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1 Megabenthic assemblages on bathyal escarpments off the West Corsican Margin
2 (Western Mediterranean)

3
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14
15 **Abstract**

16
17 Deep-sea environments in the Mediterranean Sea have been widely degraded over the
18 past decades and thus there is an urgent need to implement protection measures. Within
19 European Union's Mediterranean waters vast extensions of the deep-sea ecologically
20 relevant ecosystems have been protected by integrating them to the Natura 2000
21 network. Inside the French Exclusive Economic Zone, this network is currently
22 expanding to off-shore areas, beyond 12 nautical miles. In this study, we characterized
23 megabenthic biodiversity on target features located inside a designed site of the south
24 west Corsican margin, particularly on a volcanic promontory on the south flank of the
25 Ajaccio submarine canyon and a wall of the Valinco Canyon, between 1990 and 2250 m
26 depth. By means of a fine scale three-dimensional photogrammetric analysis, four
27 megabenthic assemblages segregated by substrate were identified. Hard substrate
28 assemblages were characterized by the presence of sponges, polychaetes, gastropods
29 and the squat lobster *Munida tenuimana* while soft sediment assemblages were
30 characterized by the elpidiid holothurian *Penilpidia ludwigi* and an unidentified
31 sabellid. Highest densities were registered on serpulid thanatocoenoses, which hosted
32 widespread patches of an unidentified encrusting sponge. Lebensspuren had a diverse
33 origin likely deriving from the activity of epibenthic, infaunal and bathypelagic

34 organisms. In general, litter was not abundant at these offshore sites: in the Valinco site,
35 it had both a marine and land-based origin while at the even more offshore Ajaccio site,
36 it was mainly marine based. More extensive surveys would be advisable to confirm this
37 trend. This study provides new insight on the ecology and diversity of Mediterranean
38 deep-sea environments in the 2000 m bathymetric zone, highlighting the enduring
39 knowledge gap surrounding orographically complex deep-sea escarpments in the basin.

41 **Keywords**

42
43 Benthic Biocoenoses, Bathyal, Lebensspuren, Marine Litter, Three-Dimensional
44 Photogrammetry

46 **Introduction**

47
48 The deep sea (>200 m) is by far the most extensive biome on our planet, covering up to
49 66% of the Earth's surface (Bolgan and Parmentier, 2020). Great attention has been
50 dedicated at improving the knowledge on the biodiversity and functioning of deep-sea
51 ecosystems exposed to growing human impacts during the past decades (Ramirez-
52 Llodra et al. 2010). Consequently, benthic ecological studies in bathyal (200-3000 m
53 depth) and abyssal (3000-6000 m depth) environments have substantially increased (e.g.
54 Amon et al., 2017, Fernández-Arcaya et al., 2017; Simón-Lledó et al., 2019a).
55 Particularly, this research has mostly been focused on environments associated to high
56 diversity, high biomass and productivity, or both, such as submarine canyons, cold-
57 water coral (CWC) mounds, seamounts, mid-ocean ridges and diverse chemosynthetic
58 environments (e.g. Ramires-Llodra et al. 2010; Buhl-Mortensen et al., 2010; Fernández-
59 Arcaya et al., 2017; Levin et al., 2016; Rogers, 2018).

60 In the Mediterranean Sea, the discovery of several new CWC sites during the 1990's
61 (e.g. Etiope et al., 2010) triggered an ongoing expansion of benthic ecological research
62 on megabenthic assemblages beyond the shelf edge (> 200 m depth) using manned
63 submersible and ROVs. This work has been largely focused on the study of three-
64 dimensionally complex sessile suspension feeder assemblages (e.g. Orejas et al., 2009;
65 Bo et al., 2014; Mastrototaro et al., 2017; Santín et al., 2018). In the Gulf of Lion,

66 Ligurian and Corsican shelves, the mapping and characterization of epibenthic
67 assemblages of submarine canyons has mainly been conducted in 2008-2010 under the
68 MEDSEACAN and CORSEACAN exploration programmes led by the French Agency
69 of Marine Protected Areas (AAMP, now French Office for Biodiversity – OFB) in the
70 upper bathyal zone, between 200 and 800 m depth (Fourt et al., 2014a, b, 2017, 2019).
71 More generally, these explorations have been conducted from the lower circalittoral to
72 the upper bathyal, with few studies venturing into the lower bathyal zone
73 (Supplementary material 1).

74 Since the 1990s, most research conducted in lower bathyal Mediterranean environments
75 have focused on the characterization of crustacean and fish assemblages (Cartes, 1993;
76 Jones et al., 2003; Company et al., 2003; Sardà et al., 2004; Sion et al., 2004), however
77 other groups or multi-phyletic assemblages (Zibrowius, 1985; Olu et al. 2004; Cartes et
78 al., 2009; Tecchio et al., 2011a; b; Mecho et al., 2014; Boury-Esnault et al., 2015;
79 Sartoretto and Zibrowius, 2018) have received far less attention. Moreover, most
80 benthic ecological studies in the lower bathyal have addressed megabenthic
81 assemblages on soft sediment environments using bottom trawls and other bottom
82 contact gears (Cartes et al., 2009; Ramírez-Llodra, 2008). Due to these gears'
83 operational limitations on orographically complex hard bottoms, megabenthic
84 assemblages on lower bathyal canyon walls and seamount flanks remain widely
85 unknown (Zibrowius and Taviani, 2006). Only few underwater image-based studies
86 have provided a minor glimpse on megabenthic diversity at lower bathyal assemblages
87 of submarine canyons and seamounts (Sartoretto and Zibrowius, 2018; Bo et al., 2020).
88 Although not dedicated to biological studies, geological surveys have contributed to
89 these observations (Sosson and Guennoc, 1997), providing some clues to the occurrence
90 of habitat structuring taxa on hard substrates, on which the need for protection measures
91 is being considered.

92 In the recent decades, the number of human activities and pressures impacting bathyal
93 environments (e.g. bottom trawling, marine litter, oil and gas exploration and
94 exploitation, exploration for deep-sea mining) has increased and cumulated with large
95 scale climate-driven ocean changes (Levin and Le Bris, 2015). In the deep
96 Mediterranean, some anthropogenic pressures have substantially raised (e.g. bottom
97 trawling, marine pollution, exploration for hydrocarbons), which combine with changes

98 in water properties and basin-scale circulation (Adloff et al. 2015). There is thus a
99 pressing need for establishing a regional inventory that provides baselines for future
100 management and conservation plans, which are currently lacking (Aguilar et al., 2017;
101 Pierdomenico et al., 2019a). In the bathyal zone, canyons and seamounts are described
102 as particular hotspots of biodiversity, fulfilling several of the ecological criteria of the
103 Convention on Biological Diversity (CBD) for the identification of Ecologically or
104 Biologically Significant Areas (EBSA), as well those of Vulnerable Marine Ecosystems
105 (VMEs) from the FAO (Fernandez-Arcaya et al., 2017; Rogers, 2018; FAO 2019).
106 Within the European Union's (EU) Mediterranean waters, the protection of large areas
107 of the continental shelf and slopes, including numerous submarine canyon heads, have
108 recently been achieved through their integration within the Natura 2000 network (EC
109 2020/96), which aims at preserving at least 10% of EU's territorial waters by 2020 and
110 establish coherent protection networks, in line with the CBD and Nagoya
111 recommendations (Aichi Target 11). In order to achieve this goal, the Natura 2000
112 network will expand to offshore areas, beyond the 12 nautical miles. Within the French
113 exclusive economic zone five new offshore sites, expected to host particular biological
114 features were considered fulfilling the Reef designation criteria under the Habitat
115 directive (Fourt and Goujard, 2014). Among these new sites, several features including
116 rocky outcrops and coral thanatocoenoses with associated submarine canyons of the
117 south-western Corsican margin have been identified and an area named "Reefs of the
118 Ajaccio Seamount and of the Valinco rocky outcrops" has been proposed to the
119 European commission in 2017. It was integrated within the Natura 2000 network as a
120 Site of Community Importance in 2018 (FR94022020). The main aim of the current
121 study is to further document the largely unknown biodiversity patterns of this site. To
122 achieve this goal, in this study we (1) assess megabenthic distribution along the
123 explored bathymetric range, (2) address differences in standing stocks among different
124 substrates, (3) characterize megabenthic assemblages, (4) characterize and quantify
125 lebensspuren and (5) benthic litter, on two locations of this area corresponding to a
126 volcanic promontory on the south flank of the deep branch of the Ajaccio submarine
127 canyon and a steep wall in the Valinco Canyon (Fig. 1). We take advantage of recent,
128 three-dimensional photogrammetry approaches, which have shown to be especially
129 adequate to study megabenthic assemblages on steep bathyal environments (Robert et

130 al., 2017; Price et al., 2019). This method implemented from georeferenced still pictures
131 acquired using the new hybrid-ROV Ariane has allowed to obtain key ecological
132 information on habitat heterogeneity, fine-scale species habitat interaction and provided
133 insight into organism abundance and assemblage diversity. Additionally, we discuss the
134 significance of these results for the establishment of effective management tools and as
135 baseline for monitoring changes in the diversity of these bathyal habitats in forthcoming
136 years.

137

138 **Materials and Methods:**

139

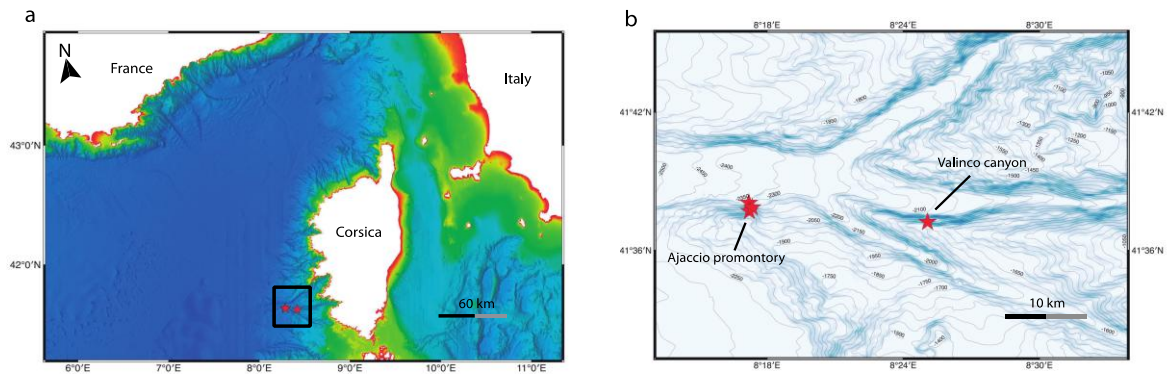
140 **Geographic setting**

141

142 The study area is located in the south-western Corsica margin (Fig. 1a). This area is
143 characterized by an extremely steep margin incised by the Valinco and Ajaccio
144 submarine canyons, which extend from the continental shelf (~100 m depth) down to
145 the foot of the island margin (2200 m depth) (Fig. 1b) where they merge into a major
146 canyon system (Kenyon et al., 2002). On this area's continental slope, numerous
147 volcanic promontories are found between 1200 m down to 2500 m depth (Rossi et al.,
148 1998). These volcanic rocks originated during the Miocene and have a broad talc-
149 alkaline character (Rossi et al., 1998; Rehault et al., 2012). These volcanic formations
150 on the south-western Corsican margin have been reported to be cemented by manganese
151 oxide coatings, as described for volcanic formations in the Ligurian, Sardinian and
152 north Corsican margins (Rehault et al., 2012; Bo et al., 2020).

153 The intermediate and lower southwestern Corsican slope is influenced by three major
154 water masses: the Levantine intermediate waters (LIW), which flow northward,
155 between 200 – 800 m depth, the Tyrrhenian deep water found between 800 and 1500 m
156 depth, and the western Mediterranean deep water which expands from 1500 down to the
157 bottom (Millot, 1987; Send et al., 1999; Zuñiga et al., 2007).

158



159

160

161 Figure 1. a) Corsica Island, the black square indicates the section of the Corsican margin where Ajaccio
 162 and Valinco Canyons study sites are located. b) Close up of the south-western Corsican margin showing
 163 both sampling sites. Red stars indicate transect locations (bathymetric metadata and Digital Terrain
 164 Model data products have been derived from the EMODnet Bathymetry portal - [http://www.emodnet-](http://www.emodnet-bathymetry.eu)
 165 [bathymetry.eu](http://www.emodnet-bathymetry.eu) and projection from Bathy-morphologie régionale de la façade Méditerranée et Corse
 166 (édition 2014, résolution 100m) (Loubrieu et al., 2014).

167

168 This study's primary target was the summit and flank of a volcanic promontory located
 169 at 2060 - 2250 m depth range, 27 miles off Ajaccio (Fig. 1b, Table 1). Due to adverse
 170 meteorological conditions that affected access to this site, a second target in the same
 171 area but closer to the shore was visited and used for a comparative assessment. This
 172 second target is located on a steep wall of the Valinco canyon, between 1690 - 1990 m
 173 depth (Fig. 1b, Table 1).

174

175 Table 1. Transect location, depth range, on the seafloor and covered surface area. AP: Ajaccio
 176 promontory, VC: Valinco canyon, Lat.: latitude, Lon.: longitude, min.: minutes

177

Ariane Dive #	Location	Depth (start)	Depth (end)	Lat. (start)	Lon. (start)	Lat. (end)	Lon. (end)	Time (min.)	Covered surface (m ²)
104-02	AP	2256	2127	41.6349	8.2854	41.6352	8.2827	160	223
105-03	AP	2228	2050	41.6325	8.2886	41.6293	8.2902	122	3530
106-04	AP	2060	1994	41.6312	8.2889	41.6261	8.2841	230	2774
107-05	VC	1694	1950	41.6235	8.4182	41.6191	8.4257	215	1187

178

179

180 **Image acquisition**

181

182 A total of 4 ROV photographic transects (Table 1) were recorded during the Cylice-Eco
183 oceanographic survey on board of the R/V “L’Europe” of the French Oceanographic
184 Fleet (23 September 2018 to 6 October 2018). Three transects were recorded on the
185 Ajaccio volcanic promontory and one on a wall of the Valinco Canyon (Fig. 1b, Table
186 1). Transects were performed with the Hybrid Remotely Operated Vehicle (H-ROV)
187 Ariane (Ifremer), which has been designed to perform georeferenced photographic
188 surveys of the seafloor to develop 2D-3D mosaics. The Ariane is equipped with a Nikon
189 D5500 digital camera which allowed to acquire high-definition geo-referenced still
190 images every 15 seconds (surveys at about 3 m above seabed). 1041 HD (6000 x 4000
191 pixels) still images were obtained covering a total area of 7714 m² (Table 1).

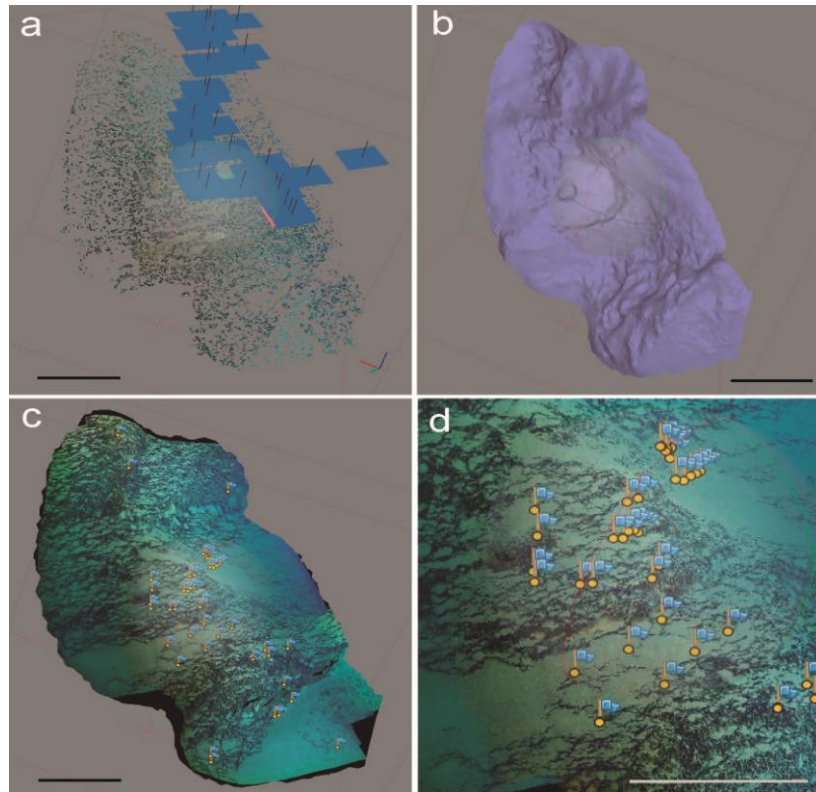
192

193

194 **Photogrammetry reconstruction and analysis**

195

196 The software Agisoft PhotoScan professional edition (v.1.2.5) was used to build 3D
197 image reconstructions. Models were constructed following a sequential workflow (Fig.
198 2) specified by Agisoft Photoscan Professional software using a MacPro equipped with
199 a 6 core Intel Xeon E5, with a processing speed of 3.5 GHz and an AMD FirePro D700
200 6144 MB image processor. The 3D reconstructions were employed to inspect fine-scale
201 spatial positioning of all megafaunal species (here defined as organisms larger than 10
202 mm), lebensspuren formations defined as traces generated by epibenthic and infaunal
203 organisms while feeding, moving or burrowing (Bell et al., 2013), and marine litter
204 items. In Agisoft Photoscan, still images were examined and markers were placed to
205 accurately georeference organisms, lebensspuren formation and marine litter items (Fig
206 2d). Once markers were placed, they were also visible in all other still images that cover
207 the same position from a different angle, avoiding item duplication. Posteriorly, markers
208 were exported as xyz text files for subsequent statistical analyses (Supplementary
209 material 2).



210

211

212 Figure 2. a) Camera alignment (blue squares) and dense point cloud construction, b) mesh creation, c)
 213 textured mesh reconstruction, d) close up of 3D reconstruction (textured mesh) with marker flags
 214 showing the position of megabenthic organisms. (Scale bars: 1 m)

215

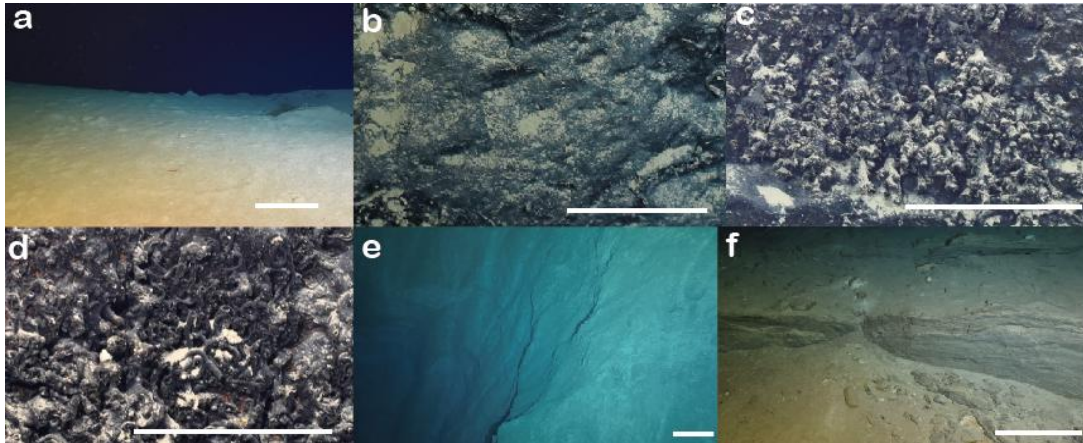
216 Megafaunal organisms were identified to the lowest possible taxonomic level. However,
 217 since organisms could not be sampled and identification to species level could not
 218 always be achieved, in some cases they were classified into morphospecies (visually
 219 distinct taxa) as it has been done in other image-based deep-sea studies (Robert et al.,
 220 2015; Simón-Lledó et al., 2019a). Lebensspuren formations were categorized based on
 221 their morphology and origin (Bell et al., 2013). Litter items were categorized based on
 222 the material they were made of and their origin. Marine litter is generally classified into
 223 two origin categories: land-based litter which originates from terrestrial sources and
 224 reaches the marine environment through wind or nearby waterways, and marine-based
 225 litter derived from discards generated in fisheries, aquaculture, marine traffic or military
 226 activities (Galgani et al., 2015). Substrates were classified into five different categories:
 227 soft sediments, bare rock, solitary coral thanatocoenosis, serpulid thanatocoenosis and
 228 compacted muds (Fig. 3). Bare rock and both types of thanatocoenoses were coated

229 with Mn-Fe oxides (Fig. 3b-d). Compacted muds occurred as vertical walls,
230 occasionally displaying slabs at their base (Fig. 3e-3f).

231

232

233



234

235 Figure 3. Substrate types categories considered. a) Soft sediments, b) bare rock, c) solitary coral
236 thanatocoenosis, d) serpulid thanatocoenosis, e) compacted muds vertical wall, f) compacted mud slabs at
237 the base of a vertical wall. (Scale bar = 50 cm).

238

239 **Statistical analysis**

240 In each 3D photogrammetric reconstruction, megabenthic morphospecies and
241 lebensspuren abundances were standardized by dividing the abundances registered in a
242 certain substrate type by the surface covered by this particular substrate, thus obtaining
243 density values. For all morphospecies and lebensspuren items, density was expressed as
244 the number of individuals ($n \text{ ind m}^{-2}$) or items ($n \text{ items m}^{-2}$) per square meter,
245 respectively. However, since encrusting sponge can undergo fission and fusion
246 processes promoting clonality (Blanquer et al., 2009), for the encrusting unidentified
247 sponge *Porifera* sp.1, density does not refer to individuals but individual patches.

248 Megabenthic assemblages were identified based on species composition by means of a
249 non-metric multidimensional scaling ordination (nMDS) of the sampling units, with
250 species abundances being square-root transformed, and ordination performed via a
251 Bray-Curtis dissimilarity matrix. Adonis permutation multivariate analysis of variance
252 and subsequent pairwise tests were used to test for significant differences amongst

253 assemblages. The nMDS and Adonis test were performed using the R-language function
254 “metaMDS” and “Adonis”, available in the vegan library of the R software platform
255 (Oksanen et al., 2016). Rare taxa, here defined as species occurring 3 times or less, were
256 excluded from the nMDS analysis.

257 The Indicator value Indice (IndVal) was used to determine which taxa were
258 representative from each assemblage. The IndVal method allows to identify
259 combinations of species that permit to discriminate a group of samples from other
260 samples in the analysis (Jordà Molina et al., 2019). IndVal measures were computed
261 using the function *indval* included in the *labdsv* package (Roberts, 2013).

262

263 **Results**

264 **Description of physical characteristics along ROV dives**

265

266 In the Ajaccio Canyon, the volcanic promontory, was explored between 1994 and 2256
267 m depth. This area was characterized by high cliffs with complex geomorphological
268 structures constituted by hard substrates and to a lesser extent gently sloping terraces
269 covered by soft sediments (Fig. 3a), which represented 28.3% of explored surface. Bare
270 rock was the most abundant substrate (Fig. 3b), covering 58% of the explored area. On
271 overhangs and tilted walls protected from sediment deposition, solitary coral and
272 serpulid thanatocoenosis (Fig. 3c and d) were found covering 6.7% and 7% of the
273 explored surface, respectively.

274 The Valinco Canyon was explored between 1694 and 1950 m depth. The area was also
275 characterized by the presence of vertical cliffs entirely constituted by compacted muds
276 (Fig. 3e), which covered 76% of the explored area. Along the cliffs several terraces
277 where observed being mostly covered by soft sediments (24% of explored surface)
278 alternated by compacted mud slabs (Fig. 3f).

279

280 **Megafaunal assessment**

281

282 A total of 4508 megafaunal organisms were observed along the 7714 m² of seafloor
283 explored during this study (Table. 2). In the Ajaccio volcanic promontory, a total of 20

284 morphospecies were identified (Table 2). Porifera and Polychaeta were the most diverse
 285 and abundant groups, being represented by 4 (Fig. 4 a-d) and 5 (Fig. 5 a-e)
 286 morphospecies and accounting 89% and 8.9% of all observed organisms, respectively
 287 (Table 2). The remaining phyla were represented by 11 morphospecies and accounted
 288 between 0.07% to 0.7% of all observed organisms (Table 2).

289 In the Valinco Canyon wall a total of 11 morphospecies were observed. Polychaeta, was
 290 the most diverse group, and along with Echinodermata were the most abundant phyla
 291 correspondingly representing 59.3% and 31.6% of observed morphospecies. The
 292 remaining phyla accounted for 1.3% and 3.9% of all observed organisms (Table 2).
 293 Rare taxa (≤ 3 records) represented 35% of the total morphospecies in the Ajaccio
 294 seamount and 73% in the Valinco canyon.

295

296 Table 2. Total abundance and taxonomic classification of megabenthic morphospecies quantified at the
 297 Ajaccio seamount and Valinco Canyon. (*) Observe that Group level has not been classified
 298 hierarchically, ranging from Phylum to species, to ease tabulation. n corresponds to the number of
 299 individuals except for Porifera sp.1 which corresponds to the number of patches.

Group (*)	Morphospecies	Canyon			
		Ajaccio		Valinco	
		n	%	n	%
Porifera	Porifera sp.1	3855	87.13	0	0
	Porifera sp.2	32	0.72	0	0
	Porifera sp.3	51	1.15	0	0
	Porifera sp.4	2	0.05	0	0
	cf. <i>Cladorhiza abyssicola</i>	0	0	1	1.3
Cnidaria	Hydrozoa	14	0.32	0	0
	<i>Desmophyllum dianthus</i>	3	0.07	0	0
	Actiniaria	0	0	1	1.3
Gastropoda	Gastropoda sp.1	24	0.54	0	0
	Gastropoda sp.2	2	0.05	0	0
Polychaeta	Polychaeta sp.1	295	6.67	27	35.5
	Amphinomid	11	0.25	0	0
	Sabellida	27	0.61	18	23.8
	Polynoid	3	0.07	0	0
	Serpulid	59	1.33	0	0
Decapoda	<i>Plesionika acanthonotus</i>	11	0.25	1	1.3
	<i>Aristeus antennatus</i>	1	0.36	0	0
	<i>Munida tenuimana</i>	11	0.09	1	1.3
Echinodermata	<i>Penilpidia ludwigi</i>	16	0.36	21	27.7
	<i>Ceramaster grenadensis</i>	4	0.09	2	2.6
	<i>Hymenodiscus coronata</i>	0	0	1	1.3
Chordata	Macrouridae	2	0.05	0	0

Mora moro
Bathypterois dubius

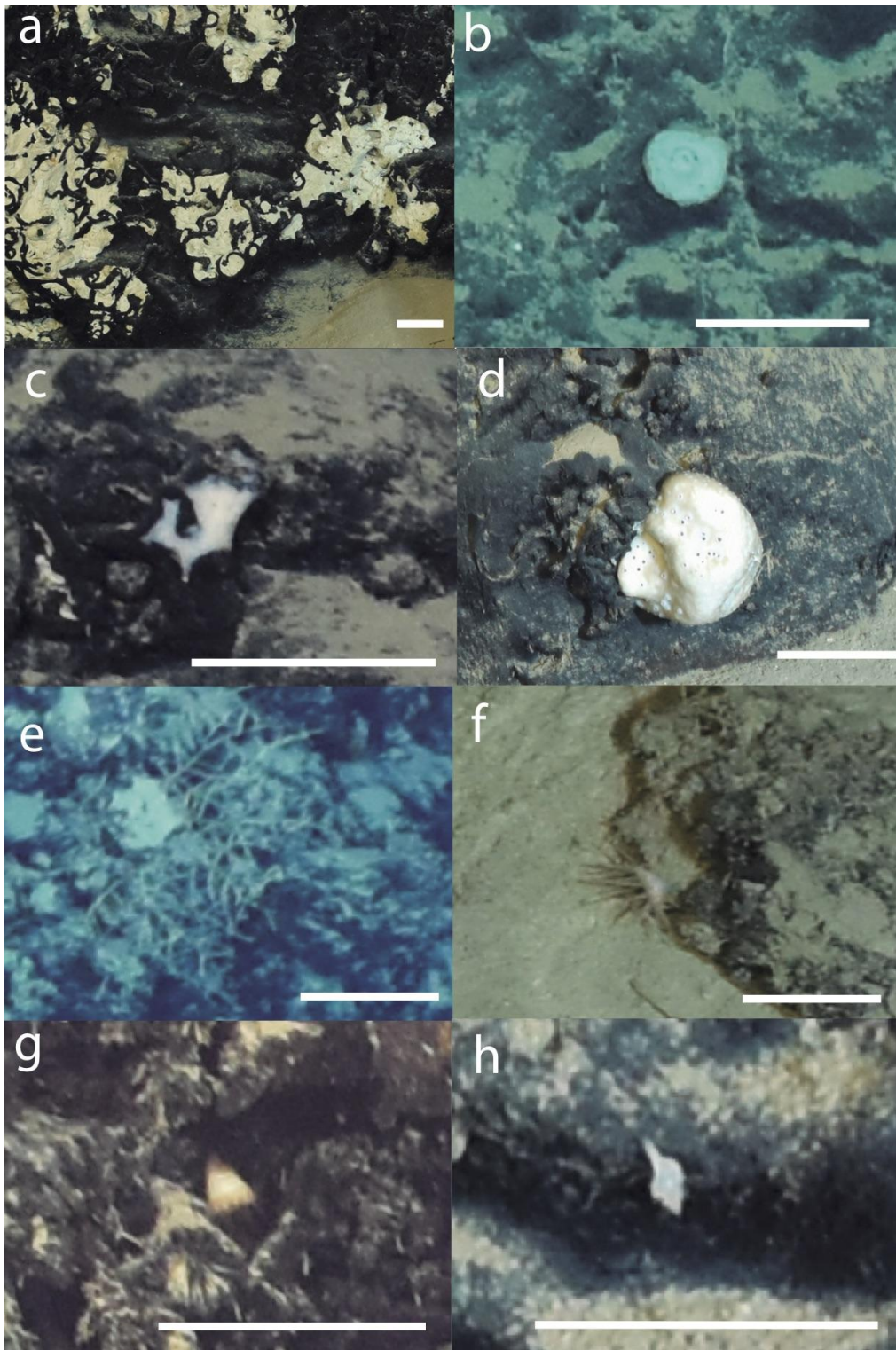
1
0

0.02
0

1
2

1.3
2.6

300

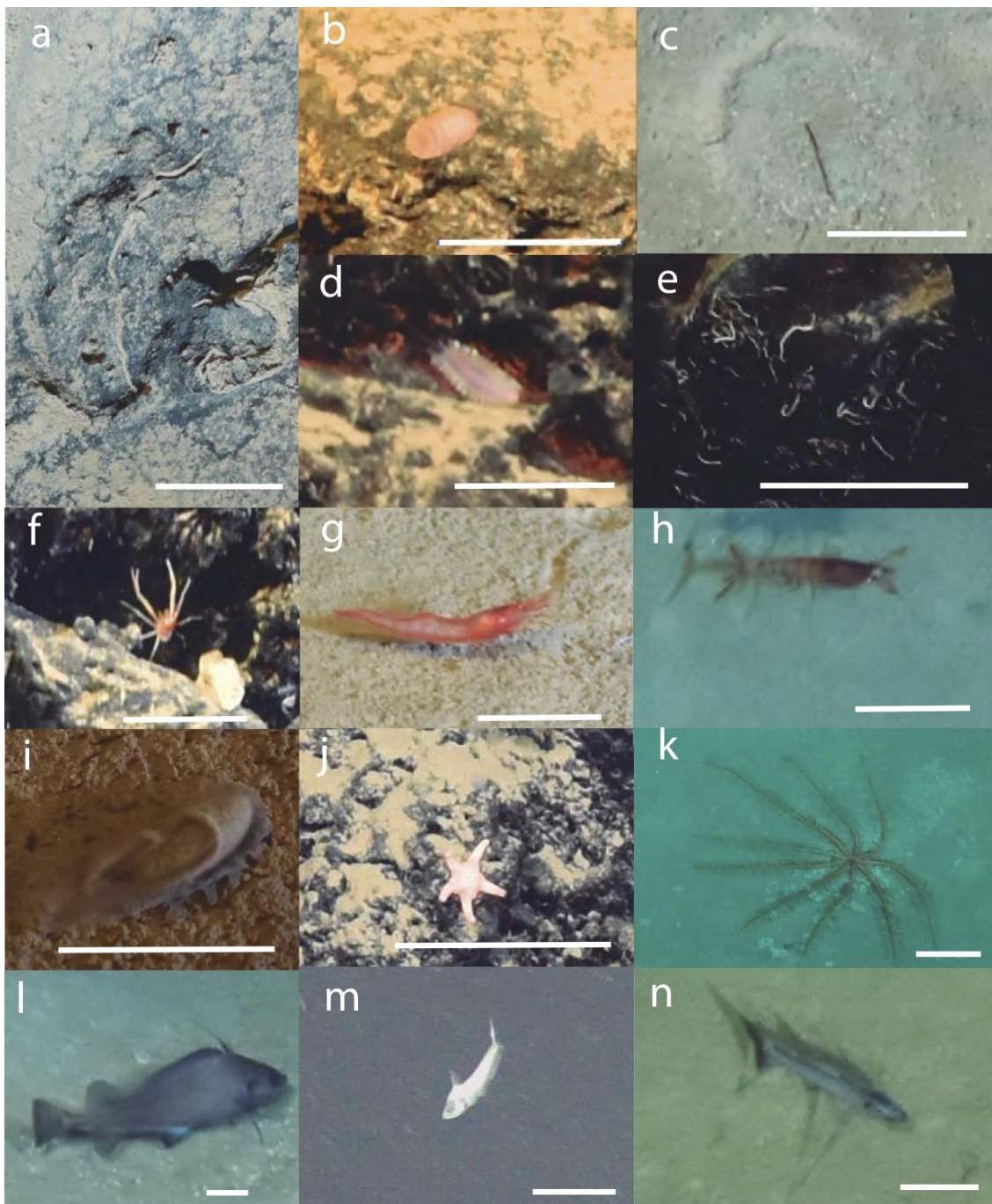


301

302

303

Figure 4. a) Porifera sp.1, b) Porifera sp.2, c) Porifera sp.3, d) Porifera sp.4, e) Hydrozoa f) Unknown actiniaria, g) *Desmophyllum dianthus*, h) Gastropoda sp.1 (Scale = 10 cm).



305

306

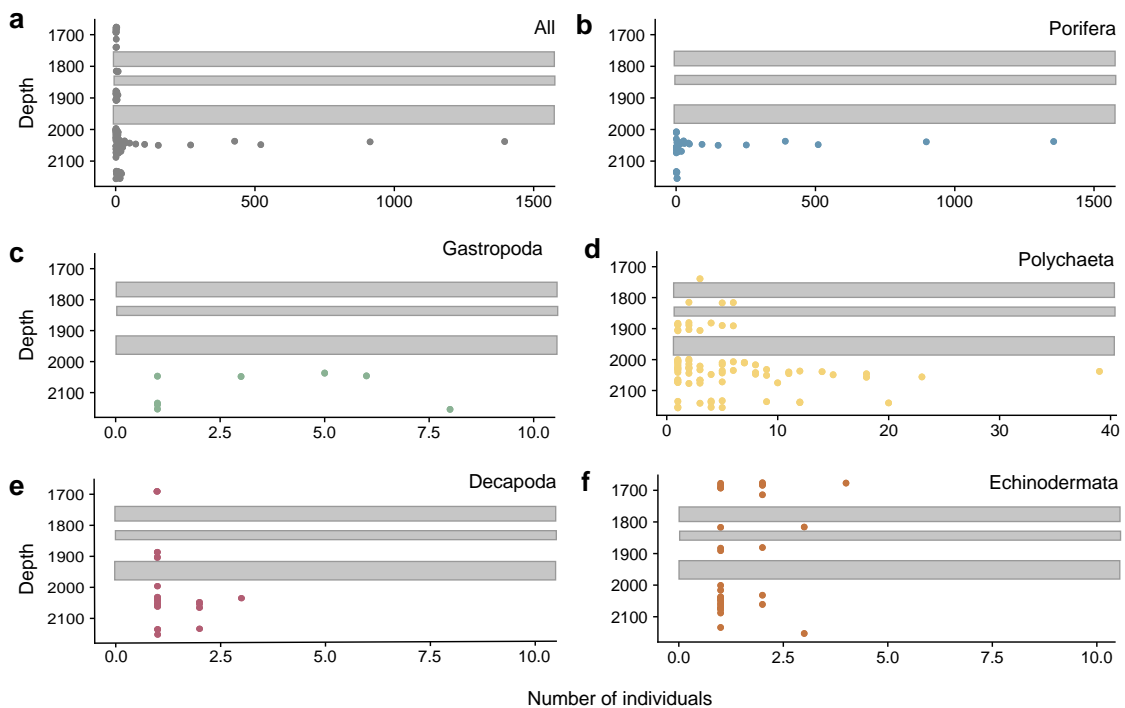
307 Figure 5 a) Polychaeta sp.1, b) Amphinomid, c) Sabellid, d) Polynoid, e) Serpulid, f) *Munida tenuimana*,308 g) *Plesionika acanthonotus*, h) *Aristeus antennatus*, i) *Penilpidia ludwigi*, j) *Ceramaster grenadensis*, k)309 *Hymenodiscus coronata*, l) *Mora moro*, g) unknown macrourid, h) *Bathypterois dubius*. (Scale = 10 cm)

310

311 **Bathymetric distribution**

312

313 Along the explored bathymetric range megabenthic morphospecies abundances
314 generally ranged between 1 and 25 individuals (Fig. 6). However, at 2030 to 2070 m
315 depth in an area that covered 155.6 m² (2% of the explored surface), Porifera registered
316 an abrupt increment in abundance reaching values of 1400 individuals (here mostly
317 Porifera sp.1 patches; Fig. 6b). This phylum presented the most restricted bathymetric
318 distribution being constrained between 2000 and 2190 m depth (Fig. 6b). The remaining
319 phyla presented a wider distribution, with Polychaeta and Echinodermata presenting the
320 widest depth range (Fig. 6e-f).



321

322 Fig. 6. Bathymetric profile representation of the abundance of different faunal groups. Organisms total
323 abundance (number of individuals) associated to each depth value has been plotted. a) All megabenthic,
324 b) Porifera c) Gastropoda d) Polychaeta, e) Decapoda, f) Echinodermata. For Porifera, Porifera sp.1
325 individual patches have been added to the number of individuals for other species. Gray bands represent
326 unexplored areas.

327

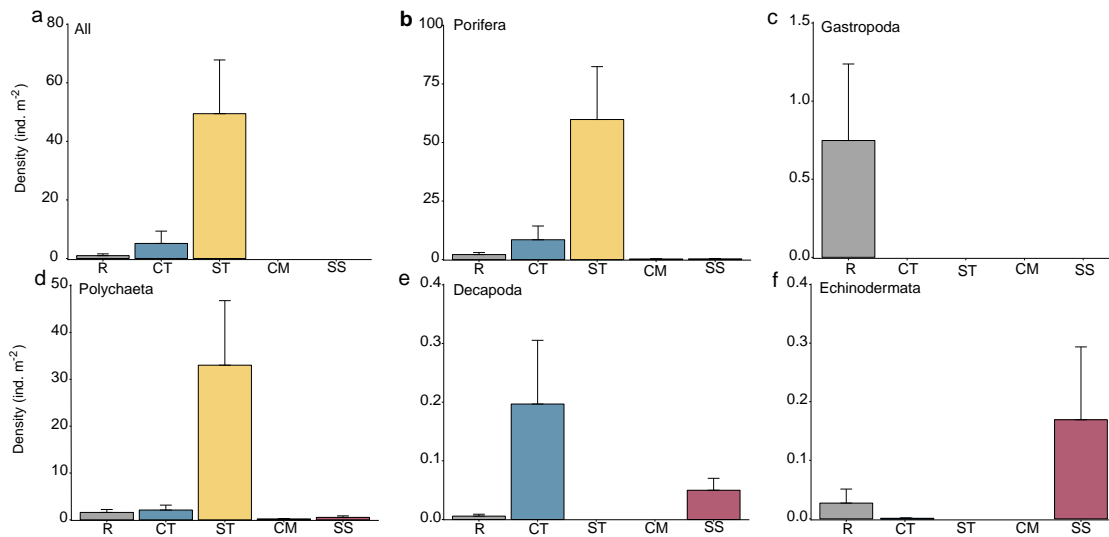
328 **Standing stock variation among substrates**

329

330 Overall morphospecies density was variable across the different substrates (Fig. 7a)
331 with mean values ranging between 0.20 ± 0.07 ind. m⁻² (SD) on compacted muds to
332 47 ± 18 ind. m⁻² (SD) in serpulid thanatocoenosis (Fig. 7a). Porifera morphospecies (Fig.

333 4a-d) were restricted to hard substrate environments, with most individuals being found
 334 on coral and serpulid thanatocoenoses (Fig. 8), where highest densities were registered
 335 (Fig. 7b). Both Gastropoda (Fig. 4h) and Polychaeta (Fig. 5a-e) morphospecies were
 336 mostly found on bare rock environments (Fig. 8), where highest densities were recorded
 337 (Fig. 7c, d). However, it should be noted that an unidentified species of Sabellida (Fig.
 338 5c) was exclusively found on soft sediment environments (Fig. 8), where it occurred at
 339 average densities of 0.08 ± 0.05 ind. m^{-2} (SD). Decapod species (Fig. 5f-g) were found
 340 on soft sediments, bare rocks and coral thanatocoenosis (Figs. 7e and 8), where highest
 341 densities were found. Finally, Echinoderms (Fig. 5i-k) were restricted to bare rock,
 342 coral thanatocoenosis and soft sediments (Fig. 7f and 8), where highest densities were
 343 registered (Fig. 7f).

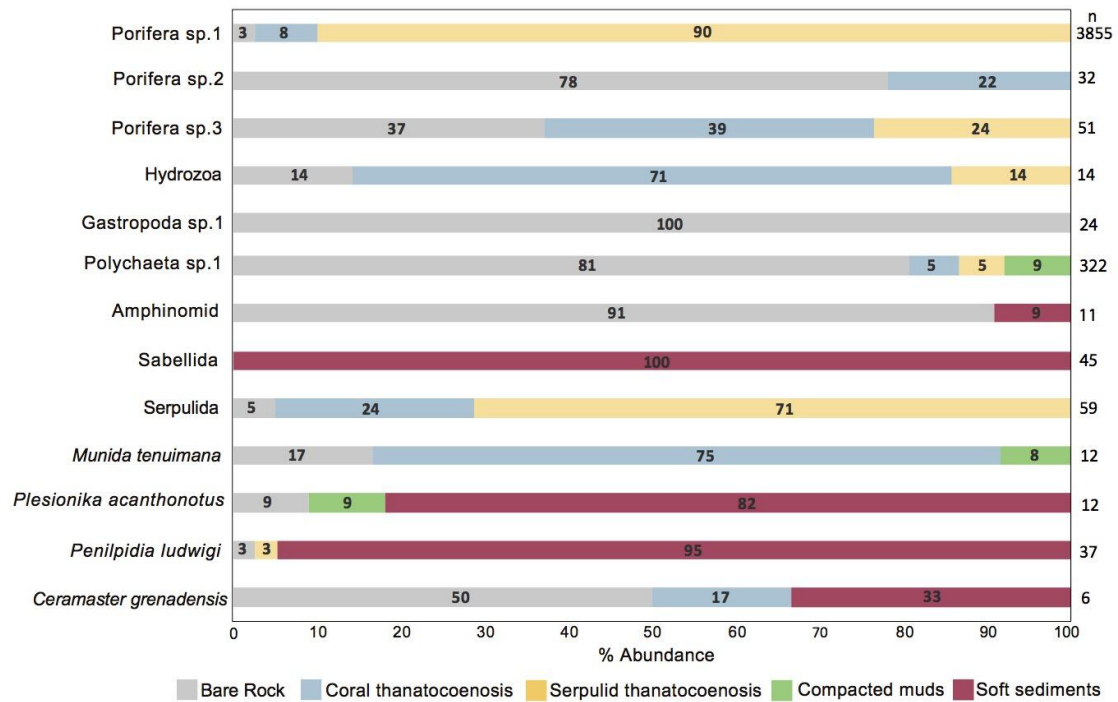
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346 Figure 7. Average densities of megabenthic organisms across the different substrate types. R: bare rock,
 347 CT: coral thanatocoenosis, ST: serpulid thanatocoenosis, CM: compacted muds, SS: soft sediments (mean
 348 \pm SD). For Porifera, densities refer to both Porifera sp.1's individual patches and individuals for the other
 349 species. Rare taxa are not included.

350



351

352 Figure 8. Relative morphospecies abundance (%) across the five substrate types. n = number of
 353 individuals (for Porifera sp.1, n represents the number of patches). Numbers within the bars: relative %
 354 within a substrate category. Rare taxa are not included.

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356 **Assemblage composition**

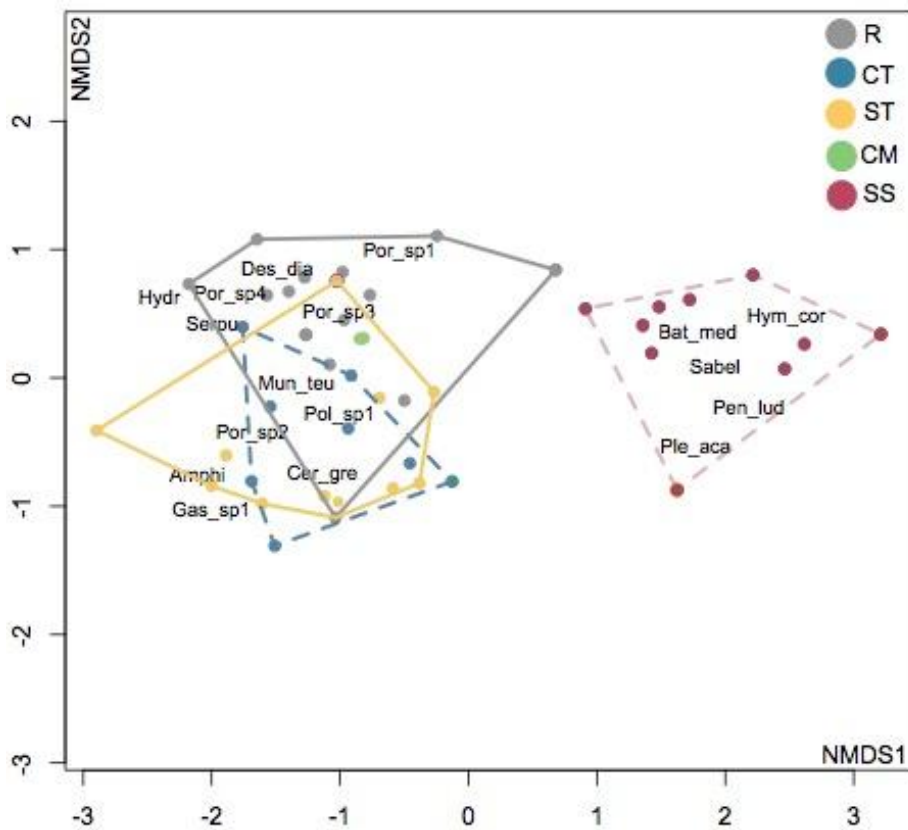
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358 In the nMDS analysis the first axis clearly segregated assemblages occurring on soft
 359 sediments from those occurring on hard substrates (Fig. 9). Permutation multivariate
 360 analysis and subsequent pair wise test revealed that for all substrate categories
 361 megabenthic assemblages significantly differed from one another ($p < 0.001$), except for
 362 rock and compacted muds, where no significant differences were found. Therefore, four
 363 megabenthic assemblages could be identified (Fig. 9):

364 Bare rock assemblage: this assemblage was mainly observed on rock substrates coated
 365 by oxides and to a lesser extent on compacted muds (Fig. 3b, 3e). A total of 12 different
 366 species constituted this assemblage (Figs. 8 and 9). Both Gastropod sp.1 and the
 367 amphinomid Polychaeta characterized this assemblage (Table 3 and Figs. 4h and 5b).

368 Coral thanatocoenosis assemblage: this assemblage was constituted by 8 different
 369 species, six of which were sessile (Figs. 8 and 9). Its characteristic species was the
 370 decapod *Munida tenuimana* (Table 3 and Fig. 5f).

371 Serpulid thanatocoenosis assemblage: this assemblage was constituted by 5 different
 372 species and was characterized by the sponge Porifera sp.1 (Table 3 and Fig. 4a). This
 373 encrusting sponge represented 98% of all observed organisms reaching densities of up
 374 to 180 patches. m⁻².
 375 Soft sediment assemblages: this assemblage was constituted by 5 different species
 376 amongst which, an unidentified sabellid and the holothurian *P. ludwigi* (Figs. 5c and 5h)
 377 were the dominant ones, respectively representing 48% and 37% of all observed
 378 organisms.



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Fig. 9 Non-metric multidimensional scaling (nMDS) ordination plot. R= bare rock, CT=coral thanatocoenosis, ST = serpulid thanatocoenosis, CM= compacted muds and SS= Soft sediments. Amphi = Amphinomid, Bat_med: *Bathypterois dubius*, Cer_gre = *Ceramaster grenadensis*, Des_dia = *Desmophyllum dianthus*, Gas_sp1= Gastropoda sp1, Hydr = Hydrozoa, Hym_cor: *Hymenodiscus coronata*, Mun_teu = *Munida tenuimana*, Pen_lud = *Penilpidia ludwigi*, Ple_aca = *Plesionika acanthonotus*, Por_sp1 = Porifera sp.1, Por_sp2 = Porifera sp.2, Por_sp3 = Porifera sp.3, Por_sp4 = Porifera sp.4, Pol_sp1 = Polychaeta sp.1, Sabel = Sabellid, Serpu= Serpulid

390

391 Table 3. Taxa characterizing each megabenthic assemblage based on their IndVal values. R:
392 bare rock, CT: solitary coral thanatocoenosis, ST = serpulid thanatocoenosis, SS: soft
393 sediments.

394

Assemblage	Species	IndVal
R	Gastropoda sp.1	0.2
	Amphinomid	0.2
CT	<i>Munida tenuimana</i>	0.4
ST	Porifera sp.1	0.6
SS	<i>Penilpidia ludwigi</i>	0.5
	Sabellida	0.4

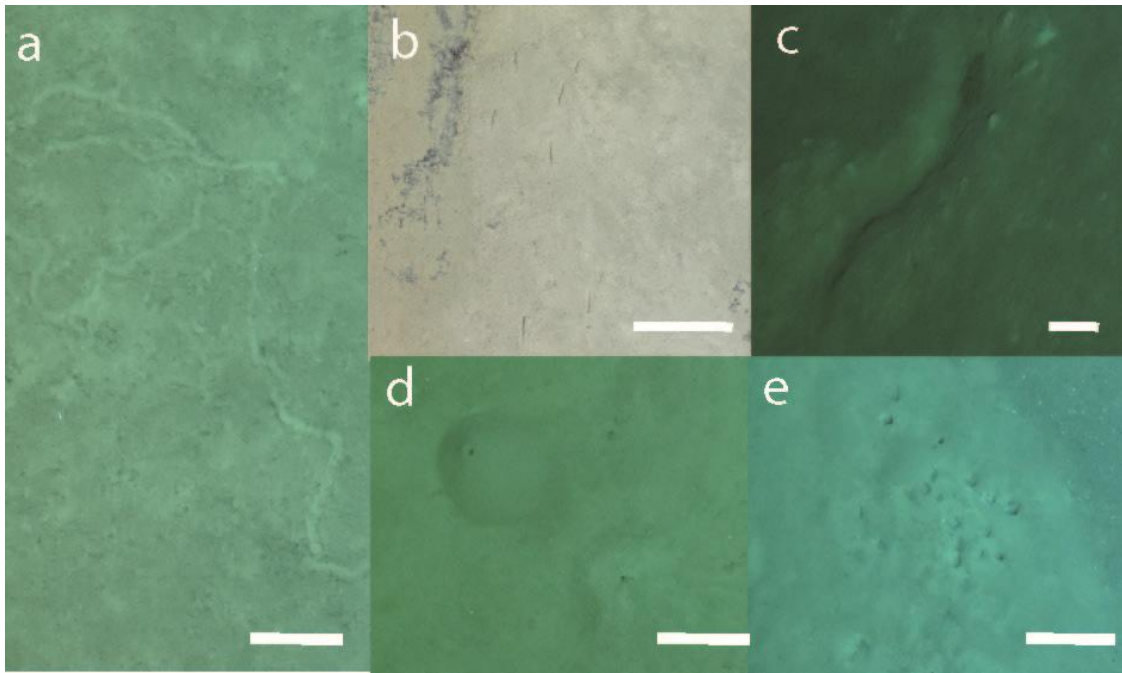
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397 **Lebensspuren**

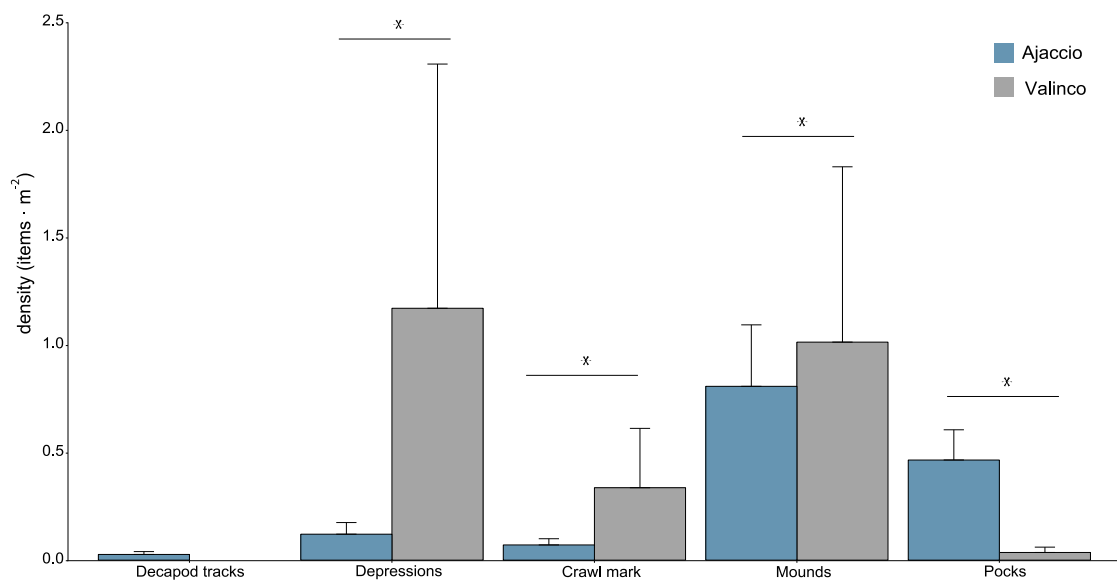
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399 Lebensspuren formations were categorized based on their morphology and origin (Bell
400 et al., 2013). Consequently, five distinct categories were identified: crawl marks,
401 decapod tracks, depressions, mounds and pocks (small holes) (Fig. 10). In the Ajaccio
402 promontory a total of 226 lebensspuren formations were observed, pocks and mounds
403 (Fig. 10d-e) being the most abundant formations representing 48% and 23% (Fig. 17) of
404 all lebensspuren formations, respectively. In the Valinco canyon a total of 282
405 lebensspuren formations were found, mounds and crawl marks (Fig. 16a and d) were the
406 most abundant formations with respectively 67% and 18% of all lebensspuren
407 formations (Fig. 17). Except for pocks and decapod tracks, lebensspuren densities were
408 significantly higher in the Valinco canyon.



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Figure 10. Categories of Lebensspuren formations a) crawl marks, b) decapod tracks, c) depression, d) mounds, e) pocks (scale bar = 10 cm).



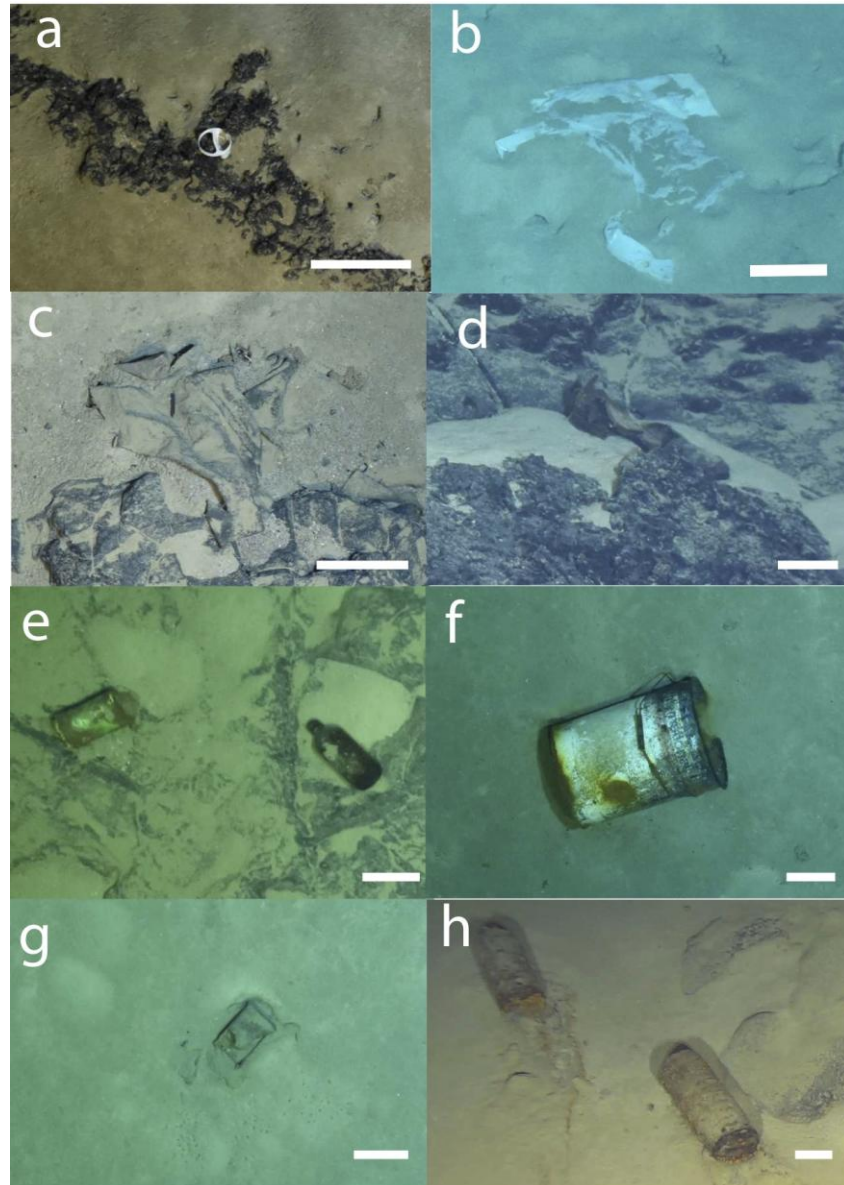
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Figure 11. Average Density of lebensspuren categories found in the Ajaccio seamount and the Valinco canyon. * represents significant differences ($p < 0.001$, uni-variate Adonis test using density as response variable). Error bars (SD).

421 **Marine litter**

422 Litter items were categorized into five different categories: single use plastics (plastic
423 wrappers, bags, small fragments), glass bottles, cans, textile (shoes and cloth fragments)
424 and military debris (Fig. 12).

425



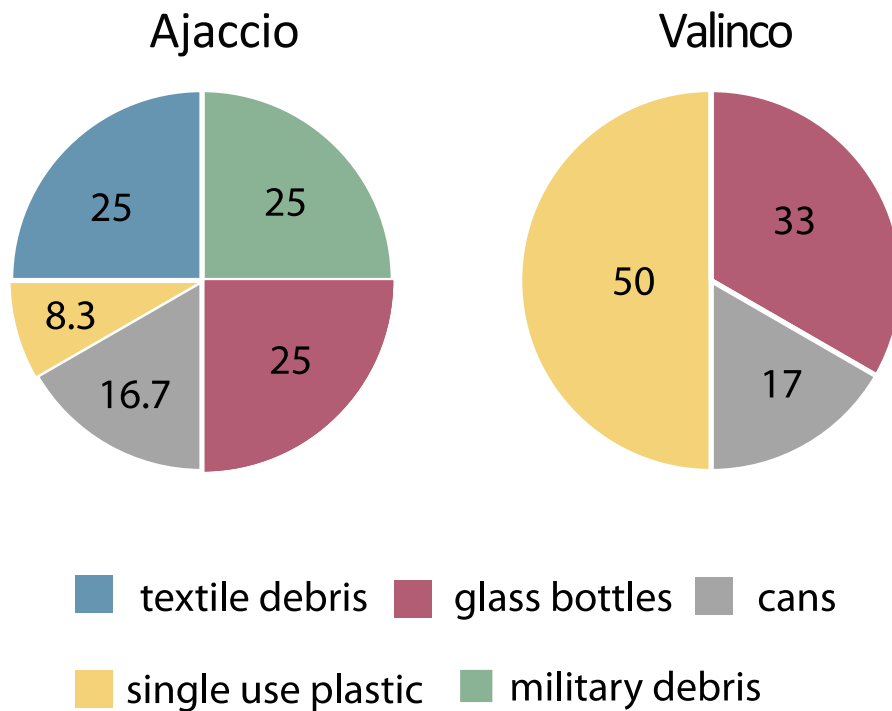
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427 Figure 12. Marine litter debris categories Single use plastic debris: a) plastic fragment, b) plastic bag.
428 Textile debris: c) cloth fragment, d) broken shoe. Glass bottles and cans: e) can and glass bottle, f) paint
429 can, g) can. Military debris: h) ammunition casing. (scale = 10 cm).

430

431 In the Ajaccio promontory twelve marine litter items belonging to 5 different categories
432 were observed (Fig. 13). Clothes, glass bottles and military debris were the most

433 abundant categories, accounting each for 25% of all litter items (Fig. 13). In the Valinco
 434 canyon six marine litter items belonging three categories were observed, plastic debris
 435 was the most abundant category (Fig. 13). Marine litter in Ajaccio and Valinco reached
 436 densities of 0.001 items m⁻² and 0.006 items m⁻², respectively.
 437



438
 439 Figure 13. Frequency of occurrence of marine litter items.

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 441

442 **Discussion**

443

444 **Diversity considerations**

445

446

447 In the study area a total of 24 epibenthic morphospecies were identified (Table 1)
 448 agreeing with previous species richness values from lower bathyal environments in
 449 other areas of the Mediterranean Sea (Ramírez-Llodra et al., 2008; Tecchio et al.,
 450 2011a). In bathyal and abyssal environments in other oceanographic basins, image-
 451 based studies with lower or similar sampling efforts (830 – 11000 m²) reported higher
 452 megabenthic species richness values, ranging between 55 to 118 species (Jones et al.,
 453 2007; Soltwedel et al., 2009; Henry et al., 2014; Simón-Lledó et al., 2019a; 2019b).
 454 These moderately low species richness values found in deep-sea Mediterranean

455 environments have been proposed to derive from the synergy of hydrodynamic
456 conditions and recent geologic history (Danovaro et al., 2010; Sartoretto and Zibrowius,
457 2018). Deep Mediterranean waters are homeothermic at relatively high temperatures
458 (ca. 13-14°C from 300 m depth to the bottom) and present high salinity from about 38 to
459 39.5, and are generally oligotrophic (Turchetto et al., 2007; Grinyó et al., 2017). These
460 environmental conditions have been suggested to prevent the colonization of deep-sea
461 Atlantic species (Danovaro et al., 2010). Consequently, it has been theorized that deep-
462 sea Mediterranean fauna comprises a fraction of deep-sea Atlantic species that have
463 been able to adapt to the warm, saltier and oligotrophic conditions of the deep
464 Mediterranean Sea (Bouchet and Taviani, 1992). Moreover, abrupt hydrological
465 oscillations that occurred during the last glaciation (70000 to 18000 years BP) are
466 thought to have harshened environmental conditions in bathyal and abyssal
467 Mediterranean environments further obstructing the entrance and establishment of deep-
468 sea Atlantic species (Zibrowius, 1980; Emig and Geistdoerfer, 2004).

469 Among the different morphospecies porifera and polychaeta were the most diverse and
470 abundant groups respectively, representing 87.4% and 9.7% of all observed organisms
471 (Table 3). This contrasts with previous knowledge on Mediterranean megabenthic
472 assemblages occurring below 1200 m and 2200 m depth, where these groups are
473 deemed to be rather scarce (Cartes et al., 2009; Tecchio et al., 2011a; 2011b). However,
474 it should be noted that most studies conducted within this bathymetric range have
475 addressed megabenthic assemblages on soft sedimentary environments (Cartes et al.,
476 2009; Tecchio et al., 2011a;b; Mecho et al., 2014) and just a handful have focused on
477 benthic assemblages on steep hard bottom environments (Sartoretto and Zibrowius,
478 2018). Thus, steep escarpments in deep bathyal environments of the Mediterranean, still
479 remain widely unknown.

480 Among the different sessile taxa, anthozoans were rather scarce being restricted to two
481 species and four observations (Table 3). This anthozoan paucity contrasts with
482 Mediterranean bathyal environments above 1500 m depth where anthozoans can make
483 up for a large proportion of megabenthic assemblages (De la Torriente et al., 2018;
484 Aymà et al., 2019; Corbera et al., 2019; Bo et al., 2020; Bilan et al., 2020).
485 Additionally, in bathyal and abyssal environments in other oceanographic basins
486 anthozoan diversity and abundance tend to be higher (Thresher et al., 2014; Durden et

487 al., 2015; Simon-Lledó et al., 2019b) than those reported in lower bathyal
488 Mediterranean environments (Sartoretto and Zibrowius, 2018). This might indicate that
489 the environmental conditions below 1500 m depth in the Mediterranean Sea limit
490 anthozoan diversity and abundance.

491 Furthermore, rare morphospecies (≤ 3 records) greatly contributed to species richness,
492 representing 33.3% and 66.6% of all morphospecies in the Ajaccio volcanic promontory
493 and the Valinco canyon, respectively (Table 3). This appears to be a common feature of
494 megabenthic assemblages on bathyal and abyssal environments where rare taxa can
495 make up for a large proportion of megabenthic assemblages (Durden et al., 2015;
496 Simón-Lledó et al., 2019a; Delavenne et al., 2019). Though, it is unclear if this high
497 representation of rare taxa derives from insufficient sampling effort or if in fact reflects
498 natural patterns in deep-sea megabenthic assemblage's species richness (Simón-Lledó et
499 al., 2019a).

500

501 **Standing stock and assemblage composition**

502

503 Megabenthic species abundance varied across the explored bathymetric range,
504 experiencing an abrupt increment between 2030 and 2075 m depth (Fig. 3) where
505 highest densities were registered (180 encrusting sponge patches m^{-2}). Although it is
506 entirely due to the occurrence of the numerous patches of the peculiar Porifera sp.1, this
507 pattern contrasts with the common conception that megabenthic organisms' density
508 decreases with depth (Rex et al., 2006). However, in seamounts and canyons in other
509 areas of the world similar situations have been observed (Santín et al., 2018; Thresher et
510 al., 2014). Megabenthic organism's depth distribution is conditioned by the joined
511 effect of several factors such as water temperature, hydrodynamic processes and the
512 availability of both food and suitable substrates (Orejas et al., 2009; Robert et al., 2017;
513 Vad et al., 2019). In the study area, 89% of the organisms that formed this peak of
514 abundance occurred on serpulid thanatocoenosis, which represented 34% of all substrate
515 within this depth range, indicating that this substrate positively influenced organism's
516 abundance.

517 In this regard, megabenthic assemblages were segregated by different substrate types
518 (Fig. 6). On hard substrate three different megabenthic assemblages were found.

519 Bare rock assemblages occurred on both Fe-Mn oxide-coated rocks (95.6%) and
520 compacted muds (4.4%) covering a surface of 3817 m². This contrasts with previous
521 research on seamounts, which clearly differentiated between assemblages occurring on
522 polymetallic crusts from those occurring on other hard substrates (Schlacher et al.,
523 2014). Furthermore, assemblages occurring on polymetallic crusts on Pacific seamounts
524 presented lower densities than those occurring on other adjacent hard substrates (Grigg
525 et al., 1987; Schlacher et al., 2014). This differs from the present study as overall
526 organism density (Fig. 4a) on Fe-Mn coated rocks and compacted muds did not
527 significantly differed (PERMANOVA, *Pseudo-F* = 0.584, *P* = 0.485). This assemblage
528 was characterized by the presence of gastropods and polychaetes (Fig. 4 and Table 3)
529 and several sponge species (Fig. 5), but other groups characteristic of shallower
530 Mediterranean Fe-Mn oxide coated environments such as bryozoans and bivalves were
531 completely absent (Toscano and Raspini, 2005).

532 In the Mediterranean Sea, thanatocoenoses are ubiquitous on hard substrate
533 environments between 200 and 3500 m depth (Zibrowius, 1985; Aghib et al., 1991;
534 Galil and Zibrowius, 1998; Toscano and Raspini, 2005). As it has been observed in the
535 study area (Figs. 2c and 2d), thanatocoenoses are generally black, resulting from a Fe-
536 Mn oxide coating (Zibrowius, 1985; Sartoretto and Zibrowius, 2018; Bo et al., 2020).
537 Thanatocoenosis constitute complex three-dimensional structures that provide habitat
538 and substrate to numerous species (Aguilar et al., 2017) being able to host diverse and
539 complex benthic assemblages (Corbera et al., 2019). However, depending on the
540 subfossil remains that constitute each thanatocoenosis benthic assemblages can differ
541 both in terms of abundance and species composition (Rosso et al., 2010). This was the
542 case of both benthic assemblages occurring on thanatocoenoses in the study area (Figs.
543 7-9 and Table 3).

544 Assemblages on solitary coral thanatocoenosis presented higher species richness than
545 those occurring on serpulid thanatocoenosis (Fig. 8) and where characterized by *Munida*
546 *tenuimana* (Fig. 5f; Table 3). This squat lobster is a common inhabitant of bathyal
547 environments in the western Mediterranean (Cartes, 1993) where it has been observed
548 to occur on both live and dead coral assemblages (Mastrototaro et al., 2010). It is likely
549 that the three-dimensional structure formed by the dead coral framework provides
550 refuge to this species (Taviani et al., 2017). Furthermore, it should be noted that 85% of

551 the observed organisms were sponges contrasting with previous reports on solitary coral
552 thanatocoenosis where this group was quite scarce (Sartoretto and Zibrowius, 2018).
553 Similarly, on serpulid thanatocoenosis, sponges were the most abundant group (Figs. 7,
554 8). This assemblage was dominated by Porifera sp.1 (Fig. 4a and Table 3), which
555 represented 98% of all observed organisms forming dense aggregates that reached
556 densities of 180 encrusting sponge patches m^{-2} (62 ± 58 MEAN \pm SD). This density value
557 is amongst the highest ever registered for encrusting sponges in Mediterranean bathyal
558 environments (Santín et al., 2018; Bo et al., 2020). This could indicate that serpulid
559 thanatocoenosis in deep bathyal environments provide a rather suitable substrate for this
560 particular encrusting sponge. It should be noted, that encrusting sponges can undergo
561 fission and fusion processes which could alter sponge patch surface area and density
562 over time (Blanquer et al., 2009). Although we do not know if Porifera sp.1 experiences
563 fission or fusion it would be advisable that future studies also considered this species'
564 patch surface area as done in other deep-sea studies addressing community dynamics
565 (Boolukos et al., 2019).

566 On soft sediment environments assemblages were constituted by typical inhabitants of
567 Mediterranean bathyal muds such as *Hymenodiscus coronata* (Fig. 5k), *Bathypterois*
568 *dubius* (Fig. 5n) and *Plesionika acanthonotus* (Fig. 5g), which have been commonly
569 encountered on experimental trawls below 1000 m depth (Cartes et al., 2009; Mecho et
570 al., 2014). This assemblage was characterized by an unidentified species of sabellid and
571 the elpidiid holothurian *Penilpidia ludwigi* (Fig. 5c, 5i), which were the most abundant
572 species. This unknown sabellid was sparsely distributed, reaching maximum densities
573 of 0.4 ind. m^{-2} , resembling previous observations on bathyal sediments in submarine
574 canyons of the Catalan margin, where sabellid reached densities of 0.5 ind. m^{-2}
575 (Mamouridis et al., 2011). Lastly, *P. ludwigi* has been recently described to occur across
576 the entire Mediterranean covering a wide bathymetric range (480 – 4760 m depth)
577 (Chimienti et al., 2019). Although, this species can form dense aggregates reaching
578 densities of 300 ind. m^{-2} (Chimienti et al., 2019), in the study area it was quite scarce,
579 reaching maximum densities of 2 ind m^{-2} .

580

581 **Lebensspuren**

582

583 In both sampling locations lebensspuren presented a similar composition but densities
584 in Valinco were generally higher (Fig. 11). Lebensspuren density is considered to result
585 from a combined effect of both the bioturbation capacity of a benthic community and
586 physical processes that regulate lebensspuren residence time (Bell et al., 2013).
587 Megabenthic assemblage composition and density have been suggested to influence
588 lebensspuren residence time and consequently its density (Bell et al., 2013).
589 Nevertheless, no significant differences in soft sediment assemblage composition (Fig.
590 9) nor organism density (PERMANOVA, Pseudo-F: 0.867; p-value: 0.489) were found
591 between both sampling locations. Moreover, among the different environmental factors
592 influencing lebensspuren density surface productivity and organic matter flux to the
593 deep-sea are thought to strongly relate to lebensspuren formation (Kitchell et al., 1978;
594 Anderson et al., 2011; Bell et al., 2013). Based on general organic carbon flux patterns
595 in submarine canyons it is possible that the Valinco sampling location, which covered a
596 shallower bathymetric range and is closer to the canyon head (Table 1 and Fig 1b),
597 receive higher organic carbon fluxes thus promoting lebensspuren formation (Smith et
598 al., 2008; Rumín-Caparrós et al., 2013). Yet, this hypothesis should be carefully
599 considered as organic carbon fluxes at these depths, in both sampling locations on the
600 oligotrophic Corsica south-west margin, are still unknown.

601 Determining the origin of lebensspuren formation can contribute to increase knowledge
602 on local deep-sea biodiversity (Przeslawski et al., 2012). Crawl marks (Fig. 10a) were
603 observed to derive from *P. ludwigi* locomotion. The other lebensspuren formations
604 could not be related with any of the other megabenthic organisms observed in the study
605 area. However, in bathyal sediment grounds in the Toulon Canyon, hole aggregations
606 such as the once encountered in this study area (Fig. 10e) were associated with the
607 decapod crustacean *Calcocaris macandreae*, which forms semi-permanent burrow
608 complexes with multiple entrances (Anderson et al., 1991; Gerino et al., 1995).

609 Mounds with an apical vent (Fig. 10d) have been identified as echiuran burrows (Gerino
610 et al., 1995). In the study area, most mound slopes were covered by radial bands (Fig.
611 10d), being consistent with proboscis imprints left by echiurans while deposit-feeding
612 (Bett and Rice, 1993).

613 On the other hand, narrow depressions (Fig. 10c) have been considered to result from
614 the interaction of bathypelagic vertebrates with the seafloor (Marsh et al., 2018).

615 Woodside et al. (2006) reported narrow oblique depressions between 1700 – 2100 m
616 depth in the eastern Mediterranean attributing their formation to Cuvier’s beaked whale
617 (*Ziphius cavirostris*) foraging on the seafloor. Although the depressions in the study
618 area morphologically resembled those reported by Woodside et al. (2006), their
619 dimension were slightly smaller reaching maximum lengths and widths of 0.7 cm and
620 0.4 cm, respectively (Fig. 10c) and thus the origin of this depressions remains unclear.

621

622 **Marine litter**

623

624

625 Marine litter was observed in all dives but in small quantities compared to previous
626 studies in the Mediterranean Sea. Unlike other canyon systems of the western
627 Mediterranean close to shore and urbanized areas, no massive aggregations were
628 observed (Pierdomenico et al., 2019a). Marine litter in the study area was scatteredly
629 distributed and densities reached values of 0.001 items m⁻² in Ajaccio and 0.006 items
630 m⁻² in Valinco. These density values were consistent with previous observations on
631 deep bathyal environments (>1000 m depth) in other oceanographic basins (Mordecai et
632 al., 2011; Pham et al., 2014) and the Mediterranean (Galgani et al., 1995; Tubau et al.,
633 2015).

634 Litter composition in both sampling stations differed (Fig. 13). In Ajaccio glass, textile
635 (mainly shoes and jeans) and military debris (ammunition casings) were the most
636 abundant components (Fig. 13). Conversely, Valinco presented a more homogeneous
637 composition with single use plastic items (plastic bags) and glass bottles (beer bottles)
638 as the most abundant component (Fig. 13), being in line with previous observations in
639 Mediterranean bathyal environments (Cau et al., 2019). Metal, glass and textile debris
640 in deep-sea environments are thought to originate from marine based anthropogenic
641 activities as they rapidly sink and do not travel long distances (Koutsodendris et al.,
642 2008). Conversely, the vast majority of single use plastics has a land-based origin (Cau
643 et al., 2019). Thus, it would be reasonable to hypothesize that in Ajaccio litter mostly
644 originated from marine-based sources, while in Valinco it has both a marine and land-
645 based origin. However, more extensive studies would be required to confirm this pattern
646 and support the hypothesis. Finally, no interactions between marine litter and motile or

647 sessile fauna were observed, in contrast with what has been observed in regions with
648 higher litter densities (Pierdomenico et al., 2019a; 2019b).

649

650 **Conservation remarks**

651

652 The broad consensus on the biological and ecological relevance of deep-sea topographic
653 structures, such as seamounts and submarine canyons, subjected to increasing levels of
654 anthropogenic impacts, reinforces the need for more exhaustive biodiversity
655 assessments, crucial for the development of conservation policies (Clark and Dunn,
656 2012; Fernández-Aracaya et al., 2017). Henceforth, the present study represents the first
657 in-depth study on benthic assemblages in deep bathyal environments (> 1000 m depth)
658 of the Corsican margin. This study has allowed to identify distinct megabenthic
659 assemblages associated to particular substrates. In this regard, it is worth remarking the
660 ecological relevance of the encountered thanatocoenoses, which hosted very extended
661 patches of unidentified encrusting sponges (Fig. 5). This result is consistent with the
662 identification of the Ajaccio site under the “reef” habitat typology (1170) of the Natura
663 2000 network and the relevance of thanatocoenoses for conservation of bathyal
664 Mediterranean habitats (SPA/RAC UN Environment/MAP 2019). This novel finding
665 contrasts with the common conception that megabenthic assemblages on deep bathyal
666 Mediterranean environments are sparsely populated and constitutes a remarkable feature
667 for conservation purposes. Although we don't know anything about the striking Porifera
668 sp.1 encountered here, deep-sea sponge aggregations elsewhere are currently listed as
669 vulnerable marine ecosystems (VMEs) by the FAO (2009).

670 As part of future surveys of this offshore Natura 2000 site (beyond 12 nautical miles
671 from shore), the use of 3D georeferenced models of benthic assemblages will provide a
672 reliable baseline for future monitoring.

673

674 **Conclusions**

675

676 - 24 morphospecies were identified, agreeing with species richness values in other areas
677 of the Mediterranean. But as observed in other deep-sea environments rare taxa (≤ 3
678 records) made up for a large proportion of all observed species.

679 - Four megabenthic assemblages were identified in the study area being segregated by
680 substrate type. Assemblages on hard substrates were characterized by the presence of
681 sponges, polychaetes, and squat lobsters while soft substrates were characterized by the
682 presence of an unidentified sabellid and the elpiidid holothurian *Penilpidia ludwigi*.
683 - Highest densities were found on serpulid thanatocoenosis, which hosted extended
684 encrusting sponge patch aggregations.
685 - In the study area, lebensspuren likely derived from biogenic processes exerted by
686 epibenthic (crawl marks), infaunal (pocks and mounds) and bathypelagic (depressions)
687 organisms.
688 - Litter occurrence was low in the studied area, with litter items in Ajaccio promontory
689 mostly being of likely marine-based origin as they were mainly (91.7%) represented by
690 fast-sinking items (glass, metal, military debris). Conversely, in Valinco canyon, litter
691 had a more mixed origin, as half of all items were single use plastics and the rest were
692 fast sinking items.

693

694

695

696 **Acknowledgements**

697

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1542 **Supplementary material caption**

1543

1544

1545 Supplementary material 1: Bibliographic compilation of benthic research in
1546 Mediterranean bathyal environments. Depth categorization is based on Emig and
1547 Geistoerfer, 2004. CS: continental shelf, SE: Shelf edge, S: slope, C: canyon, M:
1548 seamount.

1549

1550

1551 Supplementary material 2: Marker xyz txt file.

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1555 **Author contribution**

1556

1557 Jordi Grinyó: Conceptualization, methodology, data acquisition, data curation, formal
1558 analysis, data curation, Writing - original draft; Writing - review & editing.

1559

1560 Nadine Le Bris: Funding acquisition, conceptualization, methodology, data acquisition,
1561 data curation, Writing - original draft; Writing - review & editing.

1562

1563 Pierre Chevaldonné: Funding acquisition, data acquisition, writing-review & editing

1564

1565 Thomas Schohn: methodology, writing-review & editing

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