial (Tarasov *et al.*, 2005).

When hydrogen sulphide is absent, diatom mats are present. Algal-bacterial mats are associated with chemosynthetic microorganisms that can reduce or oxidize sulphur compound and usually develop at temperatures up to 55-60°C. Lastly, pure bacterial mats consist of thiobacteria of the genera *Thiobacillus*, *Thiomicrospira* and *Thiosphaera* or filamentous colourless sulphur bacteria as *Thiothrix* or *Beggiatoa*. In these mats the most significant biogeochemical processes are the oxidation of reduced sulphur compounds and organic matter synthesis. When hydrogen sulphide and organic matter concentrations are high, these sulphur bacteria function as chemo-organotrophs and mineralize the organic matter present.

The amount of food material derived from both chemosynthesis and photosynthesis processes promote the meiofauna abundance that can reach higher values compared to the background sediments (Kamenev *et al.*, 1993).

Indeed, mats can increase the biomass of meiofauna by representing an important food source, capable of influencing the trophodynamics of these extreme systems (Zeppilli and Danovaro, 2009); as a consequence, the aggregation of surrounding macrofauna is stimulated (Tarasov *et al.*, 2005). Conversely, vent activity can have a limiting effect on meiofauna assemblages because of high sediment temperature and rapid sedimentation rates (Tarasov *et al.*, 1999). Fluid emission can also alter sediment grain size (Zeppilli and Danovaro, 2009) and create extreme conditions in terms of temperatures and chemical compound, promoting the survival of the most tolerant species and/or taxa (Zeppilli *et al.*, 2018). Colangelo *et al.* (2001) found that the intermediate disturbance theory can explain the situation of meiobenthic communities exposed to increasing hydrothermal seepage.

Nematoda and Copepoda Harpacticoida are common forms of meiobenthos in diatom mats, while in algae-bacterial and bacterial mats Nematoda and Ciliata are prevailing and sedentary Polychaeta are also present with relevant population and biomass. Shallow-water vent macrofauna are characterized by low species diversity, with the species composition mostly determined by the geographical location (temperate and tropical latitudes), seabed features (hard and soft bottoms, rigid lava flows or hydrothermal constructions), temperature of bottom sediments and volcanic fluids and chemical composition of the vent fluids (Tarasov, 2006).

In these areas the most sensitive macrofauna species are replaced by opportunistic species able to thrive with a wide range of environmental factors. All these species can show adaptive traits, such as resistance to temperature and salinity fluctuations, ability to change their metabolism and food habits and an ability to survive in conditions of low oxygen content or in the presence of sulphide; they can also show biochemical or morphological alterations or the accumulation of heavy metals (Tarasov, 2006).

1.4 Shallow hydrothermal vents as natural laboratories for analysing ocean acidification

One of the most important characteristics of shallow vents is their high concentration of dissolved CO_2 and thus the usually acidic conditions found.

The ocean has represented the true sink for one-third of the anthropogenic CO_2 for the last two centuries (Sabine *et al.*, 2004). The absorption of CO_2 causes a decrease in the ocean pH, according to the following reaction:

$$CO_{2(g)} + H_2O \leftrightarrow H_2CO_{3(aq)} \leftrightarrow H^+ + HCO_3^-$$

An increase in atmospheric CO_2 is a direct cause for the acidification of surface seawater (Boatta *et al.*, 2013). Due to anthropogenic emissions, atmospheric concentrations of carbon dioxide could almost double between 2006 and 2100 according to most recent carbon-dioxide emission scenarios (IPCC, 2001).

To better understand how the increase of ocean acidification can affect marine ecosystems, Hall-Spencer *et al.* (2008) proposed to use environments naturally rich in pCO_2 such as volcanic vents.

Volcanic vents are especially abundant in the Mediterranean Sea, around Italy and Greece. Previous studies showed that the largest part of the vent emission is represented by CO_2, but other important gasses are hydrogen sulphide, hydrogen, and methane (Dando *et al.*, 1999).

Evidence suggests that the acidification resulting from dissolved CO_2 and H_2S can eliminate carbonate-secreting organisms living nearby by dissolving carbonatic structures, thus leading to potentially severe shifts in the coastal marine ecosystems (Hall-Spencer *et al.*, 2008; Price and Giovannelli, 2017). More specifically, by studying CO_2 vents with ambient seawater temperature and lacking toxic sulphur compounds in areas of Ischia (Italy), Hall-Spencer *et al.* (2008) found that organisms like *Halimeda* algae and some corals as *Caryophilla*, *Cladocora* and *Balanophyllia* were common outside the vents, but absent where the mean saturation state of aragonite was less than 2.5, near vents. Moreover, the abundance of Corallinaceae was significantly reduced at lowered pH, while other algal and plant genera (*Caulerpa*, *Cladophora*, *Asparagopsis*, *Dictyota* and *Sargassum*) seemed to be resilient to high amount of pCO_2. Regarding the benthic fauna, sea urchins (*Paracentrotus lividus* and *Arbacia lixula*) resulted to be very common outside vents, but their abundance reduced when pH levels hit low values. Juveniles of different Gastropoda were absent in area with low pH, while adults were present but with weakened shells. On the other hand, the seagrass production was enhanced and epiphytism level on them was reduced (Hall-Spencer *et al.*, 2008).

Similarly, bacterial communities showed detectable shifts, thus leading to the possibility that the biogeochemical functions of marine sediments will also be significantly affected by ocean acidification (Kerfahi *et al.*, 2014).

1.5 Meiofaunal assemblages

The term *meiobenthos* was firstly introduced by Mare (1942) to indicate the organisms of intermediate size compared to the smaller ones, *microbenthos*, and the larger ones, *macrobenthos*. The word comes from the Greek *meion* ("μειον"), that means smaller.

The size range for meiofauna goes from 30 µm (20 µm for deep-sea environments) to 0.5-1 mm, thus including both large protozoans and metazoans (Danovaro, 2019). They represent the most phyletically diverse fauna on Earth, comprising 24 of the 35 animal phyla (Giere, 2009). Their microscopic size reflects the evolutionary benefit they get from it, allowing them to live and thrive in interstitial spaces (Schratzberger & Ingels, 2018).

Quantitative size-taxon studies infer that the marine meiofauna represent a separate biologically and ecologically defined group of animals (Giere, 2009).

Meiofauna can be divided in permanent and temporary meiofauna. Permanent meiofauna are represented by organisms that keep the meiofaunal size throughout all their life, whereas temporary meiofauna are meiofaunal in size only during the first part of its life and they include larvae and juvenile forms of macrofaunal or megafaunal species (Baguley *et al.*, 2019).

Meiofauna are mostly found in and on soft sediments, but also on and among epilithic plants and other hard substrates; the surfaces of barren rocks, covered by biofilm and detritus, are suitable areas too (Giere, 2009; Bianchelli *et al.*, 2016; Bianchelli and Danovaro, 2020). They can be found in terrestrial, freshwater, and marine environments. In marine habitats they occur from the intertidal zone to the deepest trenches and in heavily polluted sediments, where they often represent the only living animal species (Baguley *et al.*, 2019). They generally represent the most abundant metazoan group in marine benthos, with a density of 10^5-10^6 individuals/m^2, or 100-1000 individuals/cm^2 (Danovaro *et al.*, 2003).

Meiofauna inhabit different kind of sediments showing several morphological adaptations. For instance, sand fauna is usually slender and elongated, in order to move through narrow interstitial openings; mud fauna is generally larger and not restricted to a particular morphology (Danovaro, 2019). Indeed, sediment size represents one of the most important environmental factors that affects the meiobenthic communities (Giere, 2009). The vertical distribution of meiobenthic taxa in marine sediments is normally limited by oxygen penetration depth in the sediment. The majority of meiofaunal species are generally encountered in the first 2 cm of sediment, with usually oxygenation levels with a RPD (redox potential discontinuity depth) higher than +400 mV

(Danovaro *et al.*, 2003). Copepoda are one of the most sensitive taxa, thus they are usually limited to the most superficial sediment stratum. However, there are organisms capable to live in hypoxic/anoxic conditions and when hydrogen sulphide is present; they belong to the so-called *Thiobios* and they comprehend Nematoda, Oligochaeta, Bivalvia, Gnathostomulida and Polychaeta (Powell & Bright, 1981; Wetzel *et al.*, 1995, 2002; Windoffer *et al.*, 1999; Krieger *et al.*, 2000). Nematoda are usually the dominant taxon in the meiofauna, and they can represent the 90% of total meiobenthic populations. The second group is generally represented by Copepoda Harpacticoida, followed by Polychaetea (Danovaro *et al.*, 2003).

Meiofaunal organisms can show different feeding strategy: most of them are deposit feeder, but also grazers and bacterivores constitute well represented groups (Danovaro *et al.*, 2003). It has been estimated that meiofaunal grazing on bacterial and algal community can remove up to 3% of bacterial biomass and 1% of diatom stock is per hour (Montagna, 1984). This activity stimulates microbial growth rate, keeping it in a logarithmic phase (Danovaro *et al.*, 2003).

Meiofauna naturally show a patchy distribution (Danovaro *et al.*, 2003; Giere 2009). Many different factors have been proposed to explain this patchiness: (i) micro-spatial variation in physical factors such as oxygen and grain size;

(ii) food distribution; (iii) presence of biogenic structures in the habitat such as worm tubes; (iv) predation or biotic disturbance; (v) interspecific competition and (vi) aggregations.

1.6 The ecological role of meiofauna

Many ecosystem processes that take place in marine sediments, such as reworking of sediments, recycling of nutrients, food web dynamics, degradation and distribution of pollutants, decomposition, mineralisation, burial, and storage of organic matter are important on a global scale and are essential to sustain life on Earth (Giere, 2009).

Nowadays, it is well-known that degradation of marine benthic compartment will cause the loss of many ecosystem services, since they harbour organisms that play functions essential to benthic ecosystem processes (Hooper *et al.*, 2005).

Meiofauna can have effect on physical, chemical, and biological properties (Schratzberger & Ingels, 2018):

- physical properties: sediment texture and cohesion, shear strength, permeability and pore space, and distribution in sediment size.
- chemical properties: levels of organic matter, inorganic nutrients, and oxygen.

- biological properties: density and composition of other benthic fauna and microbes.

Meiofaunal organisms can perform an active sediment particle reworking through burrowing, construction and maintenance of burrows, ingestion and defecation of particles, and excretion of metabolic wastes (Schratzberger & Ingels, 2018). Many meiobenthic species secrete extracellular polymeric substances (EPS) that bound together sediment particles (Nehring *et al.*, 1990; Nehring, 1993). The vertical movements of meiobenthic organisms may produce a substantial transport of water into the upper centimetres of sediment, thus acting as conveyors affecting nutrient cycle and biogeochemical fluxes; in this way they can change chemical gradients into the sediment (Schratzberger & Ingels, 2018).

Moreover, meiofauna have an important role in marine food webs, by affecting the structure of microbial communities in different ways: (i) mechanical break-down of detrital particles, making them more liable to bacterial action; (ii) direct excretion of nutrients, ready for microbial use (De Troch *et al.*, 2005); (iii) production of mucus (EPS), that can attract and sustain bacterial growth (Moens *et al.*, 2005); (iv) sediment bioturbation; (v) maintaining bacterial growth in the logarithmic phase, (Coull, 1999). Montagna (1984) found that meiofauna can eat their body weight equivalent in microbes each day causing a stimulatory effect on the microbial community.

Meiofauna have a key ecological role in the benthic domain as they represent a link to higher trophic levels (Danovaro *et al.*, 2003), directly feeding on microalgae, on indirectly feeding on secretions of primary producers (Schratzberger & Ingels, 2018). Meiofauna can act as a prey for macrofauna, but also fish and even some shore birds (Schratzberger & Ingels, 2018, Ptatscheck *et al.*, 2020). Meiofauna are characterized by fast turn-over times allowing a rapid population replacement (Coull, 1999). Indeed, due to its small size, the meiofauna turnover (i.e., production:biomass ratio) is 5 times higher compared to that of macrofauna (Gerlach, 1978), resulting in high production rates (Giere 2009). Macrofauna-meiofauna interactions typically include competition for resources, macrofauna predation on meiofauna, physical disturbance and biogeochemical alteration of benthic environment and organisms' habitable niches (Schratzberger & Ingels, 2018). Some meiobenthic organisms, such as Turbellaria and predator Nematoda, have been shown to have a significant impact on some of the macrofauna juvenile populations, thus shaping the structure of macrofaunal community by altering density and acting selectively on a few families of macrofaunal juveniles (Danovaro *et al.*, 1997). Meiofauna can thus be seen as a strong ecological interactor, by occupying a unique position in benthic food webs (Schratzberger & Ingels, 2018).

1.7 Meiofauna characterizing the shallow-water vents

The abundance and taxonomic structure of meiobenthos inhabiting shallow-water vents are strictly linked to the temperature of the seabed and to the content of hydrogen sulphide in the fluids, along with abundance of food material and to unstable habitat conditions (Tarasov, 2006). Often, meiofauna species found in shallow vent areas represent a subset of those present in the surrounding non-vent area (Dando *et al.*, 1995, Zeppilli & Danovaro, 2009). Nematoda represent an important component in the meiofauna of shallow vents, with abundance values that can vary from $2 \bullet 10^3$ individuals/m^2 to $1.8 \bullet 10^6$ individuals/m^2 (Tarasov *et al.*, 2005). This group presents a wide range of morphological and biochemical adaptations to extreme environmental conditions, thus enabling them to master new biotopes and sources of food (Tarasov, 2006).

Kamenev *et al.* (1993) documented an increase in the number of meiobenthic animals with a dominance of Nematoda in volcanic vent areas of McEwans Bay, as reported in other studies (Spies & DesMarais, 1983; Jensen, 1986; Fricke *et al.*, 1989; Montagna *et al.*, 1989; Shirayama & Ohta, 1990). In all these studies, an increased number of meiobenthic organisms, particularly

Nematoda, coupled with a reduction of meiofaunal diversity have been reported.

Conversely, Thiermann *et al.* (1997) registered a general decrease in Nematoda abundances moving from the distal seagrass end to the proximal vent area. In this case, the hydrothermal activity was reflected by a decrease in both the abundance and diversity of fauna. Similarly, Tarasov *et al.* (1999) recorded low meiofauna numbers in areas of hydrothermal fluids and volcanic gases discharge; in this case Nematoda, Copepoda Harpacticoida and Ostracoda represented 80 to 90% of the total meiofauna community. Authors hypothesized that the hot sediment temperature, a rapid sedimentation rate and the lack of hard substratum were major factors inhibiting the development of benthic communities. However, they concluded that the effects of hydrothermalism on primary production and biota in shallow-water systems is most marked in areas significantly isolated from the open sea, while the effect is reduced when the isolation is lower or absent.

Generally, Nematoda dominate sites with high fluid emissions, whereas Copepoda are prevalent in sediments with moderate emissions (Coull 1985; Colangelo *et al.* 2001; Zeppilli and Danovaro 2009, Zeppilli *et al.*, 2018). In the exhalative fields of the Panarea’s caldera, Copepoda resulted to be the dominant taxon, with a high diversity in areas with a moderate gas seepage or sulphur deposit (Colangelo *et al.*, 2001). Sediment characteristics have a master role in driving the composition of meiofauna assemblages (Wieser, 1959; Colangelo *et al.*, 2001), indeed the coarse grain size characterizing this caldera could provide a reason for the copepod dominance. Nematoda densities, conversely, appeared to be more relevant at stations with presence of bubble streams.

In shallow-vent environments vertical meiofaunal distribution can increase from the surface sediments to intermediate layers, to decrease in the deeper ones (Baldrighi *et al.*, 2020). Copepoda and their *nauplii* prefer the well oxygenated surface sediment layer (Grego *et al.*, 2014; Baldrighi *et al.*, 2020), while Nematoda become dominant at subsurface depths (Ingels *et al.*, 2009; Rosli *et al.*, 2016; Baldrighi *et al.*, 2020).

In conclusion, meiofauna communities of shallow vents highly vary depending on local characteristics, that can widely differ within sites. Shallow water vents are heterogeneous marine environments, and their presence can have an impact on local biodiversity.

2. AIM OF THE THESIS

Meiofauna in coastal vent environments have received low attention in the past, compared to the deep-sea one. In particular, in the Aeolian archipelago, only the meiofauna community characterizing Panarea island has been investigated (Colangelo *et al.*, 2001).

The aim of this study is to investigate, for the first time, meiofaunal assemblages of Vulcano and Salina islands. The following objectives have been achieved:

1. to characterize the diversity of meiobenthic assemblages inhabiting different shallow vents;
2. to describe the meiofauna spatial distribution along a vertical into the sediment column and along a horizontal transect at increasing distance from vent areas;
3. to assess if and how the presence of vent activity can have a certain influence on the distribution and diversity of the meiofauna.

3. MATERIALS AND METHODS

3.1 Site description and sampling strategy

The study area is in the Aeolian Islands archipelago, on the north side of Sicily Island (fig. 3). The sampling was carried out during the AEO19 Expedition, in September 2019. Sediment samples were collected by SCUBA divers from two different sites located at Vulcano and Salina islands (Table 1).

Figure 3 - Map of the southern Italian region and location of the sampled stations in the Aeolian Archipelago

At each site, stations were located along transects from inside to outside the vent areas. In both sites the distance between the three stations varied considering venting activity: the first one was collected in the active area, the second one in an area affected by the activity and the third one in an unaffected, or almost unaffected, area.

Vulcano Island sampled site was located in Levante Port and was characterized by gas emission and the presence of white microbial mat. The temperature in this site was 52°C and it showed an acidic pH of 5,22. It is characterised by suboxic conditions, as indicated by 24% of DO and -202mV of ORP. Station 1 was from the centre of actively visible venting; station 2 was from ca. three meters inside a thick white microbial mat; station 3 was located outside the vent field and characterized by the presence of *Zostera* meadow. During the extraction procedure carried out in the laboratory it was possible to note that sediment in this site was characterised by visible yellow deposits, probably due to sulphur compounds.

The sampling site at Salina Island was in the Bay of Pollara, within an ancient partially collapsed marine crater. Diffuse degassing characterised the area, represented by a large rocky flat. No visible microbial mats were present, and the emission temperature seemed to conform to the background seawater temperature (~30 °C), suggesting that the venting is dominated by CO_2. Also in this case the venting point showed an acidic pH of 5,6. Station 1 was directly on the active degassing site; station 2 was located ca. 15 meters away from the degassing site even if the effect of bubbling was still evident, and station 3 sampled outside the venting field (Lingua) but at a similar water depth compared to station 1 and 2 and near *Posidonia* mats.

Station	Island	Site name	Latitude (°N)	Longitude (°E)	Shallow vent type	Depth (m)	Temperature (°C)	Salinity (PSU)	Dissolved oxygen (% DO)	Oxidation-reduction potential (mV)	pH
PL	Vulcano	Levante port, Vulcano	38,4161941	14,9611976	high temp, high sulphide	6.1	52	37.7	24.4	-202	5.22
PO	Salina	Pollara, Salina	38,574516	14,799716	low temp, CO_2 dominated	10	28	39	48	121	5.6

*Table 1 – **Location, depth, and physic-chemical characteristics of the sampled stations.** Parameters were measured in the hydrothermal fluids. Of the sampled sites, PO was never reported in the literature before.*
Shallow-water hydrothermal vent classification according to Giovannelli & Price, 2019.

The local water masses of the Aeolian Islands are characterised by the presence of strong currents from Messina strait, responsible for the large exchange of waters in the archipelago and they confer unique characteristic in the chemistry and oceanography of local waters (Italiano and Nuccio, 1991; Ferrillo, 2020). Furthermore, the strong geochemical gradient from East to West through the Aeolian Volcanic Arc and the great difference in rock composition and trace elements within each island, all contribute to a creation of unique ecosystem around these islands.

3.2 Sampling method

Sediment samples were collected by SCUBA divers by using core tubes with an internal diameter of 4.5 cm, to analyse meiofaunal communities and total organic carbon (TOC). Two replicates have been collected for each station and layer, with the exception for station PL1 layers 3-5, 5-10- 10-15 cm and station PO1 layer 10-15 cm. In this case, only one replicate was collected because of the hard nature of the sediment that prevented to push the core deeper into the sediment.

Sediment cores were divided into five layers (0-1, 1-3, 3-5, 5-10 and 10-15 cm) and fixed in buffered 4% formalin and seawater. The fixative solution is generally obtained by using prefiltered marine water with a $Na_2B_4O_7$ buffer to reach an 8,2 pH (Higgins & Thiel, 1988).

3.3 Meiofaunal analysis

The samples were rinsed from the fixative solution, then sieved through a 1 mm mesh over a beaker to exclude the larger organisms and over a 30 µm mesh to retain the smallest ones. The retained fraction was divided in 50 ml tubes, Ludox HS40 was added with a 1:3 ratio and then the sample was centrifuged for 10 minutes at 3000 rpm (Heip, Vincx & Vranken, 1985). The supernatant fraction was filtered with the 30 µm mesh and rinsed thoroughly with water. The sediment fraction still in the Falcon was centrifuged again, after Ludox addition, for at least two times. The collected sample was stained with Rose Bengal and stored in 4% formalin (Danovaro *et al.*, 2003). Meiofaunal organisms were counted and classified by higher taxa under a stereomicroscope. Foraminifera and Ciliata have been included in the analysis.

3.4 Environmental data

To characterise the sampling area an estimation of total organic carbon (%TOC) was performed for each sample. Sediment samples were previously dried at 60 °C for 48 hours, then weighted and muffled at 450°C for four hours and weighted again (Danovaro, 2010).

3.5 Data analysis

Univariate and multivariate analyses were carried out to assess differences in TOC content and meiofaunal variables – such as total abundance, number of taxa and community composition.

A linear regression analysis was carried out to test the presence of significant correlations between TOC content and meiofauna total abundances or the number of taxa present.

The sample design included three factors as main source of variance: “site” (fixed, 2 levels: PL and PO), “station” (random and nested in “site”, 3 levels: 1, 2 and 3) and layer (random and nested in “station”, 5 levels: 0-1, 1-3, 3-5, 5-10, 10-15). The distance-based permutation analysis of variance (PERMANOVA, Aderson, Gorley & Clarke, 2008) was used to test for differences in TOC content, total meiofauna abundances, taxa richness and community structure between sites, stations and layers. The analyses were carried out on Euclidean distances (for all the following univariate measures: TOC content, meiobenthic abundance as total number of individuals on 10 cm^{-2}) or Bray–Curtis similarity matrices (for multivariate measures: meiofauna community composition), using 999 permutations of the residuals under a reduced model. Prior to the analyses environmental data were normalised, whereas biotic data were fourth root transformed; the fourth root transformation of the abundance was chosen in order to give more relevance to rare taxa in the analysis (Anderson *et al.*, 2008, Baldrighi et al, 2021).

Although aware that random factors have been considered in this analysis, pairwise tests have been forced in the attempt to investigate the differences among stations and layers.

P values for pairwise comparisons were obtained from Monte Carlo asymptotic distributions, because of the restricted number of unique permutations (Anderson, 2006, Baldrighi *et al.*, 2021). To further investigate meiofauna composition differences between layers a SIMPER analysis has been conducted on couples of layers that showed a significant P value after the PERMANOVA pairwise comparisons.

All the analyses were performed using the routines included in the software PRIMER 6 and PERMANOVA+ (Clarke and Gorley, 2006).

4. RESULTS

4.1 Environmental parameters

Even if any grain size analysis was performed, the sediment characterizing PO samples appeared to be coarser than the sediment characterizing PL samples (personal observation).

TOC values ranged from 0.55% to 4.85% and appeared to be generally higher in PO stations but always lower than 2%, except for the deepest layers of PO3 that showed a value of 4.85% (Table 2).

Sample	**TOC**	Sample	**TOC**
PL 1 0-1 cm	0.55%	PO1 0-1 cm	0.84%
PL1 1-3 cm	0.57%	PO1 1-3 cm	0.88%
PL1 3-5 cm	0.62%	PO1 3-5 cm	0.92%
PL1 5-10 cm	0.63%	PO1 5-10 cm	0.95%
PL1 10-15cm	0.63%	PO1 10-15cm	0.95%
PL2 0-1b	0.67%	PO2 0-1 cm	1.00%
PL2 1-3 cm	0.69%	PO2 1-3 cm	1.09%
PL2 3-5 cm	0.71%	PO2 3-5 cm	1.18%
PL2 5-10 cm	0.71%	PO2 5-10 cm	1.25%
PL2 10-15cm	0.73%	PO2 10-15cm	1.32%
PL3 0-1 cm	0.74%	PO3 0-1 cm	1.36%
PL3 1-3 cm	0.75%	PO3 1-3 cm	1.44%
PL3 3-5 cm	0.78%	PO3 3-5 cm	1.57%
PL3 5-10 cm	0.80%	PO3 5-10 cm	1.96%
PL3 10-15cm	0.81%	PO3 10-15cm	4.85%

*Table 2 – **TOC values***

The PERMANOVA test results indicated significant differences in TOC content only between layers (PERMANOVA, p=0.001) at stations PL1, PL2, PO1 and PO2, as reported in Table 3. Generally, most differences among layers occurred when comparing superficial layers to deep ones.

4.2 Meiofauna analysis

Total meiofaunal abundance ranged from 644.67 ± 88.81 ind./10 cm^2 at PL2 station to 2873.61 ± 918.45 ind./10 cm^2 at PL3 station; PL shows more variable values, while PO ranges from 1282.19 ± 237.20 ind./10 cm^2 at PO3 to 1562.80 ± 182.12 ind./10 cm^2 at PO2 (fig. 4). Significant differences occurred between stations (PERMANOVA, p=0.008) and layers (PERMANOVA, p=0.001). Particularly, differences between stations occurred when comparing PL2 *versus* PL3 (PERMANOVA, p=0.024), while significant differences between layers are reported in Table 3.

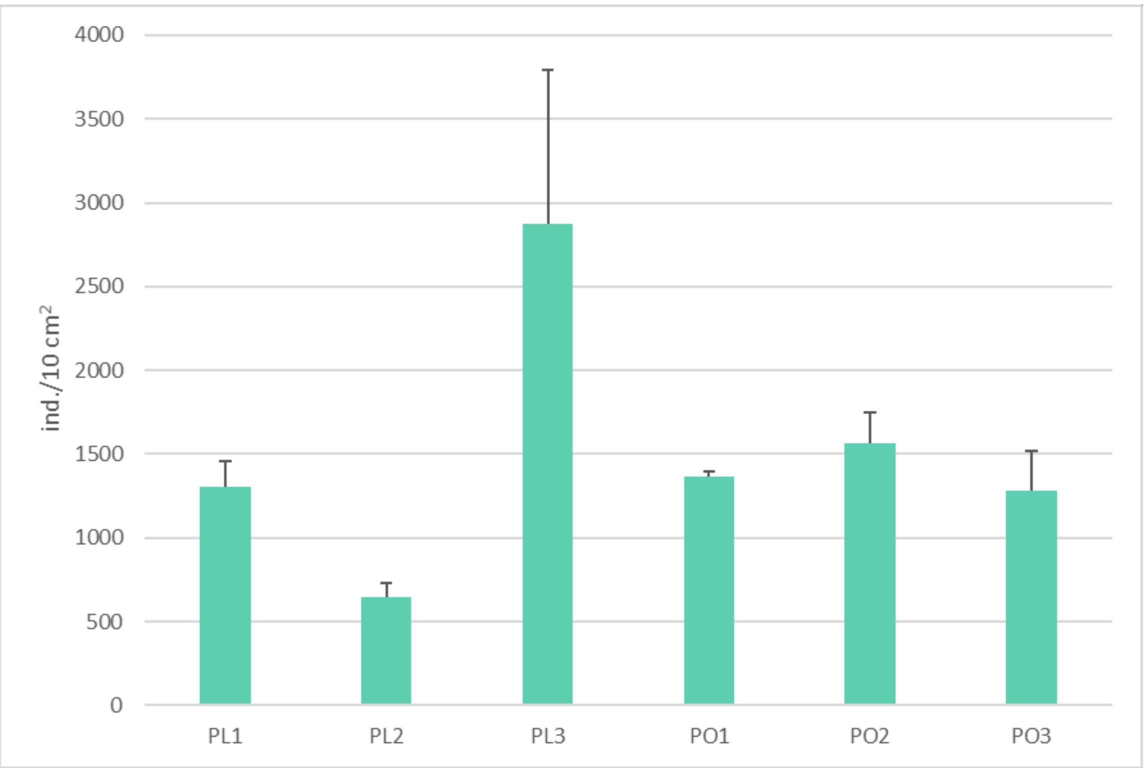

*Figure 4 - **Total meiofaunal abundance per site.** Reported are mean values at all the investigated stations. Vertical bars are standard deviations.*

	Source	df	SS	MS	F	P(MC)
TOC	si	1	2.10E+00	2.10E+00	9.46E-01	0.988
	st(si)	4	90'166	22'541	13'717	0.306
	la(st(si))	24	40'544	16'893	81'933	***0.001***
	Res	26	53'608	0.20619		
	Total	55	55			
Pair-wise test						
PL1	0-1 *vs* 1-3 cm					***0.043***
	0-1 *vs* 3-5 cm					***0.032***
	0-1 *vs* 5-10 cm					***0.007***
	0-1 *vs* 10-15 cm					***0.019***
PL2	0-1 *vs* 10-15 cm					***0.048***
PO1	1-3 *vs* 5-10 cm					***0.021***
	1-3 *vs* 10-15 cm					***0.048***
PO2	0-1 *vs* 1-3 cm					***0.033***
Total meiofauna abundance	si	1	2088.3	2088.3	12'944	0.303
	st(si)	4	6558.6	1639.6	31'228	***0.008***
	la(st(si))	24	12828	534.5	23'247	***0.001***
	Res	26	5977.9	229.92		
	Total	55	27052			
Pair-wise test	PL2 *vs* PL3					***0.024***
PL1	0-1 *vs* 5-10 cm					***0.015***
	0-1 *vs* 10-15 cm					***0.021***
	1-3 *vs* 3-5 cm					***0.036***
	1-3 *vs* 5-10 cm					***0.037***
	1-3 *vs* 10-15 cm					***0.037***
PL2	0-1 *vs* 1-3 cm					***0.003***
	0-1 *vs* 3-5 cm					***0.005***
	0-1 *vs* 5-10 cm					***0.002***
PL3	1-3 *vs* 3-5 cm					***0.045***
PO2	0-1 *vs* 10-15 cm					***0.014***
	1-3 *vs* 10-15 cm					***0.024***
	3-5 *vs* 10-15 cm					***0.004***
PO3	3-5 *vs* 5-10 cm					***0.021***

	Source	df	SS	MS	F	P(MC)
Taxa richness	si	1	420.47	420.47	12'352	0.327
	st(si)	4	1371.7	342.93	15'334	0.184
	la(st(si))	24	5378.8	224.12	10'742	0.411
	Res	26	5424.3	208.63		
	Total	55	12558			
Meiofauna community structure	si	1	14467	14467	28'748	***0.047***
	st(si)	4	20466	5116.5	37'506	***0.001***
	la(st(si))	24	33321	1388.4	2'283	***0.001***
	Res	26	15812	608.14		
	Total	55	82065			
Pair-wise test	PL1 *vs* PL3					***0.022***
	PL2 *vs* PL3					***0.005***
	PO1 *vs* PO3					***0.006***
	PO2 *vs* PO3					***0.019***
PL1	1-3 *vs* 5-10 cm					***0.034***
	1-3 *vs* 10-15 cm					***0.044***
PL2	0-1 *vs* 1-3 cm					***0.044***
	0-1 *vs* 3-5 cm					***0.03***
PO2	0-1 *vs* 5-10 cm					***0.0465***

Table 3 – ***Results of the PERMANOVA test*** *carried out to ascertain differences in meiofaunal assemblage (i.e. total abundance, taxa richness and meiofaunal community structure between sites (si), stations (st) and sediment layers (la). Reported are df = degree of freedom; MS = mean square; F = F statistic; P = probability level. In italic and bold significant P values.*

Sampling stations in PO showed an increase of total meiofaunal abundance from the surface sediment to the intermediate strata (maximum value at 3-5 cm in PO1 and at 1-3 cm in PO2 and PO3 stations). PL1 showed higher values in 0-1 and 1-3 layers, while from the 3–5-layer abundances were very low; similarly, PL2 showed larger values only in the 0-1b; PL3 was characterized by values increasing from 0-1 to 1-3 layer and then decreasing towards the bottom (fig.5).

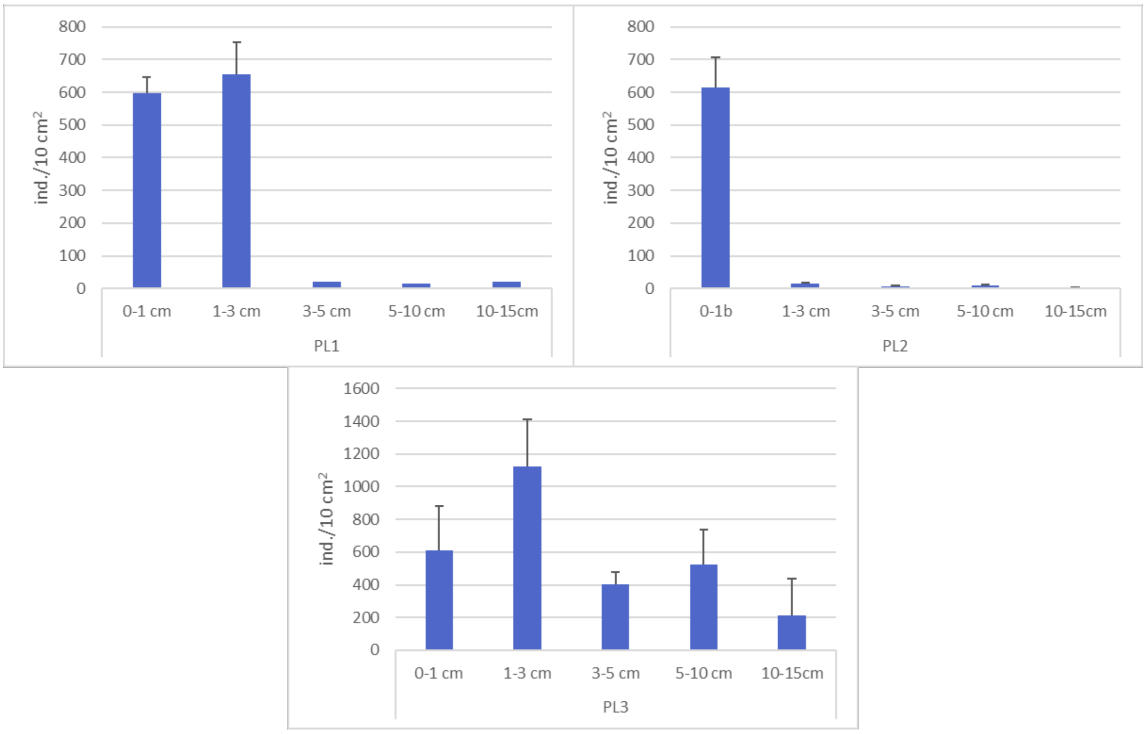

*Figure 5 – **Vertical distribution of total abundances at all PL sites.***

A total of 21 higher taxa, including Foraminifera and Ciliata, were found. The total number of taxa ranged from 8 at PL1 to 17 at PL2. At PO site the number of taxa increased moving away from the vent (from 9 to 16), while at PL site, from PL2 the highest total number of taxa was reported (17) and from PL1 the lowest (8). At PL a total of 19 taxa were identified: Nematoda, Foraminifera, Copepoda and their *nauplii,* Amphipoda, Cnidaria, Ciliata, Polychaeta, Oligochaeta, Ostracoda, Halacarida, Sipuncula, Platyhelminthes, Rotifera, Bivalvia, Tanaidacea, Gastrotricha, Cladocera, Gasteropoda, and Cumacea, while at PO 18 taxa were present: Nematoda, Foraminifera, Copepoda and their *nauplii*, Amphipoda, Ciliata, Polychaeta, Oligochaeta, Ostracoda, Halacarida, Sipuncula, Platyhelminthes, Rotifera, Bivalvia, Gastrotricha, Tardigrada, Cladocera, Priapulida and Gasteropoda.

Even though the PERMANOVA did not reveal any significant differences, in PL1 and PL2 the total number of taxa appeared to decrease strongly with depth layer (fig. 6).

*Figure 6 – **Changes in the total number of taxa for all stations.***
Blue: PL
Light blue: PO

Meiofauna abundances and number of taxa appear to be mostly unrelated, particularly at PL site where PL2 shows the lowest total abundance and the higher total number of taxa (fig. 7).

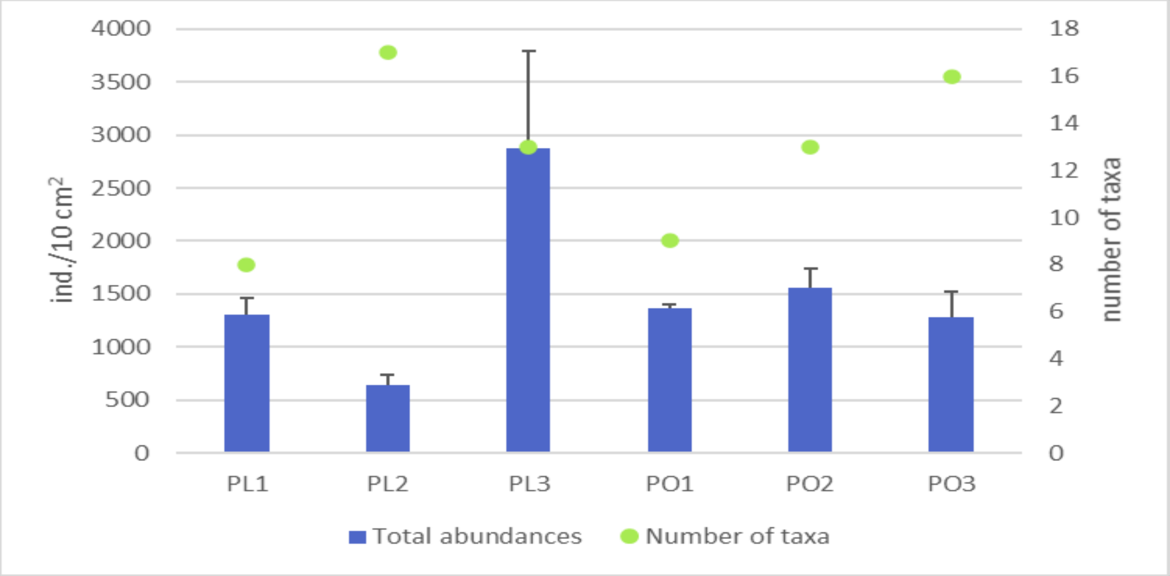

*Figure 7 – **Total abundance and number of taxa per site**.*

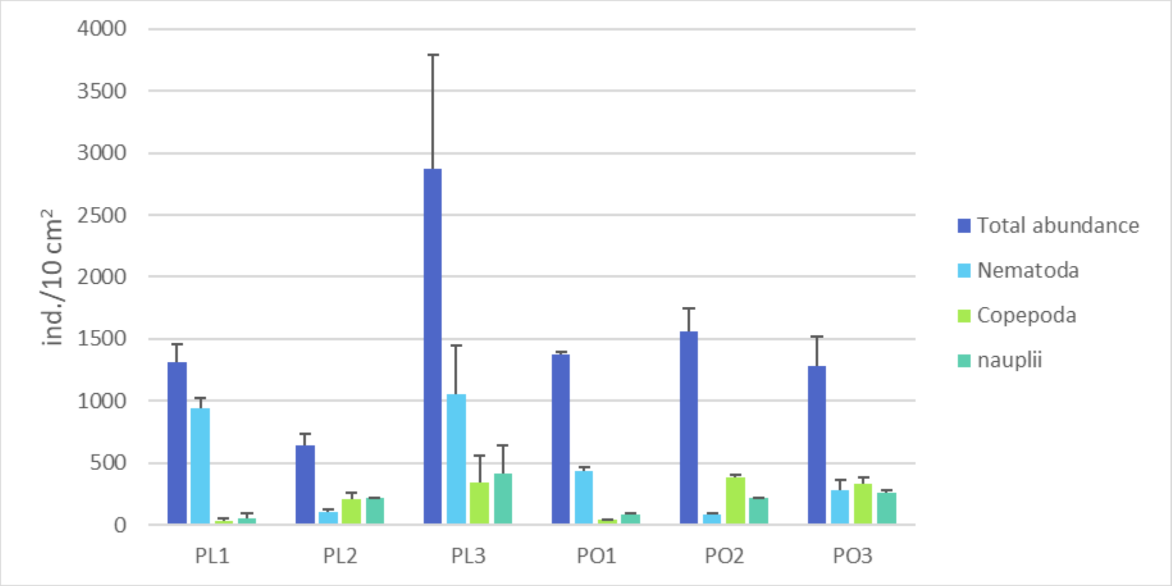

*Figure 8 – **Nematoda, Copepoda, nauplii and total meiofaunal abundances per site.***

The most represented taxa were Nematoda and Copepoda (adults and their *nauplii*). Total Copepoda abundances always increased when moving away from the vent station, while Nematoda did not show a clear trend, but their lowest abundances were registered at intermediate stations at both sites (fig.8).

Nematoda were the most representative taxon at PL1 (71.9%) and showed a high contribution at PL3 too (36.63%), Copepoda and their *nauplii* dominated in PL2 and PO3 (65.7% and 46.3%), while in PO1 and PO2 these taxa combined did not reach 50% of contribution, even if at PO1 Nematoda were more relevant than Copepoda and their *nauplii* while the opposite happened at PO2. Ciliata were found in very high abundances at PL1 and PL3 and

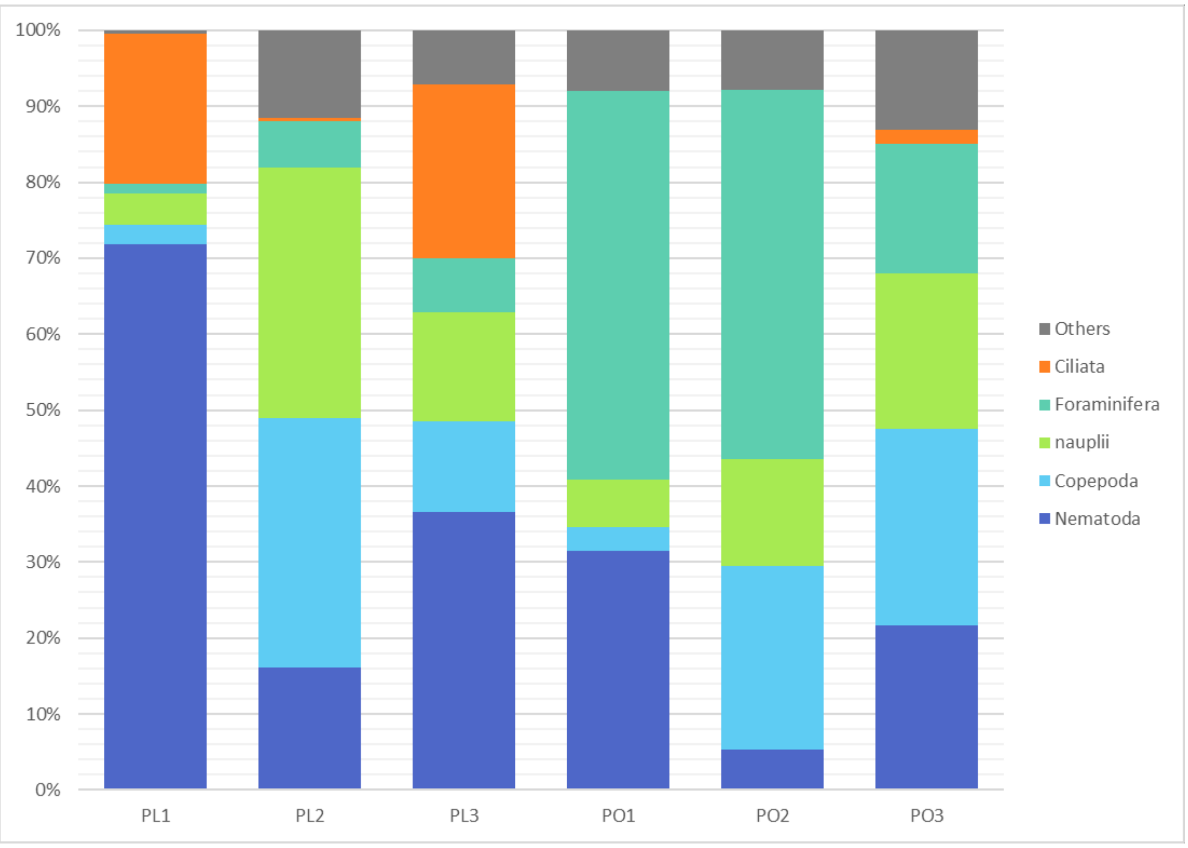

*Figure 7 – **Meiofaunal assemblages at all investigated stations.** Others: Amphipoda, Cnidaria, Polychaeta, Oligochaeta, Ostracoda, Halacarida, Sipuncula, Platyhelminthes, Rotifera, Bivalvia, Tanaidacea, Gastrotricha, Tardigrada, Cladocera, Priapulida, Gasteropoda and Cumacea.*

Foraminifera at PL2, PO1, PO2 and PO3 (Fig. 9). Copepoda abundances appeared to be lower in the vicinity of vent activity.

Polychaeta and Ostracoda occurred at every station, Gasteropoda were present at PL2 and PO3 and Rotifera were found at every station but PL1. Oligochaeta, Halacarida, Sipuncula appeared at four stations, while all other groups were present at three or less stations (Fig. 10).

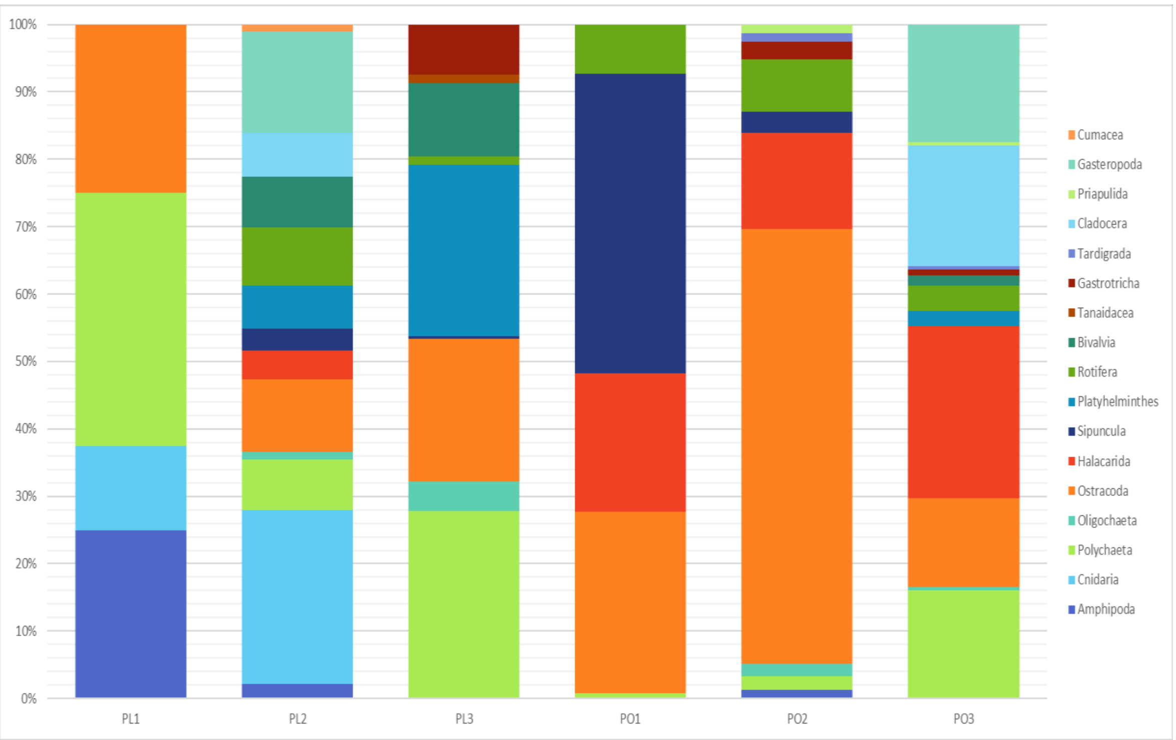

*Figure 8 – **Focus on the meiofaunal assemblages of "others" category,** from fig. 9.*

Nematoda abundances showed a different vertical distribution depending on the site: in PL1 they decreased with depth, while in PL2 and PL3 they increased going deeper into the sediment; in PO1 they showed a bell-shaped curve – an increase towards sub-superficial layers followed by a decrease from 1-3 cm layer to the bottom; in PO2 they showed low abundances as well as with increasing sediment depth and in PO3 there was an increase with depth. On the other hand, Copepoda abundances showed a decreasing pattern with depth at all sites, even though at PO3 they increased in the 1-3 cm layer and they dropped at the deepest layer (Fig. 11).

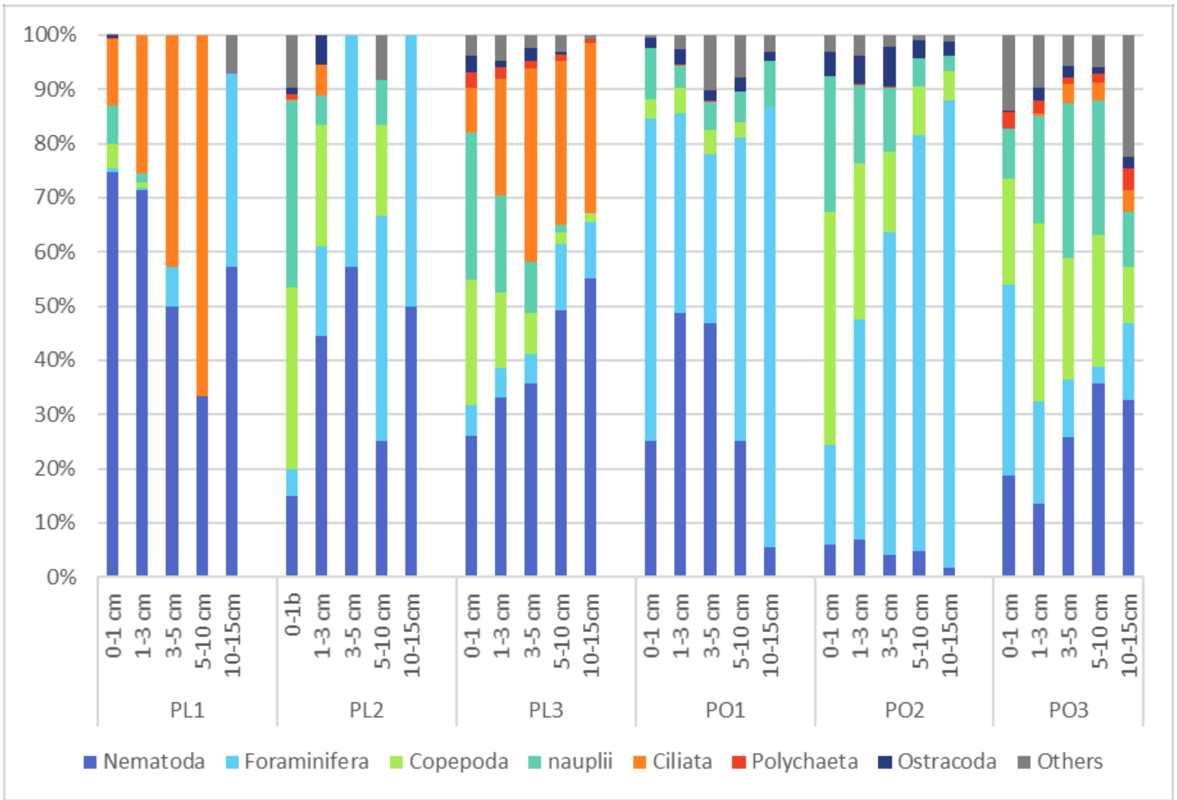

*Figure 9 – **Vertical meiofaunal community structure.** Others: Amphipoda, Cnidaria, Oligochaeta, Halacarida, Sipuncula, Platyhelminthes, Rotifera, Bivalvia, Tanaidacea, Gastrotricha, Tardigrada, Cladocera, Priapulida, Gasteropoda, Cumacea.*

PERMANOVA, carried out on the whole meiobenthic taxonomic composition, revealed significant differences between sites, stations and layers (PERMANOVA, p= 0.047, p=0.001 and p=0.001 respectively). Particularly, SIMPER analysis showed for PL and PO an average dissimilarity of 56.04%, mainly due to the different contribution of Foraminifera, Copepoda and their *nauplii*, Ciliata and Nematoda. For both PL and PO sites differences between stations appeared when comparing stations 1 *versus* 3 and 2 *versus* 3 (PERMANOVA: p=0.022 for PL1 *versus* PL3, p=0.005 for PL2 *versus* PL3, p=0.006 for PO1 *versus* PO2, p=0.19 for PO2 *versus* PO3). Significant differences between layers are reported in Table 3; SIMPER average dissimilarities for significant differences are reported in Table 4.

	Source	Average dissimilarity
	PL1 *vs* PL3	48.09%
	PL2 *vs* PL3	68.14%
	PO1 *vs* PO3	40.82%
	PO2 *vs* PO3	40.26%
PL1	1-3 *vs* 5-10 cm	40.51%
	1-3 *vs* 10-15 cm	61.22%
PL2	0-1 *vs* 1-3 cm	35.66%
	0-1 *vs* 3-5 cm	54.74%
PO2	0-1 *vs* 5-10 cm	35.53%

Table 4 – ***Average dissimilarities calculated by SIMPER analysis for comparisons with significant differences*** *(see Table 3).*

Considering PL 1 and 3 stations, Nematoda were more abundant at PL1 while Copepoda and their *nauplii* and Foraminifera at PL3; PL2 *versus* PL3 is mainly due to higher abundances of Copepoda and their *nauplii* in PL2 and of Nematoda and Ciliata in PL3.

Moving to PO, PO1 *versus* PO3 was due to higher abundances of Copepoda and their *nauplii* and Polychaeta in PO3 and of Foraminifera in PO1, while Cladocera were present only at PO3 site; PO2 *versus* PO3 difference can be explained by Foraminifera, Copepoda and their *nauplii* and Polychaeta higer abundances in PO3 and Cladocera absence in PO2 but not in PO3.

The differences between layers in PL1 station were mainly due to Nematoda, Copepoda and their *nauplii* and Ciliata: Copepoda and their *nauplii* disappeared, Ciliata decreased in the 5-10 cm layer and disappeared in the 10-15 cm sediment layer and Nematoda showed in both cases a significant reduction in their abundances.

The differences in 0-1 *versus* 1-3 cm PL2 layers were mainly due to Copepoda and their *nauplii*, Cnidaria and Polychaeta: Cnidaria and Polychaeta disappeared completely, while Copepoda and their *nauplii* decreased; considering the 0-1 *versus* 3-5 cm PL2 layers, the differences were a consequence of Copepoda and their *nauplii* and Ciliata that disappeared, while Nematoda abundances decreased strongly.

For PO stations, only the comparison 0-1 *vesrus* 5-10 cm in PO2 appeared significant and was due to Copepoda and their *nauplii*, Sipuncula, Rotifera and Ostracoda: Copepoda and Ostracoda show a reduction in their abundances, while Sipuncula and Rotifera both disappeared in the 5-10 layer.

5. DISCUSSION

5.1 Effects of vents on TOC

The total organic carbon appeared to be low if compared with values registered at other vent sites (Dando *et al.*, 1995). Any significant correlation was detected between TOC (%) and total meiofaunal abundance and/or meiofaunal diversity (i.e. number of taxa) (data not shown; $R^2 < 0.05$).

5.2 Effects of vents on meiofaunal distribution and diversity

Previous studies reported different effects of venting on the meiofauna density inhabiting sediments surrounding deep vents or shallow-water vents and also to the presence of vent obligate meiofauna taxa at deep sea vents and their lack at shallow depths (Tarasov *et al.*, 2005). In the deep-sea, vent emissions negatively impact faunal abundance (Tarasov *et al.*, 2005), while in shallow environments they can promote meiofauna abundances, with higher values compared to the background sediments, coupled with a reduction in meiofaunal diversity and a dominance of nematodes (Kamenev *et al.*, 1993).

Meiofauna naturally show a patchy distribution (Danovaro *et al.*, 2003; Giere, 2009). In the present study, a heterogeneous distribution is present, and it can reflect the small-scale environmental heterogeneity that typically characterizes hydrothermal vent habitats (Gollner *et al.*, 2010), with different conditions present over a few meters distance.

Significant differences in total meiofaunal abundances within sites were detected only between stations 2 and 3 at the PL site, with PL2 showing considerably lower abundance values than PL3. The interaction between the sandy bottoms and the differences in pressure generated by the vigorous gas discharge — usually found at shallow-water vent systems — creates microcirculative patterns and small convective cells that ultimately influences microbial diversity and distribution (Price and Giovannelli, 2017). PL2 station was located at the edge of one of these convective cells, which can justify the presence of the biofilm at this station. Moreover, PL site showed a much higher fluid temperature than PO indeed, a high sediment temperature could be plausible, which is also known to be a major factor limiting the distribution of benthic organisms (Kamenev *et al.*, 1993; Dando *et al.*, 1995; Tarasov *et al.*, 1999). The presence of convective cells that create physical disturbance coupled with high temperature may explain the low meiofauna abundance found at this station. Conversely, vent activity itself did not seem to have a major impact on meiofauna abundances, since the stations located closer to the emission site did not show significant differences with any other station.

Total abundances appeared higher than those present in other shallow vent environments (Kamenev *et al.*, 1993; Thiermann *et al.*, 1997; Tarasov *et al.*, 1997; Colangelo *et al.*, 2001, Zeppilli and Danovaro, 2009), but consistent with those reported in a study conducted in the Gulf of Naples (south of Italy) (Baldrighi *et al.*, 2020).

In most of the investigated stations, with the only exception for PL1 and PL2, the vertical distribution of the meiofauna showed similar patterns previously described in Baldrighi *et al.* (2020): an increase in the total abundance moving deeper into the sediment layer. This phenomenon can be explained as a migratory response by meiobenhtic organisms from the more disturbed sediment surface layers to the intermediate and less impacted layers (Leduc and Pilditch, 2013). Conversely, vertical abundances of PL1 and PL2 were higher in the superficial layers, and they dropped along the sediment depth profile (Table 3). High sediment temperature can be taken into account as a major factor shaping the meiofaunal vertical distribution at both stations PL1 and PL2, due to their proximity (3 meters distance between them). During the sampling procedure, researchers noticed a rapid temperature increase going deeper in the sediment. In the light of this, it can be hypothesised that superficial layers presented temperatures lower enough to allow organisms to survive.

Considering the meiofaunal diversity, as total number of taxa, both investigated sites were characterized by higher values than that reported in Kamenev *et al.* (1993), Thiermann *et al.* (1997), Tarasov *et al.* (1999), *Colangelo et al.* (2001) and Zeppilli and Danovaro (2009). Even though no significant differences were detected between sites and stations, it is worth noticing that vent stations showed the lowest number of taxa, in accordance with Kamenev *et al*. (1993). The vent fluid emissions could prevent settlement of higher taxa sensitive to high temperatures, low pH, and/or high sulphide concentrations (Gollner *et al.*, 2010).

Moreover, the number of taxa at PL2 station were much higher than those found at all the other stations, except for the control station PO3. In this second case values were linear with those found in other similar environments (Mascart *et al.*, 2013; Baldrighi *et al*., 2020). The presence of a bacterial biofilm could explain the marked diversity reported at PL2 station, even if the total meiofaunal abundance was the lowest value registered compared to all the other stations. Indeed, the biofilm can act as a food source for the meiobenthic organisms (Zeppilli and Danoaro, 2009), creating favourable conditions for a well-diversified community at the very surface sediment layer in PL2.

PO total variation in the number of taxa were consistent with what Thiermann *et al.* (1997) described in Milos (Greece), as they recorded a general trend of decreasing species diversity from the seagrass end of their transect towards the hydrothermal area.

Considering the relationship between the total number of taxa and total abundance, at higher values of abundance did not always correspond higher values in diversity. If this relationship was respected at PO site, at PL site, and in detail at PL2 station, the lowest abundance in meiofauna was related to the highest number of taxa. This difference can be addressed by taking in consideration the distinct features characterizing the two sites: PO showed less-extreme conditions and no bacterial mat, while PL showed a combination of biofilm presence and high sediment temperature. Microbial mats are known as food source for different taxa (Nematoda: Zeppilli and Danovaro, 2009; Copepoda: Heptner and Ivanenko, 2002; Ciliata: Bernhard *et al.*, 2000, Foraminifera: Torres *et al.*, 2003; Rotifera: Pascal *et al.*, 2014) and a positive effect can be hypothesised for others, thus representing an aggregating factor, since the background fauna may concentrate around sites where the production of chemosynthetic or methanotrophic bacteria is added to the photosynthetic primary production (Tarasov *et al.*, 1999). Conversely, high sediment temperature acts as a limiting factor for meiofaunal abundances and in this case it could have limited the sediment layers with viable conditions.

As previously reported (Kamenev *et al.*, 1993; Tarasov *et al.*, 1999; Tarasov *et al.*, 2005), Nematoda dominated at almost all investigated stations. However, at PL2 and PO3 stations Copepods and their *nauplii* were the most represented taxa. Similar results were reported in Colangelo *et al.* (2001) and Zeppilli and Danovaro (2009).

Colangelo *et al.* (2001) found high copepod abundances in areas with moderate gas seepage or sulphur deposit confirming the preference of copepods for coarser sediment (Coull, 1985). In the present study, PL2 and PO3 did not show gas seepage. Even if any grain size analysis was performed, PO site was clearly characterized by coarse sediment (personal observation). At PL2, sulphur deposits were noticed during the meiofauna extraction from sediment, along with the presence of biofilm. It is known that copepods have developed specific adaptation to feed on bacterial mats (Heptner and Ivanenko, 2002), this might explain their dominance at that station.

At PO1 and PO2 stations, Foraminifera displayed particularly high abundances. Even if this group is rarely considered in meiofaunal analysis since they are unicellular, Foraminifera constitute environmentally a key ecological group in marine ecosystems and well adapted to CO_2 emissions (Di Bella *et al.*, 2016).

It is worth highlighting the contribution of another unicellular group of organisms, the Ciliata, as they give a great contribution to total abundance at PL1 and PL3 stations. Ciliata have often been reported as the most diverse group of microbial eukaryotes in different hydrothermal vents (López-García *et al.*, 2003, López-García *et al.*, 2007, Sauvadet *et al.*, 2010, Zhao and Xu, 2016) and protists can represent a trophic link between prokaryotes and higher trophic levels (Anderson *et al.*, 2012).

Community structure of taxa included in “others” seems to present a general variation among stations.

Meiofauna community structure showed significant differences at all levels of investigation.

Foraminifera were the main taxon responsible for the dissimilarity between PL and PO sites, as their contribution was much higher in PO than in PL. One possible explanation might be an effect of sediment grain size on the Foraminifera distribution variability. Grain size variations is known to be an important factor controlling foraminiferal distribution (Di Bella *et al.*, 2016), but granulometry analyses are needed to give more precise explanations.

On the other hand, the presence of Nematoda and Ciliata characterized PL site, and this could be partially explained by the presence of biofilm. The presence of bacteria can provide not only food for Nematoda (Zeppilli and Danovaro, 2009) but can also supported abundant communities of Ciliata, (Bernhard *et al.*, 2000). Also the group Copepoda and their *nauplii* contributed to the dissimilarity between sites: Copepoda appeared to be more abundant at PO site, while *nauplii* al PL.

Major differences between stations occurred at both sites between stations 1 *versus* 3 and stations 2 *versus* 3, highlighting the influence of vent activity on meiofaunal assemblages. Stations 3 were in both cases out of venting activity and characterized by the presence of seagrass mats, while stations 1 and 2 were respectively from active centres or in areas still affected by venting or degassing activity. Copepoda and their *nauplii* were reported in lower abundances in proximity of vent activity, while Nematoda dominated at PL1 and Foraminifera at PO1, probably suggesting a better resistance of these taxa to venting conditions, such as bubble stream and high fluid temperatures for Nematoda at PL1.

Differences between sediment layers were usually detected between surface and subsurface layers and they were due to a reduction or disappearance of certain taxa. Indeed, most of the taxa disappeared with increasing depth layer. Copepoda showed a strong decrease with sediment depth, while Nematoda had a slight reduction. Copepoda usually occupied the well oxygenated surface sediment layer (Grego *et al.*, 2014; Baldrighi *et al.*, 2020), whereas Nematoda, adapted to thrive with extreme environmental conditions (Tarasov *et al.*, 2006), were reported till the deepest layers.

6. CONCLUSIONS

This study documents, for the first time, the meiofauna abundance, diversity and distribution inhabiting vent areas around Vulcano and Salina Islands.

Some patterns in the meiofaunal distribution were confirmed, such as a general migration of meiobenthic organisms to sub-superficial layers, as well as a heterogeneous distribution on a small spatial scale reflecting the environmental heterogeneity that characterises these extreme environments.

On the other hand, some findings were in contrast with most of the literature on shallow hydrothermal vents: the investigated sites showed overall higher values in meiofaunal abundance and diversity (i.e. number of taxa) compared to previous studies.

These preliminary results confirmed that each vent habitat presents unique features of benthic communities inhabiting the surrounding sediments.

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