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## Colonization of synthetic sponges at the deep-sea Lucky Strike hydrothermal vent field (Mid-Atlantic Ridge): a first insight

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### Abstract :

The main objective of the present study was to investigate invertebrate colonization processes at deep-sea hydrothermal vents in response to environmental factors and to the presence of complex artificial substrata (i.e., synthetic sponges). We set out a pilot experiment at 1700 m depth on the Lucky Strike vent field (Eiffel Tower, Mid-Atlantic Ridge). Synthetic sponges were deployed in 2011 at five sites along a gradient of hydrothermal activity and were recovered in 2013, and the composition of macro- and meiofauna was assessed on four of them. The influence of temperature and fluid inputs on colonizer faunal abundance and diversity was analyzed. Faunal abundance and diversity decreased with increasing distance from vent emission. The colonizers were represented by a subset of species characterizing the natural populations at the Eiffel Tower edifice. Some taxa (e.g., pycnogonids, ophiuroids, cnidarians, foraminiferans) represented new records not yet found on deployed substrata on the Eiffel Tower. Synthetic sponges harbored a high percentage (from 17.5% to 55%) of juveniles and larval stages of polychaetes, molluscs, and copepods. A mature nematode community (mainly *Cephalochaetosoma* and *Halomonhystera*) in a reproductive stage was found. Variability in faunal composition was significantly correlated with distance from fluid emission. We hypothesize that the complex structure of inorganic sponge substrata may have favored settlement of juveniles and larvae. Sponge substrata may, therefore, help sample a wider range of organisms than other substrata, and, thereby, provide a more complete picture of vent biodiversity. The results provided in this study might improve our understanding of mechanisms that govern faunal colonization processes at vents.

**Keywords :** Synthetic sponges, Colonization, Lucky Strike, Meiofauna, Macrofauna, Substratum type

## Introduction

Hydrothermal vents (HVs) are hot spots of high productivity and biomass when compared to the surrounding deep-sea benthos (Tunnicliffe 1991; Van Dover et al. 2002). As vent fluid emissions are transient, hydrothermal sites have ephemeral lifespans ranging from years (e.g. the East Pacific Rise (EPR); Lutz et al. 2008) to decades or centuries (e.g., the Mid-Atlantic Ridge, (MAR); Humphris et al. 2002). Vents are patchily distributed and isolated from each other with large differences in spatial frequency of venting between ocean ridges (Beaulieu et al. 2015). On fast spreading ridges like the East Pacific Rise (EPR), characterized by frequent eruptions (Shank et al. 1998), vents are generally separated by a few kilometres (Tolstoy et al. 2006). Conversely, on slow spreading ridges (e.g. Mid-Atlantic Ridge, MAR), vent sites are more distant from each other (i.e. 100-350 kilometres; Beaulieu et al. 2013). In the Pacific, even when the nearest populated HV is situated several kilometres away (Marcus et al. 2009), nascent vent sites appear to be rapidly (months/years) colonized by vent organisms issued from a pool of regional species (Tunnicliffe et al. 1997; Mullineaux et al. 2010; Gollner et al. 2013). As in most ecosystems, colonization processes are intimately linked to reproduction, larval dispersal and recruitment as well as to immigration from surrounding environments (Gaudron et al. 2010), data for which there are still major knowledge gaps. Moreover, biological interactions between vent colonizers contribute to determine and maintain the composition and diversity of hydrothermal communities (Govenar and Fisher, 2007 and literature therein). Shank et al. (1998) suggested that successful vent faunal colonization may be strongly influenced by physical oceanographic processes and hydrothermal conditions, and also by temporal changes in geochemical composition of fluid emissions. In addition to the influence of fluid chemistry, the modification of substrata by microbial alteration or a preceding faunal species is an important mechanism that influence the colonization by a succession of species (Shank et al. 1998). However, our knowledge of colonization processes in the vent environment is still limited since natural recolonization observations are restricted to the

70 Pacific Ocean were major volcanic eruptions lead to the formation of new colonization areas. At  
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271 more temporally stable vent sites (MAR for example, Cuvelier et al. 2011), other means have to be  
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572 found to gain insights about recruitment dynamics.  
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773 Over the last decades, several colonization experiments have been used to help identifying the  
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1074 factors that influence the recruitment and settling of species in the vent environments. These studies  
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1275 focused on the deployment of substrata, using a variety of experimental designs, substratum types  
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1576 (i.e. organic and inorganic) and durations (e.g. from months to years). There were done mainly on  
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1777 the EPR (East Pacific Rise; Govenar and Fisher 2007; Gollner et al. 2013, 2015), on Juan de Fuca  
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1978 Ridge (northeast Pacific; Kelly and Metaxas 2008) and along the MAR (Gaudron et al. 2010;  
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2279 Ivanenko et al. 2011; Cuvelier et al. 2014; Zeppilli et al. 2015; Plum et al. 2016). On EPR and Juan  
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2480 de Fuca Ridge, the type of substratum and their structural complexity heavily influenced the vent  
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2781 faunal colonization in term of abundance and diversity (Govenar and Fisher 2007, Kelly and  
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2982 Metaxas 2008). In the Govenar and Fisher (2007) case study, artificial tube worms were deployed  
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3283 along a chemosynthetic primary productivity gradient including areas in which *R. pachyptila* does  
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3484 not occur. The authors demonstrated that complex physical structures could support the highest  
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3785 colonizers' density and diversity in areas of high chemosynthetic primary production. Moreover, a  
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3986 similar species richness was reported between natural aggregations of *R. pachyptila* and artificial  
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4187 aggregations in intermediate- and high-productivity zones, suggesting that complex physical  
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4488 structure alone can support local species diversity in active venting areas. On the MAR,  
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4689 colonization experiments on different organic and inorganic substrata have shown that after two  
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4990 years, the environmental conditions rather than the type of substratum were the most important  
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5191 factors influencing the settlement and colonization of fauna (Ivanenko et al. 2011; Cuvelier et al.  
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5492 2014; Plum et al. 2016). In contrast, the same experimental design showed that after 9 months, the  
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5693 density and composition of colonising nematodes were rather significantly influenced by the type of  
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5894 substratum (Zeppilli et al. 2015). Differences in conclusions from these studies emphasized the fact  
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6195 that deployment duration is an important factor to consider when examining colonization processes.  
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96 In addition, to abiotic and biotic factors, habitat complexity, including habitat provision by other  
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27 species, is known to play a key role in facilitating species abundance and diversity (Hull 1997;  
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98 Bertness et al. 1999). Complex habitats contribute to increase the area available for settlement,  
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79 benefit the retention of propagules (Eckman 1987; Tsurumi and Tunnicliffe 2003) and create a  
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100 variety of microhabitats that favour species interactions (Kelly and Metaxas 2008). Moreover, the  
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101 provision of space may also offer protection from predators and contribute to the concentration of  
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14 food resources (Van Dover 2002; Govenar et al. 2005; Govenar and Fisher 2007).  
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183 In the present study, we continue the examination of factors that influence colonization processes  
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204 on a particular substratum (artificial sponge) as part of a larger integrative study that was initiated in  
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105 2006 (Cuvelier et al. 2014) and it is still on-going. The overall objective of this global study is to  
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256 better understand colonization processes at deep-sea hydrothermal vents in response to  
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2707 environmental factors such as temperature, fluid flow and the presence/structure of different  
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308 substrata. This was experimentally assessed by using different types of substrata (wood, bones,  
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309 slates and sponges) that were deployed along a gradient of venting activity in the vicinity of the  
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3510 Eiffel Tower edifice at 1700 m depth on the Lucky Strike vent field located on the Mid-Atlantic  
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3711 Ridge (MAR). The results presented here concern only those obtained on the sponges between 2011  
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112 and 2013. We first examined the abundance and diversity of faunal assemblages, i.e. meio- and  
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4213 macrofaunal compartments, found on synthetic sponges after a two-year deployment time and we  
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4414 explored the relation between estimated environmental conditions (temperature, fluid inputs) and  
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4715 faunal abundance and diversity. In the discussion, we compared our results with those obtained in  
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116 preliminary and on-going experiments. Although the absence of duplication limits our conclusions,  
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517 this study presents a first insight about how a complex 3D structure, not directly deployed on the  
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5418 seafloor, may influence colonization processes in the vicinity of vents.  
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## 5719 58 5920 **2. Material and methods**

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## 121 2.1 Study site

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The Lucky Strike vent field is located on the MAR, south of the Azores (37°17.5'N, 32°16'W; Fig. 1). This vent field is characterized by the presence of multiple sulphide edifices located around a fossilized lava lake, at a mean depth of 1700 m (Ondréas et al. 2009). The 11-m high Eiffel Tower is a well-defined active edifice located south-east of the lava lake. Hydrothermal activity on the structure occurs through black smokers, flanges or diffusion zones (Cuvelier et al. 2009) and the temperatures of the focused emissions can reach 324°C (Charlou et al. 2000). The entire edifice is colonized by different faunal assemblages that were characterised by a series of ecological studies (Cuvelier et al. 2009; Cuvelier et al. 2011a; Sarrazin et al. 2015; Husson et al. 2016). Out of the six assemblages characterised by Cuvelier et al. (2009), five are visually dominated by mussels, differing in size and in the presence or absence of microbial mats. These assemblages colonise a narrow range of low temperature habitats, ranging from 4.8°C to 8.8°C in the mussels (Sarrazin et al. 2015). A sixth assemblage is composed of shrimp, mainly *Mirocaris fortunata* that inhabit warmer habitats, with temperature reaching up to 9.5°C (Cuvelier et al. 2011a). The diversity varies strongly along the fluid mixing gradient, with higher densities and species richness observed in low temperature habitats (Sarrazin et al. 2015). Since 2006, a series of colonization experiments were deployed on and around this edifice (Cuvelier et al. 2014, Zeppilli et al. 2015; Plum et al. 2016). The results presented here represent only a snap-shot of the experiment done between 2011 and 2013. Data on copepods from the same experiment but on the other substrata (slate, wood, bones) are presented in Plum et al. (2016).

## 5142 2.2. Experimental set-up

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Five single substrata (slate, wood, cow and pig bone, sponge) were deployed during the Momarsat 2011 cruise at five sites (1 to 5) located along a gradient of hydrothermal activity, representing a single sponge substratum per site. These sites were selected in previous experiments (Cuvelier et al.

146 2014; Zeppilli et al. 2015; Plum et al. 2016, Fig. 1), allowing for the characterization of the activity  
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147 gradient between the sites. Site 1 was the least active area located at the base of the edifice (low  
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148 fluid input). Site 2 (high emission) was the most active area among the selected sites. It is located  
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149 on the north-west side of the Eiffel Tower on top of the edifice. This site harboured the denser  
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150 assemblages of *Bathymodiolus azoricus* mussels. The substrata at site 3 (intermediate emission)  
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11 were placed near a crack with diffuse fluid flow characterized by the presence of a low abundance  
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14 of *Bathymodiolus azoricus* surrounded by microbial mats. Site 4 (inactive) was located 25 m from  
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153 two active edifices (Eiffel Tower & Montsegur) and was chosen as an external site with limited  
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154 hydrothermal input. A fifth site, located away from any hydrothermal influence was added to the  
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21 previous colonization experiments (see site 5, Fig. 1). This new site 5 (external) is situated in the  
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24 lava lake and characterized by the absence of detectable hydrothermal influence (Table 1). To  
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27 facilitate deployment and recovery, the synthetic sponges were tied by a ~ 15 cm long nylon rope to  
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30 the wood substrata (Fig. 1). The latter was equipped with an autonomous temperature probe (HOBO  
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33 U12-015-02, Onset), which recorded the local temperature on each site (as a proxy of hydrothermal  
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36 activity) at 15 min intervals during the entire deployment period. The synthetic sponges (namely E1  
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39 to E5) are similar to those used in the shower (mesh bath sponges). They are made in polyethylene,  
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42 a chemically resistant thermoplastic that can be very durable. These sponges are characterized by  
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45 the presence of numerous holes of ~1 mm diameter, creating a net forming convolution. The  
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48 estimated planar colonization surface of each sponge is approximately 0.455 m<sup>2</sup>. Before 2011, no  
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51 sponges were deployed on the Eiffel Tower colonization experiment. The idea behind deploying  
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54 these sponges was to offer a complex 3D substratum to the colonizing fauna and also a substratum  
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57 that was not directly laid on the rock substratum as the others but rather floating at approximately  
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60 ~50 cm from the seafloor. We postulated that our chance to trap larvae was increased in comparison  
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63 with the other type of substratum and also, that the complex structure of the sponge would offer  
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66 better protection against predators and a more suitable habitat for smaller organisms. The results  
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69 presented here concern only those found on the sponges. All 2011 substrata were recovered during  
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172 the BIOBAZ 2013 cruise with the Remotely Operative Vehicle (ROV) Victor6000. A few substrata  
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 173 were loss, including a bone from site 5 and the sponge from site 1 (E1) that was lost during  
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 174 recovery. This study is based on data available from 4 (sites 2-5) of the 5 initial sites.  
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### 1076 2.3. Evaluation of environmental conditions

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1477 In our dataset, the highest temperature ( $7.3 \pm 1.6^\circ\text{C}$ ) was found at site 2 which is concordantly the  
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 178 site with the highest fluid inputs. Site 3 was characterized by intermediate temperatures ( $5.5 \pm$   
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 1979  $0.6^\circ\text{C}$ ) while the inactive site 4 and external site 5 were characterized by the lowest temperatures  
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 180 ( $4.7 \pm 0.1^\circ\text{C}$  and  $4.3 \pm 0.1^\circ\text{C}$ , respectively), representing low to no hydrothermal influence (Table  
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 181 1). Mean temperature values reported in the present study (2011-2013) fell in the range of  
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 182 temperatures reported in previous experimental studies conducted between 2006 and 2011 and  
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 183 characterizing the investigated sites (Cuvelier et al. 2014; Zeppilli et al. 2015). Previous studies  
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 184 have demonstrated that temperature at the Lucky Strike vent field is a valuable proxy of the  
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 185 chemical characteristics of vent fluids (Sarradin et al. 2009). For instance, temperature correlates  
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 186 positively with total dissolved sulphide and iron concentrations (De Busserolles et al. 2009). Fluid  
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 187 input can also be estimated using the formula proposed by Sarradin et al. (2009):  $\% = 0.314 * T - 1.38$ ,  
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 188 calculated with the Eiffel Tower end-member temperature of  $324^\circ\text{C}$  reported in Charlou et al.  
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 189 (2000) and ambient temperature of  $4.4^\circ\text{C}$ . Indeed, fluid inputs are very low in diffuse flow areas,  
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 190 varying from 0.9% at our most active site 2 to 0.05% at the external site (Plum et al. 2016; Table 1).  
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### 5092 2.4 Sample processing

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5593 Upon recovery, all substrata were put in a thermally insulated sampling box and brought to the  
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 194 surface. On board, macrofauna (organisms retained on a  $250\ \mu\text{m}$  mesh) was sorted and separated  
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 195 into major taxa. The rinse-off of each substratum was put into separate flasks. Half of the samples  
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196 were fixed in buffered seawater formalin (4%) and the other half was preserved in 96° ethanol. In  
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 197 the laboratory, samples were analysed in details and passed over 250 µm and 20 µm sieves to  
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 198 separate the macrofaunal from the meiofaunal fraction. The limit of 250 µm and 20 µm for  
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 199 separating the faunal pool into macrofaunal and meiofaunal size classes were chosen in order to  
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 200 easily compare our results with previous studies (Cuvelier et al. 2014; Sarrazin et al. 2015; Zeppilli  
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 201 et al. 2015; Plum et al. 2016). In particular, the use of a 20 µm sieve for deep-sea meiofaunal  
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 202 fraction is recommended to avoid underestimation of biodiversity (Sarrazin et al. 2015). Juveniles  
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 203 of macrofauna found in the meiofaunal fraction were considered as temporary meiofauna. All  
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 204 faunal organisms retained on the sieves were identified under a Leica Wild 10 stereomicroscope.  
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 205 For nematode identification, 150 randomly collected individuals were mounted on slides after  
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 206 formalin–ethanol–glycerol treatment. They were identified to the genus level according to Platt and  
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 207 Warwick (1983, 1988), Warwick et al. (1998), and the recent literature dealing with new nematode  
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 208 genera and species from the Atlantic Ocean (NeMys database, Deprez et al. 2005). Different faunal  
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 209 morphotypes and/or unknown species were reported as sp1, sp2, etc. Furthermore, a colonization  
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 210 rate index (CI) was calculated by dividing the average number of colonists (per m<sup>2</sup>) by the number  
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 211 of days the sponges stayed at the seafloor (as proposed in Cuvelier et al. 2014 and adapted from a  
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 212 recruitment rate index from Romey et al. 1991; Table 2).

#### 2.4 Statistical analyses

215 Meio- and macrofaunal abundances were expressed as individuals/m<sup>2</sup> and reported in Table 2.  
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 217 Meio- and macrofaunal diversity was expressed as taxonomical richness (TR) and the rarefaction  
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 219 biodiversity indices for theoretical samples of  $n= 50$  and  $n=100$  individuals were calculated. All  
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 221 indices were calculated using the PRIMER6 software (Plymouth Marine Laboratory, UK; Clarke,  
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 223 1993). Larvae and nauplii were not included in the taxonomic richness or in other diversity indices.



220 Due to the lack of replicate, statistical analyses were limited to a principal component analysis  
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 221 (PCA) and a non-parametric multivariate multiple regression analysis. The PCA, based on square-  
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 222 root transformed data, was used to visualize between-sponge variations in meio- and macrofaunal  
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 223 composition (PRIMER6 software, Plymouth Marine Laboratory, UK; Clarke, 1993). The  
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 224 relationship between meiofaunal and macrofaunal abundance and diversity and environmental  
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 1225 variables (temperature, fluid inputs) was evaluated with a non-parametric multivariate multiple  
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 226 regression analysis (DistLM: distance-based linear model) using the PERMANOVA + add-on  
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 1227 package for PRIMER6 software (McArdle and Anderson 2001; Anderson et al. 2008). For total  
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 228 abundance and diversity indices, the Euclidean distance was used as a resemblance measure,  
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 229 whereas for species composition, the analysis was based on Bray-Curtis dissimilarities (with  
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 230 square-root transformed abundance data). Forward selection was carried out and the adjusted  $R^2$   
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 231 was selected as the criterion to enable fitting of the best explanatory environmental variables in the  
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 232 model (Anderson et al. 2008). The results are provided as marginal and sequential tests. The  
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 233 marginal test revealed how much each variable explains individually, ignoring all other variables.  
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 234 Following the results of this test, a sequential test was performed which examined whether the  
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 235 addition of a particular variable contributes significantly to the explained variation (Anderson et al.  
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 236 2008).

### 3. Results

#### 3.1 Faunal communities

240 **Taxonomic composition-** A total of 35 faunal taxa colonized the sponges (Table 3). Among this,  
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 241 19 taxa were found exclusively in the macrofaunal size class and 4 exclusively in the meiofaunal  
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 242 one (Table 4). The macrofauna was dominated by polychaetes with 10 taxa followed by gastropods  
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 243 (4 taxa), chelicerates (2 taxa), ophiuroids, mytilids and cnidarians (1 taxa each). In the meiofaunal,  
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 244 only nematodes (3 taxa) and one polychaete (Hesionidae sp. 1) were restricted to this fraction.  
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245 Larvae of polychaete and bivalve settlers were found as well as numerous copepod nauplii (Table  
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 246 3). Polychaetes, crustaceans, foraminiferans and cnidarians were found either on active or on  
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 247 inactive sites (Table 4). However, chelicerates, ophiuroids, mytilids and most gastropods were  
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 248 restricted to the substrata located at active and intermediate sites (2 and 3). No copepod nauplii and  
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 249 almost no nematodes were found on the substrata at inactive and external sites (4 and 5). With the  
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 1250 exception of five polychaete taxa (Glyceridae sp. 2, *Ophryotrocha* sp., Hesionidae sp. 2 and sp. 3.  
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 251 Trichobranchidae undet.), only a few taxa (*Lepetodrilus* sp., Nematode undet.) appear to be  
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 1252 exclusive to inactive sites (Table 4).

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 2053 **Density-** The highest faunal density (175 818 ind./m<sup>2</sup>), including juveniles and nauplii, was found  
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 254 on substrate E2 (high emission) and the lowest was found at the inactive site E4 (532 ind./m<sup>2</sup>)  
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 255 (Table 2 and Fig. 2). Overall, the abundance of organisms belonging to the meiofaunal size class  
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 2756 decreased with the diminution of fluid emissions. With the exception of site 5, the meiofaunal  
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 3057 fraction dominated the total faunal abundance, varying from 166 736 ind./m<sup>2</sup> on E2 (high emission  
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 3258 site) to 371 ind./m<sup>2</sup> on E4 (low hydrothermal influence) (Fig. 2). The density of organisms found in  
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 359 the macrofaunal size class showed a similar trend, varying from 9 081 ind./m<sup>2</sup> on E2 to 160 ind./m<sup>2</sup>  
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 3260 on E4 (Table 2). They showed a slight increase on site 5 (473 ind./m<sup>2</sup>) (Fig. 2).

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 4061 In more details (see also Tables 3 and 4), densities on E2 were dominated by Draconematidae  
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 4362 nematodes (*Cephalochaetosoma* sp.) as well as by copepod nauplii and adults. The macrofaunal  
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 4563 fraction was dominated by Dorvilleidae polychaetes. A similar result was reported on substratum  
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 464 E3 for the meiofaunal fraction but the macrofaunal fraction was rather dominated by *Bathymodiolus*  
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 5065 *azoricus* and *Protolira* sp. gastropods. For external site 4, the meiofauna on E4 was dominated by  
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 5266 bivalve settlers as well as by adult copepods and ostracods. The macrofaunal density was low with  
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 5367 relatively few representatives of bigger size copepods, ostracods, nematodes, foraminifera and  
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 5768 bivalve settlers. No polychaetes were present. On E5 (inactive site), the meiofauna was also  
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 6069 dominated by adult copepods and ostracods as well as bivalve settlers. No nematodes were present.

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270 For the macrofauna, 5 families of polychaetes as well as adult copepods and bivalve settlers were  
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272 **Diversity-** A higher total taxonomic richness was reported on the sponges located at the most  
 5 active sites E2 and E3 (Table 5). However, the rarefaction diversity indices showed the highest  
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 273 value at the external site E5 (Table 5). Lower values in the rarefaction diversity indices at E2 and  
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 274 E3 can be explained by a dominance of nematodes, particularly of the genus *Cephalochaetosoma*  
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 275 (representing 61% and 32% of the total abundance at E2 and E3, respectively) and copepods  
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 276 (representing 25% and 13% of the total abundance at E3 and E2, respectively) at the most active  
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279 **Community structure-** The structure of communities on the sponge substrata changed along the  
 23 emission gradient (Fig. 3a). Nematodes, mostly represented by the genera *Cephalochaetosoma*,  
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 280 *Halomonhystera* and *Oncholaimus*, highly abundant (>70%) at site E2, were replaced by  
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 27  
 281 crustaceans (i.e. especially copepods) away from the vent emission. At all sites, the densities of  
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 282 larvae and juveniles was remarkable, varying from a minimum of 127 ind./m<sup>2</sup> on E5 (representing  
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 283 18% of the abundance) to a maximum of 49 043 ind./m<sup>2</sup> on E3 (representing 55% of the abundance)  
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 36  
 284 (Fig. 3b). It included larvae of polychaetes and juveniles of nematodes (mostly *Cephalochaetosoma*  
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 38  
 385 and *Halomonhystera*), bivalve settlers as well as copepod nauplii and copepodid stages. Polychaetes  
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 286 had very low abundance on all substrata, except E5 where they represented 29% of the total  
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 43  
 287 abundance. Macrofaunal fraction represented a low proportion (~5%) of the total faunal abundance  
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 46  
 288 at both active (E2) and intermediate (E3) sites, but increased its contribution at the inactive (E4,  
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 289 30% of the total abundance) and external (E5, 65% of the total abundance) sites.  
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291 The PCA analysis showed that sponges situated at the high (E2) and intermediate (E3) emission  
 53 sites were strongly separated from the other substrata (Fig. 4), revealing a discrimination between  
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 292 sponges near the vent emissions with those located away from hydrothermal activity. The presence  
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 293 of high densities of *Cephalochaetosoma* explains the separation of sponge E2 while the extremely  
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295 high abundance of nauplii and copepods on both E2 and E3 sponges explained their separation from  
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 296 the substrata at other sites (E4 and E5).

297 **Colonization index-** The highest colonization index (CI) was found at the most active site E2,  
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 298 while lower values were found at the inactive and external sites (Table 2). Also, the meiofaunal CI  
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 299 was higher compared to that of the macrofauna, with the exception of substrata E5 where the  
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 300 macrofaunal CI was higher than that of meiofauna (Table 2).

### 302 *3.2 Links with environmental conditions*

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 203 Environmental variables are reported in Table 1. The DistLM analysis was performed to assess the  
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 304 influence of environmental variables on faunal descriptors (i.e. faunal abundance, diversity index  
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 205 and taxa composition). Results showed that changes in taxonomic composition were significantly  
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 306 correlated (66%) by the position of sponges from the fluid emission (Table 6), as observed in Figure  
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 307 5. No other significant correlations were found between the other environmental predictors  
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 33  
 308 (temperature, fluid inputs) and the abundance and diversity of fauna (Table 6).

## 310 **Discussion**

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 313 This pilot study showed preliminary results on deep-sea fauna (meio- and macrofaunal size classes)  
 314 colonizing artificial sponges deployed in a gradient of environmental conditions in the vicinity of an  
 315 active hydrothermal edifice on the Lucky Strike vent field (MAR). The role of environmental  
 316 features on the composition, density and diversity of the recruited fauna was considered. The  
 317 consideration of the meio- and macrofaunal size classes in our study differs from several others in  
 318 which they are considered separately. This dual approach is fundamental since both size classes

319 may have different life-histories linked to their different dispersal patterns (Warwick 1984; Gollner  
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 320 et al. 2015) and therefore, exhibit different colonization patterns.

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### 322 ***Insights on community composition and diversity***

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 323 The meiofaunal fraction was the most abundant fraction on the sponges, representing 70% to 95%  
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 324 of the total densities, with the exception of site 5 in which the macrofaunal fraction dominated  
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 325 (representing 65% of the total density). The dominance of meiofauna (copepods & nematodes) was  
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 326 similar to that found in a previous study on natural faunal assemblages on the same edifice (Sarrazin  
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 327 et al. 2015) and on deployed artificial substrata (Cuvelier et al. 2014). Nematodes are known to be a  
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 328 widespread dominant taxon that can cope with many habitat conditions (Zekely et al. 2006; Copley  
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 329 et al. 2007; Vanreusel et al. 2010) and able to quickly (within months) colonize artificial substratum  
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 330 deployed at vents (Zeppilli et al., 2015). Two genera (*Cephalochaetosoma* and *Halomonhystera*)  
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 331 dominated at the high and intermediate emission sites. This corresponds to what was already  
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 332 reported at the Eiffel Tower both from colonization experiments (Cuvelier et al. 2014) and natural  
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 333 communities (Sarrazin et al. 2015), confirming the dominance of these two genera near the Eiffel  
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 334 Tower edifice. In this study however, nematodes were almost absent from the substrata found at the  
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 335 external sites. This result differed from our previous colonization studies in which they were  
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 336 represented along the hydrothermal gradient (Cuvelier et al. 2014; Zeppilli et al. 2015).

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 337 Hydrodynamic processes play a key role in species distribution and dispersal (Marsh et al., 2001).

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 338 The colonization of sponges placed in the vicinity of vent fluids may have facilitated meiofaunal  
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 339 groups with less dispersal potential such as nematodes (Giere 2009), thanks to the transfer of  
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 340 organisms by local turbulence. Horizontal currents and fluid flux are known to affect faunal  
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 56  
 341 distribution and diversity in hydrothermal communities (Sarrazin et al. 2014, 2015) and several  
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 342 studies showed that, despite their limited active dispersal (Higgins and Thiel, 1988), nematodes  
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 343 were present in the water column, mainly suspended by water currents or bioturbation (Sibert, 1981;

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344 Palmer et al., 1988; Fonseca-Genevois et al. 2006). Moreover, Boeckner and co-authors (2009)  
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345 showed that different meiofaunal taxa, including nematodes, are able to colonize substrata  
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346 suspended at different distances (from 0.5 m to 3 m) above the sea floor. In their study, very weak  
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347 currents, along with the effect of tides, were sufficient to suspend and transport the meiofauna into  
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348 the water column and enhance their dispersal (Boeckner et al. 2009). In our study, nematodes were  
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349 apparently unable to settle on the sponges, located above the seafloor, in areas located away from  
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14  
350 hydrothermal activity. Weak hydrodynamic processes encountered away from vents may have  
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351 limited their settling.

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352 As frequently noted for hydrothermal vents, copepods were the second most abundant meiofaunal  
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353 taxon after nematodes (Vanreusel et al. 1997; Zekely et al. 2006; Gollner et al. 2007). They can  
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354 thrive in different hydrothermal microhabitats (Sarrazin et al. 2015) and are able to colonize  
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355 different organic and inorganic substrata (Plum et al. 2016). Similarly to nematodes, copepods  
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356 showed the higher abundances at the active sites but unlike them, they were still present, at lower  
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357 densities, at the inactive and external sites. This pattern was opposite to that reported by Plum et al.  
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34  
358 (2016) in which copepod densities from wood and slate substrata tended to increase with decreasing  
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359 fluid inputs. This observation seems to support that the coupling between the type of substratum  
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360 and the gradient of fluid emission also has a role in affecting the density patterns of copepods (Plum  
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41  
361 et al. 2016).

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362 The macrofaunal community composition on sponge substrata changed according to vent emissions  
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363 and its abundance decreased at the inactive and external sites. The most represented macrofaunal  
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364 taxa were those usually encountered at the Eiffel Tower vent site: the ‘engineering’ species *B.*  
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365 *azoricus*, lepetodrilid gastropods and polychaetes (Cuvelier et al. 2009, Sarrazin et al. 2015) and  
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366 reported also in a previous colonization study (Cuvelier et al. 2014). However, despite their  
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367 abundance at Eiffel Tower, no shrimp were extracted from the sponges. This may represent a  
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368 sampling bias as the shrimp are mobile and may have escaped during sponge recovery but it is also

369 likely that the microhabitat they offer does not correspond to that of the shrimp which are found in  
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370 the warmer habitats of Eiffel Tower (Sarrazin et al. 2015). Conversely, taxa such as ophiuroids and  
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371 pycnogonids that were never reported from our other substrata (i.e. wood and slate; Cuvelier et al.  
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372 2014) were collected. We can hypothesize that the convolutions of the sponges acted like a trap for  
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373 these taxa, as it was initially expected. These organisms, that are part of the natural Eiffel Tower  
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374 fauna, are difficult to sample (Sarrazin et al. 2015), so the use of such heterogeneous substrata may  
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375 offer a strategy for their collection. Indeed, the complex structure of synthetic sponges could  
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376 represent a suitable habitat and their complexity may have favoured the presence of a unique faunal  
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377 community (Zekeley et al. 2006) and increased the area available for settlement (Kelly and Metaxas  
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378 2008). Furthermore, in environments subjected to physical stress, habitat complexity could increase  
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379 the frequency of positive interactions enhancing faunal diversity (Kelly and Metaxas 2008 and  
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380 literature therein). Indeed, the presence of these taxa, new to the substrata (i.e. ophiuroids and  
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381 pycnogonids), was detected only on the sponges deployed at the most active sites and subject to  
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382 harsher environmental conditions. Sponges may also have been use as a protection against predators  
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383 (Van Dover 2003; Govenar and Fisher 2007; Kelly and Metaxas 2008). Moreover, as stated for  
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384 nematodes, ophiuroid and pycnogonid propagules could have taken advantage from the vicinity of  
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385 vent fluids to colonize the synthetic sponges.

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386 Gastropods (and few other groups) appear to be restricted to the active areas, while the polychaete  
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387 community appears to shift from one group to the other. Indeed, no redundancy in the polychaete  
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388 taxa between the sponges located at the active and inactive sites is observed as if there were two  
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389 distinct communities. Indeed, some families such as Ampharetidae, Polynoidae and Spionidae are  
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390 restricted to the venting areas. Others, such as Glyceridae, Dorvilleidae and Hesionidae have  
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391 different morphotypes between the active and inactive ones. A better resolution in polychaete  
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392 identification would help to describe these communities with more precision.

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393 Even if the macrofauna found on synthetic sponges showed lower abundance values compared to  
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394 the meiofauna, its diversity was almost twice that of the meiofauna, as observed in the natural Eiffel  
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395 Tower communities (Sarrazin et al. 2015). Nevertheless, this result could change once copepods are  
 1 identified at a lower taxonomic level, i.e. genus or species (see Plum et al. 2016), revealing a similar  
 396 2 identified at a lower taxonomic level, i.e. genus or species (see Plum et al. 2016), revealing a similar  
 3 or even higher meiofaunal diversity when compared to the macrofaunal one. Taxonomic richness  
 397 4 or even higher meiofaunal diversity when compared to the macrofaunal one. Taxonomic richness  
 5 values on sponges were lower than those reported at the Eiffel Tower edifice (19 macrofaunal taxa  
 398 6 values on sponges were lower than those reported at the Eiffel Tower edifice (19 macrofaunal taxa  
 7 versus 41 in Sarrazin et al. 2015) but similar to those found in our previous colonization experiment  
 399 8 versus 41 in Sarrazin et al. 2015) but similar to those found in our previous colonization experiment  
 9 (20 macrofaunal taxa in Cuvelier et al. 2014).  
 10 (20 macrofaunal taxa in Cuvelier et al. 2014).  
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1401 A total of 35 faunal taxa colonized the sponges, representing 44% of the faunal richness identified  
 15 at the Eiffel Tower edifice (79 meio- macrofaunal taxa; Husson et al. 2016). This was slightly  
 1402 16 at the Eiffel Tower edifice (79 meio- macrofaunal taxa; Husson et al. 2016). This was slightly  
 17 higher than those found on inorganic sponges deployed on the Juan de Fuca vent site (30 taxa, Kelly  
 1403 18 higher than those found on inorganic sponges deployed on the Juan de Fuca vent site (30 taxa, Kelly  
 19 and Metaxas 2008) and to those found on organic and inorganic substrata deployed at the Eiffel  
 1404 20 and Metaxas 2008) and to those found on organic and inorganic substrata deployed at the Eiffel  
 21 Tower edifice (Cuvelier et al. 2014). The repartition of macrofauna/meiofauna on the edifice shows  
 1405 22 Tower edifice (Cuvelier et al. 2014). The repartition of macrofauna/meiofauna on the edifice shows  
 23 that the number of taxa in the macrofauna dominates, representing ~59% of the identified taxa  
 1406 24 that the number of taxa in the macrofauna dominates, representing ~59% of the identified taxa  
 25 (Sarrazin et al. 2015). The repartition macrofauna/meiofauna was approximately the same here  
 1407 26 (Sarrazin et al. 2015). The repartition macrofauna/meiofauna was approximately the same here  
 27 (54%), although we did not reach a similar taxonomic resolution. In particular, while 12 taxa of  
 1408 28 (54%), although we did not reach a similar taxonomic resolution. In particular, while 12 taxa of  
 29 copepods were found in Eiffel Tower habitats (Sarrazin et al. 2015) and 45 on wood, slate and bone  
 1409 30 copepods were found in Eiffel Tower habitats (Sarrazin et al. 2015) and 45 on wood, slate and bone  
 31 substrata from the same sampling sites (Plum et al. 2016), in the present study the copepods were  
 1410 32 substrata from the same sampling sites (Plum et al. 2016), in the present study the copepods were  
 33 only identified at the subclass level. This lack of taxonomic resolution leads to an underestimation  
 1411 34 only identified at the subclass level. This lack of taxonomic resolution leads to an underestimation  
 35 of taxonomic richness, particularly in the meiofaunal compartment. Even if nematodes were  
 1412 36 of taxonomic richness, particularly in the meiofaunal compartment. Even if nematodes were  
 37 identified at the lowest taxonomic level, only a low proportion of the natural vent nematode  
 1413 38 identified at the lowest taxonomic level, only a low proportion of the natural vent nematode  
 39 community was found on the sponges (4 taxa on sponges/15 taxa on Eiffel Tower in Husson et al.  
 1414 40 community was found on the sponges (4 taxa on sponges/15 taxa on Eiffel Tower in Husson et al.  
 41 2016).  
 1415 42 2016).  
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#### 1417 ***Influence of environmental conditions***

1418 The community structure on the sponge substrata changed along the emission gradient. Half of the  
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 1419 61 taxa were indifferently present on active or inactive sites. For the rest of the fauna, a similar  
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420 proportions of taxonomic groups (~23%) were restricted either to areas influenced by hydrothermal  
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 421 activity or to those with little or no influence. For example, copepod nauplii and nematodes were  
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 422 restricted to the sponges from the active sites and over 35% of the polychaete taxa were only found  
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 423 on the sponges located outside the venting influence. Curiously, most of the bivalve settlers were  
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 424 found on the inactive sites. Whether they were representative of *Bathymodiolus azoricus* or of other  
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426 Four of the taxa (*Bathymodiolus azoricus*, *Pseudorimula midatlantica*, *Lurifax vitreus* and  
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441 Among the few taxa (i.e. mainly polychaetes) confined on the sponges at inactive sites (4 and 5),  
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446 2010) and recognized by the authors as a non-typical vent taxon. This could explain its presence  
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447 only at the inactive site.  
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448 The total faunal taxonomic richness decreased with distance from vent emissions (i.e.  
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449 E2>E3>E5>E4), the inactive site exhibiting the lowest taxon number. Concerning the rarefaction  
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450 diversity indices, the highest values were at the external site (i.e. E5>E2>E3>E4). This finding was  
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451 not totally in line with what reported by Cuvelier et al. (2014) in which high densities but low  
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452 diversity characterized the substrata at the most active sites. The highest faunal density was found  
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453 on the sponge from the most active site while the lowest was found at the site with low  
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454 hydrothermal influence (site 4). Both faunal size classes followed the same trend, exhibiting a slight  
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455 increase on the sponge from site 5. This decreasing pattern of density with decreasing vent  
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456 emissions was observed in most of our colonization studies at Eiffel Tower (Cuvelier et al. 2014,  
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457 Zeppilli et al. 2015, present study). Indeed, a higher faunal abundance at the proximity of vent  
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458 emissions is considered a typical feature of hydrothermal ecosystems (Tsurumi and Tunnicliffe  
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459 2001). Hence, areas with higher vent fluid emissions favour the recruitment of vent fauna (Metaxas  
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460 and Kelly, 2010). However, the patterns were different for the Plum et al. 2016 study, in which  
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461 trends in copepods density were linked to the substratum type. That is, an increasing density with  
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462 decreasing fluid emission was reported from wood substrata; on bone and slate substrata copepod  
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463 density tended to decrease from high and intermediate vent activity sites to the external ones. A  
19  
464 higher taxonomic richness was reported on the sponges located at the most active sites. The  
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465 dominance of certain groups, such as bivalve settlers on E4 or ostracods on E5 has an impact on the  
21  
466 rarefaction diversity indices, so that the highest diversities are found on the site with no  
22  
467 hydrothermal influence for the total fauna and macrofauna and at site 4 for the meiofauna. The  
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468 colonization index was also higher on the substrata from the active sites than on those from the less  
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469 active to inactive sites, suggesting that the presence of fluids is favourable to recruitment.  
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470 Variations in vent fluid composition is one of the main driver of faunal composition at Eiffel Tower  
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471 (Cuvelier et al. 2011b, Sarrazin et al. 2015, Husson et al. 2016). This is in accordance with several  
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472 vent ecological studies showing that thermal conditions (and associated factors) play a key role in  
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473 defining spatial distribution of the hydrothermal fauna. Similarly, we found that the variability in  
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474 faunal composition could be explained mainly by the position of our sponges from fluid emission.  
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475 This was confirmed by the PCA analysis that support a significant difference in community  
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476 composition (abundance, diversity, composition) between the sponges from the active (2 & 3) and  
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477 inactive (4 & 5) sites. Gradients of temperature and hydrothermal flux also influenced faunal  
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478 abundance and diversity in other vent colonization experiments (Shank et al. 1998; Mullineaux et  
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479 al. 2010; Kelly et al. 2007). In addition to the environment, the distribution, abundance and  
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480 diversity of settlers are also determined by other factors, including biological interactions  
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481 (Mullineaux et al. 2003; Bates et al. 2005).  
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#### 483 *4.3 Influence of substratum heterogeneity: some preliminary considerations*

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484 The presence of complex physical structures at hydrothermal vents may lead to the formation of  
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485 microhabitats (Kelly and Metaxas 2008). This increased heterogeneity may contribute to the  
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486 provision of space and accumulation of food sources and offer protection against predators (Van  
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487 Dover 2003; Govenar and Fisher 2007; Kelly and Metaxas 2008). Therefore, substratum  
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488 heterogeneity is expected to positively influence diversity, richness and abundance of associated  
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489 fauna (Govenar et al. 2005; Bergquist et al. 2007).  
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490 This study shows that the complex structure of synthetic sponges supports colonization by the vent  
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491 fauna. Studies with inorganic sponges as colonizing substrata were previously performed on the  
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492 East Pacific Rise (Kelly and Metaxas 2008; Gollner et al. 2013, 2015). These studies showed that  
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493 artificial sponges were a suitable colonization substratum as they significantly contribute to enhance  
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494 the abundance (higher abundance compared to basalts), diversity (higher number of taxa on  
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495 sponges) and evenness of colonizers compared to other inorganic substrata (e.g. basalt).  
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496 Kelly and Metaxas (2008) reported that the complex structure of sponges contributed to the  
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497 successful colonization of smaller species of polychaetes, larvae of gastropods and meiofaunal taxa.  
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498 Similarly, the sponges deployed at Eiffel Tower (present study) harboured a high percentage of  
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499 juveniles and larval stages (e.g. larvae of gastropods). A sex ratio biased in favour of nematode  
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500 females was found in our sponge samples and high percentages of gravid nematode females of  
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501 *Cephalochaetosoma* (27%-50%) and *Halomonhystera* (65%-84%) were observed at the high and  
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502 intermediate vent sites, indicating a mature community in reproductive stage. The presence of  
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503 abundant nauplii and juvenile copepod stages on sponges from active sites supported previous  
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504 observations from other inorganic and organic substrata (Plum et al. 2016) and from natural  
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505 community (Ivanenko et al. 2012, Sarrazin et al. 2015). This finding indicates that the Eiffel Tower  
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506 copepod community is well established and is able to thrive in different microhabitats (Sarrazin et  
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507 al. 2015, Plum et al. 2016) and also contradict previous assumptions that copepod larval stages  
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508 would only inhabit micro-habitats outside the hydrothermal influence (Tsurumi et al. 2001).  
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509 Although better replication and an in depth taxonomic identification are needed, results from our  
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510 pilot study suggest that synthetic sponges can be a suitable colonizing substratum for some taxa not  
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511 found on other organic and inorganic substrata (e.g. ophiuroids, pycnogonids, cnidarians and  
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512 foraminiferans). Moreover, sponges can act as a trap for juveniles and larvae of benthic fauna likely  
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513 due to their 3-dimensional/convolute shape and their position at ~ 50 cm above the bottom which  
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514 may have contributed to the retention of swimming larvae. Substratum properties (e.g. roughness,  
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515 heterogeneity, presence of small interstitial spaces) rather than their nature (e.g. organic vs  
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516 inorganic) may be more important in favoring larval settlement (Balazy and Kuklinski 2017). As  
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517 they favor settlers from the water column compared to benthic immigrants (regardless of their life  
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518 stage), sponge substratum floating above the seafloor may provide valuable insights in terms of  
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519 export of colonists from the benthic community to the benthic-pelagic compartment and import of  
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520 planktonic colonists to the benthic communities. This might significantly improve our  
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521 understanding of mechanisms and sources of recolonization in challenged benthic habitats.  
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750 **Tables**

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751 **Table 1** Location, depth and temperature of the sites where the substrata were deployed in the vicinity of the

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752 Eiffel Tower edifice (Lucky Strike vent field, MAR). Sponge E1 was lost during recovery. T°C was

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753 measured with autonomous temperature probes deployed at each site. Standard deviations are given in

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754 parenthesis. Fluid inputs (%) have been estimated using the formula provided by Sarradin et al. (2009).

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<b>Substratum</b>	<b>E2</b>	<b>E3</b>	<b>E4</b>	<b>E5</b>
Emission	High	Intermediate	Inactive	External
Latitude (N)	37°17.3484'	37°17.3404'	37°17.3181'	37°17.465'
Longitude (W)	32°16.5333'	32°16.5379'	32°16.5331'	32°16.800'
Depth (m)	1699	1698	1705	1741
T°C	7.3 (±1.56)	5.5 (±0.55)	4.7 (±0.13)	4.3 (±0.07)
% Fluid	0.91	0.35	0.096	0.05

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**Table 2** Meiofaunal, macrofaunal and total faunal abundances on the sponge substrata recovered after 24 months. The colonization rate index (CI) is also reported and calculated by dividing the number of animals (per m<sup>2</sup>) by the number of days the substrata stayed at the seafloor.

<b>Site code</b>	<b>Meiofauna (ind./m<sup>2</sup>)</b>	<b>Macrofauna (ind./m<sup>2</sup>)</b>	<b>Total fauna (ind./m<sup>2</sup>)</b>	<b>Meiofauna CI (ind./m<sup>2</sup>/day)</b>	<b>Macrofauna CI (ind./m<sup>2</sup>/day)</b>	<b>Total fauna CI (ind./m<sup>2</sup>/day)</b>
E2	166 736	9081	175 818	218.2	11.9	230.7
E3	84 622	4226	88 846	110.8	5.5	116.3
E4	371	160	532	0.5	0.2	0.7
E5	255	473	727	0.3	0.6	0.95

769 **Table 3** Taxonomic composition and densities of meiofaunal and macrofaunal organisms colonizing the  
 1  
 270 inorganic sponges deployed at the Eiffel Tower edifice (Lucky Strike vent field, MAR) after a two-year  
 3  
 471 experiment. Higher values are indicated in bold. In the group of ‘others’ are included: molluscs and  
 5  
 772 miscellaneous specimens too damaged to be identified.

Taxon	Species	Densities (ind./m <sup>2</sup> )				
		E2	E3	E4	E5	
<b>Annelida</b>						
<b>Polychaeta</b>						
	Glyceridae	Glyceridae sp1	2.2	0.0	0.0	0.0
		Glyceridae sp2	0.0	0.0	0.0	6.6
	Ampharetidae	Undetermined sp.	679.1	347.3	0.0	0.0
	Dorvilleidae	Undetermined sp.	1907.7	301.1	0.0	0.0
		<i>Ophryotrocha</i> sp.	0.0	0.0	0.0	74.7
	Polynoidae	<i>Branchipolynoe</i> cf. <i>seepensis</i>	19.8	17.6	0.0	0.0
		Undetermined sp.	2.2	0.0	0.0	0.0
	Spionidae	<i>Laonice</i> sp.	2.2	6.6	0.0	0.0
	Hesionidae	Hesionidae sp1	35.2	0.0	0.0	0.0
		Hesionidae sp2	0.0	0.0	0.0	44.0
		Hesionidae sp3	0.0	0.0	0.0	30.8
	Trichobranchidae	Undetermined sp.	0.0	0.0	0.0	4.4
	Polychaete larvae	Undetermined sp.	709.9	167.0	0.0	52.7
<b>Arthropoda</b>						
<b>Crustacea</b>						
<b>Maxillopoda</b>						
	Copepoda	Undetermined sp.	21 863.7	23 356.0	162.6	191.2
	Nauplii	Undetermined sp	27 013.2	<b>29 580.2</b>	0.0	0.0
	Ostracoda	Undetermined sp.	740.7	120.9	134.1	<b>208.8</b>
<b>Malacostraca</b>						
	Amphipoda	Undetermined sp.	0.0	2.2	0.0	33.0
<b>Chelicerata</b>						
<b>Arachnida</b>						
	Halacaridae	Undetermined sp.	241.8	76.9	0.0	0.0
	Pycnogonida	Undetermined sp.	0.0	2.2	0.0	0.0
	Hexapoda	Undetermined sp.	4.4	0.0	0.0	0.0
<b>Echinodermata</b>						
	Ophiuroidea	Undetermined sp.	2.2	2.2	0.0	0.0
	Foraminifera	Undetermined sp.	83.5	24.2	33.0	0.0
<b>Mollusca</b>						
	Mytilidae	<i>Bathymodiolus azoricus</i>	241.8	692.3	0.0	0.0
	Bivalve settlers	Undetermined sp.	0.0	2.2	<b>180.2</b>	74.7
<b>Gastropoda</b>						
		<i>Lepetodrilus</i> sp.	0.0	0.0	0.0	6.6
	Lepetodrilidae	<i>Lepetodrilus atlanticus</i>	33.0	149.5	0.0	0.0
		<i>Pseudorimula midatlantica</i>	4.4	0.0	0.0	0.0

	Orbitestellidae	<i>Lurifax vitreus</i>	30.8	22.0	0.0	0.0
1	Skeneidae	<i>Protolira</i> sp.	112.1	661.5	17.6	0.0
2	<b>Nematoda</b>	Undetermined sp.	0.0	0.0	4.4	0.0
3	Draconematidae	<i>Cephalochaetosoma</i> sp.	<b>106 977.2</b>	28 299.0	0.0	0.0
4	Monhysteridae	<i>Halomonhystera</i> sp.	14 313.7	5008.7	0.0	0.0
5	Oncholaimidae	<i>Oncholaimus</i> sp.	715.7	0.0	0.0	0.0
6	<b>Cnidaria</b>	Undetermined sp.	2.2	0.0	0.0	0.0
7	<b>Others</b>	Undetermined sp.	79.1	6.6	0.0	0.0
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11	<b>Total density</b>		<b>175 817.6</b>	88 846.2	531.9	727.5

**Table 4** Distribution of the different taxa on the sponges substrata at active (E2), intermediate (E3), inactive (E4) and external (E5) sites. Only a few taxa are shared between active (E2 and E3) and inactive sites (E4 and E5). Ma: organisms found exclusively in the macrofaunal size class (> 250 µm), Me: organisms found exclusively to the meiofaunal size class (between 20 µm and 250µm), Me/Ma: organisms found in both meiofaunal and macrofaunal size classes.

Organism	E2	E3	E4	E5
<b>Polychaetes</b>				
Glyceridae sp 1	Ma			
Glyceridae sp2			Ma	
Ampharetidae	Me/Ma	Me/Ma		
Dorvilleidae undet	Me/Ma	Me/Ma		
Dorvilleidae : <i>Ophryotrocha</i> sp				Ma
Polynoidae undet	Ma			
Polynoidae : <i>Branchipolynoe seepensis</i>	Ma	Ma		
Spionidae : <i>Laonice</i> sp.	Ma	Ma		
Hesionidae sp. 1	Me			
Hesionidae sp 2				Ma
Hesionidae sp 3				Ma
Trichobranchidae undet				Ma
Polychaete larvae	Me/Ma	Me/Ma		Me/Ma
<b>Crustacea</b>				
Copepoda undet	Me/Ma	Me/Ma	Me/Ma	Me/Ma
Copepoda nauplii	Me/Ma	Me/Ma		
Ostracoda undet	Me/Ma	Me/Ma	Me/Ma	Me/Ma
Amphipoda undet		Ma		Ma
<b>Chelicerata</b>				
Halacaridae undet	Me/Ma	Me/Ma		

Pycnogonida undet		Ma		
Hexapoda undet	Ma			
<b>Echinodermata</b>				
Ophiuroidea undet	Ma	Ma		
<b>Foraminifera</b>				
Foraminifera undet	Me/Ma	Me/Ma	Me/Ma	
<b>Mollusca</b>				
Mytilidae : <i>Bathymodiolus azoricus</i>	Ma	Ma		
Bivalve settlers		Me/Ma	Me/Ma	Me/Ma
<i>Lepetodrilus sp.</i>				Ma
<i>Lepetodrilus atlanticus</i>	Ma	Ma		
<i>Pseudorimula midatlantica</i>	Ma			
<i>Lurifax vitreus</i>	Ma	Ma		
<i>Protolira sp.</i>	Me/Ma	Me/Ma	Me/Ma	
<b>Nematoda</b>				
Nematoda undet.			Me	
<i>Cephalochaetosoma</i>	Me/Ma	Me/Ma		
<i>Halomonhystera</i>	Me	Me		
<i>Oncholaimus</i>	Me			
<b>Cnidaria</b>				
Cnidaria undet	Ma			
<i>others'</i>	Me/Ma	Me/Ma		

**Table 5** Meiofaunal, macrofaunal and total faunal diversity colonizing the inorganic sponges at the Eiffel Tower. Taxonomic richness (TR, no larvae and nauplii) and the rarefaction biodiversity indices ( $n=50$  and  $n=100$ ) are reported. Higher values are indicated in bold.

	Substratum	TR	ES(50)	ES(100)
Meiofauna	E2	<b>13</b>	3.1	3.9
	E3	10	2.9	3.7
	E4	5	<b>4.4</b>	<b>4.8</b>
	E5	2	2.0	2.0
Macrofauna	E2	<b>19</b>	5.5	7.1
	E3	16	6.0	7.4
	E4	2	2.0	–
	E5	9	<b>7.8</b>	<b>8.6</b>
Total fauna	E2	<b>25</b>	5.4	6.5
	E3	21	5.2	6.3
	E4	6	5.1	5.5
	E5	11	<b>8.8</b>	<b>9.7</b>

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**Table 6** Results of the DistLM analysis (Selection criterion:  $R^2$ ; Selection procedure: step-wise) highlighting the effect of environmental variables on faunal abundance and diversity on inorganic sponges at the Eiffel Tower edifice (Emission: position from fluid emission; SS: sum of squares; F: F statistic; P: probability level; \* $P < 0.05$ ; ns: not significant).

	Variables	SS	F	P		Variance (%)
Faunal taxa composition	Emission	5825.5	3.645	<b>0.042</b>	*	<b>66</b>
	Fluid (%)	881.48	0.381	0.840	ns	8
Faunal abundance	Emission	5331.9	4.704	0.175	ns	70
	Fluid (%)	370.59	0.195	0.904	ns	5
Rarefaction indices ( $n=50$ ; $n=100$ )	Emission	55.821	2.081	0.311	ns	51
	Fluid (%)	40.481	3.074	0.379	ns	37

806 **Figure captions**

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808 **Fig. 1** Location of the Lucky Strike vent field on the Mid Atlantic Ridge (MAR). Pictures showing  
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809 the sampling sites at the Eiffel Tower where the inorganic sponges have been deployed in 2011. Site  
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810 2: high hydrothermal fluid emission; Site 3: intermediate hydrothermal fluid emission; Site 4:  
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811 inactive site; Site 5: external site

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813 **Fig. 2** Meio- and macrofaunal density (ind./m<sup>2</sup>) reported from the synthetic sponges deployed at the  
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814 Eiffel Tower edifice.

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816 **Fig. 3** (a) Faunal community structure characterizing the inorganic sponges deployed in the vicinity  
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817 of Eiffel Tower. The contribution of the major taxa is expressed as %; the group ‘others’ include all  
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818 taxa representing less than 1% (i.e. cnidarians, echinoderms, foraminifers, chelicerates, hexapods);  
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819 (b) percentage of juveniles/larvae found (i.e. polychaetes, bivalves, nematodes and nauplii) vs  
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820 adults colonizing the sponges

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822 **Fig. 4** PCA based on taxa composition of synthetic sponges’ substrata deployed in the vicinity of  
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823 the Eiffel Tower edifice on the Lucky Strike vent field, Mid-Atlantic Ridge

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825 **Fig. 5** DistLM and dbRDA showing the effect of environmental variables on faunal taxa  
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826 composition. The position from fluid emission explained significantly (66%) the differences in taxa  
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827 composition.

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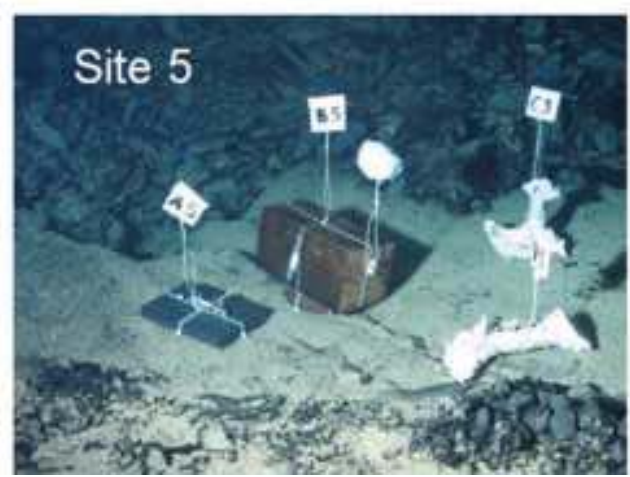
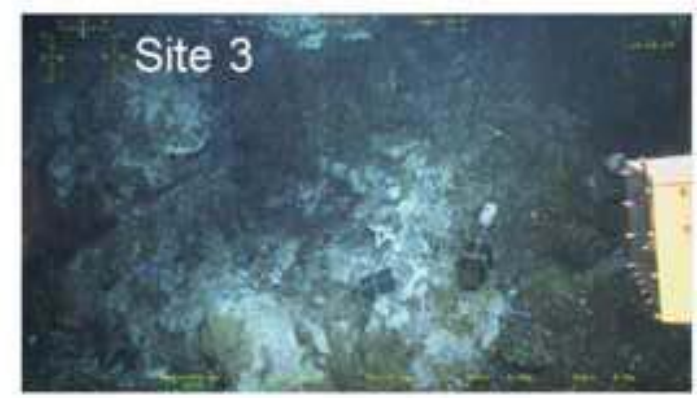
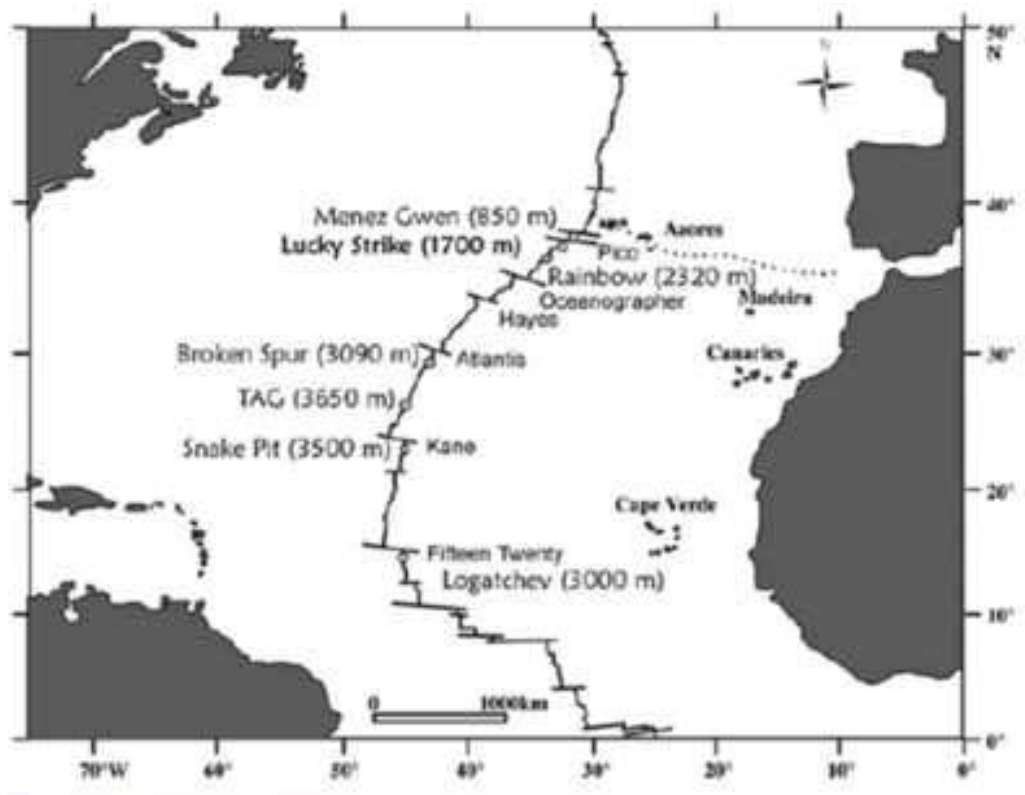
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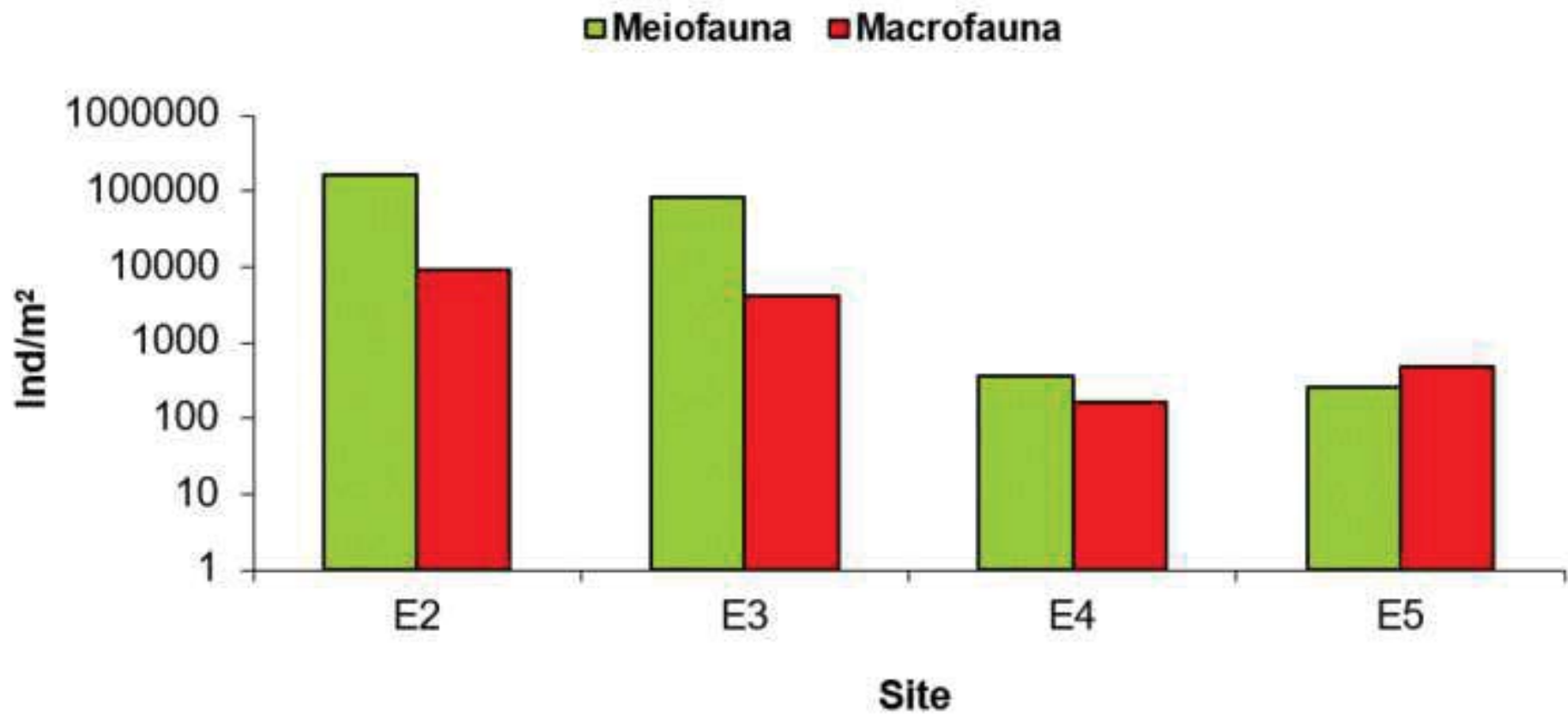


Figure 3

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