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1 Diversity, distribution and population size structure of deep  
2 Mediterranean gorgonian assemblages (Menorca Channel, Western  
3 Mediterranean Sea)

4

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23

24 **Abstract**

25 Gorgonians are a key group of organisms in benthic marine communities with a wide  
26 bathymetric and geographical distribution. Although their presence on continental  
27 shelves and slopes has been known for more than 100 years, knowledge concerning  
28 the ecology of deep gorgonian species is still in a very preliminary stage. To overcome  
29 this situation, gorgonian assemblages located at 40–360 m depth were studied over a

30 large geographical area on the continental shelf and upper slope of the Menorca  
31 Channel (Western Mediterranean Sea). A quantitative analysis of video transects  
32 recorded by a manned submersible and a remotely operated vehicle, were used to  
33 examine the diversity, distribution and demography of gorgonian species. Results  
34 showed high gorgonian diversity within this depth range (a total of nine species were  
35 observed) compared to Mediterranean coastal areas. Gorgonian assemblages on the  
36 continental shelf and upper slope were mostly monospecific (respectively 73% and  
37 76% of occupied sampling units contained one single species), whereas shelf edge  
38 assemblages were highly multispecific (92% of occupied sampling units contained  
39 several species). This contrasts with the monospecificity of Mediterranean coastal  
40 gorgonian assemblages. Gorgonian populations on the continental shelf were mostly  
41 dominated by small colonies (88% of measured colonies) with few intermediate and  
42 large colonies (12% of measured colonies). In deeper areas small colonies were still  
43 dominant (60% of measured colonies), but intermediate and large colonies were much  
44 more abundant (40% of measured colonies). This suggests high recruitment rates on  
45 the continental shelf, but perturbations (trammel nets, long lines and strong storms)  
46 may limit the presence of intermediate and large colonies. Conversely, on the shelf  
47 edge and upper slope a more stable environment may allow colonies to reach larger  
48 dimensions. The identification and ecological characterization of these deep  
49 assemblages further extends the current knowledge about Mediterranean gorgonians,  
50 and is fundamental in improving the management and conservation of deep benthic  
51 ecosystems.

52

### 53 Keyword

54 Continental shelf; shelf edge; continental slope; animal populations; geographical and  
55 vertical distribution.

56

## 57 1. Introduction

58

59 Gorgonian assemblages play an important structural and functional role in several  
60 marine benthic ecosystems all over the world, promoting a high diversity and biomass  
61 of associated fauna (Gili and Coma, 1998). From a structural point of view,  
62 gorgonians act as ecosystem engineers (*sensu* Jones et al., 1994) and foundation  
63 species (*sensu* Dayton, 1972) forming complex three-dimensional structures that  
64 provide a suitable habitat and refuge for numerous species (Buhl-Mortensen and  
65 Mortensen, 2005; Roberts et al., 2009; De Clippele et al., 2015). Current flow, food  
66 availability, and sediment re-suspension, vary widely within the complex structures  
67 formed by the gorgonian colonies, and this heterogeneity increases the abundance and  
68 functional diversity of the associated fauna (Witherell and Coon, 2001; Stone et al.,  
69 2006; Cerrano et al., 2010). From a functional point of view, gorgonians promote a  
70 significant flow of matter and energy from the pelagic to the benthic system by  
71 capturing plankton and suspended particulate organic matter (Lewis, 1982; Ribes et  
72 al., 1999; Sherwood et al., 2008), playing a paramount role in benthic-pelagic coupling  
73 processes and biogeochemical cycles (Gili and Coma, 1998; Coma et al., 2001; Hill  
74 et al., 2014).

75 Knowledge about diversity, distribution, ecology and state of conservation of  
76 gorgonian assemblages in coastal areas has significantly increased in recent decades  
77 based on the research carried out within the depth range of traditional scuba diving  
78 (~40 m depth) (e.g. Grigg, 1977; Yoshioka and Yoshioka, 1989; Linares et al., 2008).  
79 Far less is known about deep gorgonian assemblages located on the continental shelf  
80 and slope (e.g. Mortensen and Buhl-Mortensen, 2004; Matsumoto et al., 2007;  
81 Salomidi et al., 2009; Stone et al., 2014), where gorgonian presence was mostly  
82 known due to specimens by-cached by fishermen or withdrawn by blind destructive

83 techniques (Relini et al., 1986) for taxonomical studies (Carpine and Grasshoff, 1975;  
84 Grasshoff, 1992). The most recent technological development and increased  
85 availability of remotely operated vehicles (ROVs), manned submersibles, and video-  
86 equipped towed gears have significantly increased accessibility to deeper areas,  
87 allowing for controlled sampling and quantitative study of deep rocky bottoms  
88 communities (e.g. Reed et al., 2006; Mortensen et al., 2008; Orejas et al., 2009).  
89 Abiotic features change considerably with depth (Bell and Barnes, 2000; Garrabou et  
90 al., 2002; Bak et al., 2005), and the overall variability in environmental conditions is  
91 dampened at greater depths (below ~100 m depth) because temperature, currents, and  
92 other water column features are more constant than in shallower areas (e.g. Puig et al.,  
93 2000; De Mole et al., 2002; Fernández de Puelles et al., 2007). Such stability in the  
94 main environmental conditions could allow deep gorgonians to grow larger and  
95 develop populations dominated by medium and large-sized colonies (Grigg, 1975;  
96 Watanabe et al., 2009; Gori et al., 2011b). Toppling and detachment by strong currents  
97 or wave action is considered one of the main causes of mortality of large gorgonian  
98 colonies (Grigg, 1977; Weinbauer and Velimirov, 1996; Weinberg and Weinberg,  
99 1979). Indeed, both the environmental suitability and stability of a habitat may be  
100 reflected in the size structure of gorgonian and coral populations, because the size  
101 structure reflects the factors affecting recruitment, growth, and mortality rates in a  
102 particular habitat for a period of time matching the longevity of the population (Grigg,  
103 1975; Gilmour, 2004; Alvarado-Chacón and Acosta, 2009).

104 Earlier ecological studies on deep gorgonian assemblages in the  
105 Mediterranean Sea revealed that they can reach density values as high as those  
106 observed in littoral environments (e.g. Bo et al., 2009; Angiolillo et al., 2014).  
107 However, both the continental shelf and upper slope are areas where fishing is more  
108 intense (Watling and Norse, 1998; Hall-Spencer, 2002). Gorgonians are among the  
109 most common species of the by-catch of bottom trawling, trammel nets, and long line

110 fishing (Van Dolah et al., 1987; Krieger, 2001; Mytilineou et al., 2014). Since  
111 gorgonians are usually long-lived and slow growing (Linares et al., 2007; Risk et al.,  
112 2002; Sherwood and Edinger, 2009), fishing impacts can have far-reaching and long-  
113 lasting effects (Althaus et al., 2009). Consequently, deep gorgonian assemblages  
114 located on the continental shelf and upper slope are nowadays highly threatened by  
115 fishing activity (Hall-Spencer et al., 2002), and knowledge about their diversity,  
116 distribution and state of conservation is urgently needed to implement effective  
117 management and conservation measures of deep benthic ecosystems.

118 To this purpose, the aims of this study were: (1) to characterize the diversity  
119 and quantify the abundance of gorgonians forming Mediterranean gorgonian  
120 assemblages on a large area of the continental shelf and upper slope at 40–360 m depth  
121 (2) to assess the geographical and vertical distribution patterns of the observed  
122 species; (3) to appraise their population size structure, and (4) to gain insight into the  
123 possible factors affecting their abundance and distribution.

124

## 125 2. Material and methods

126

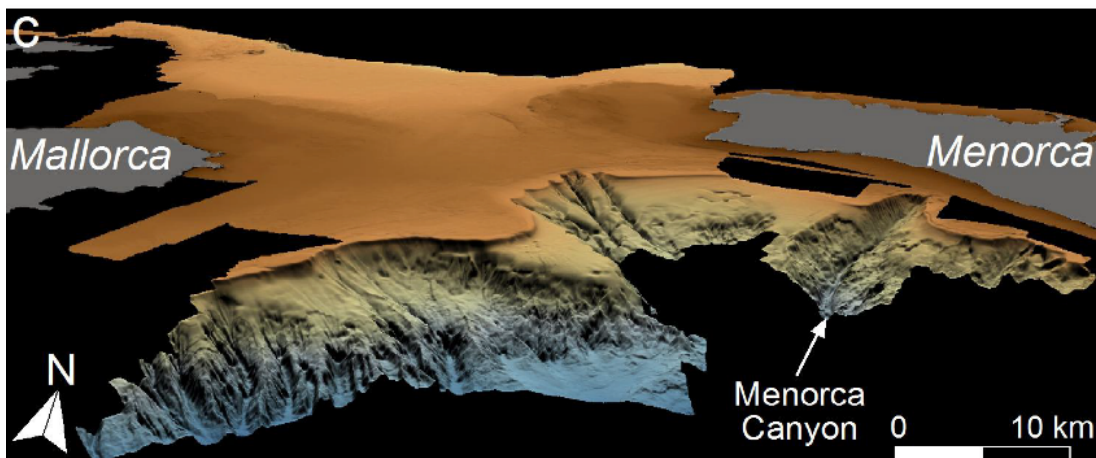
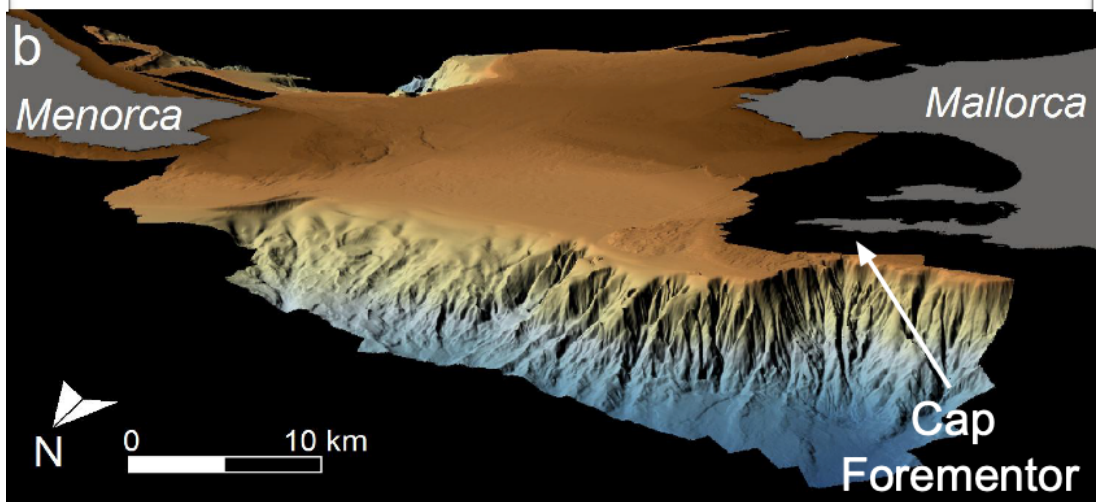
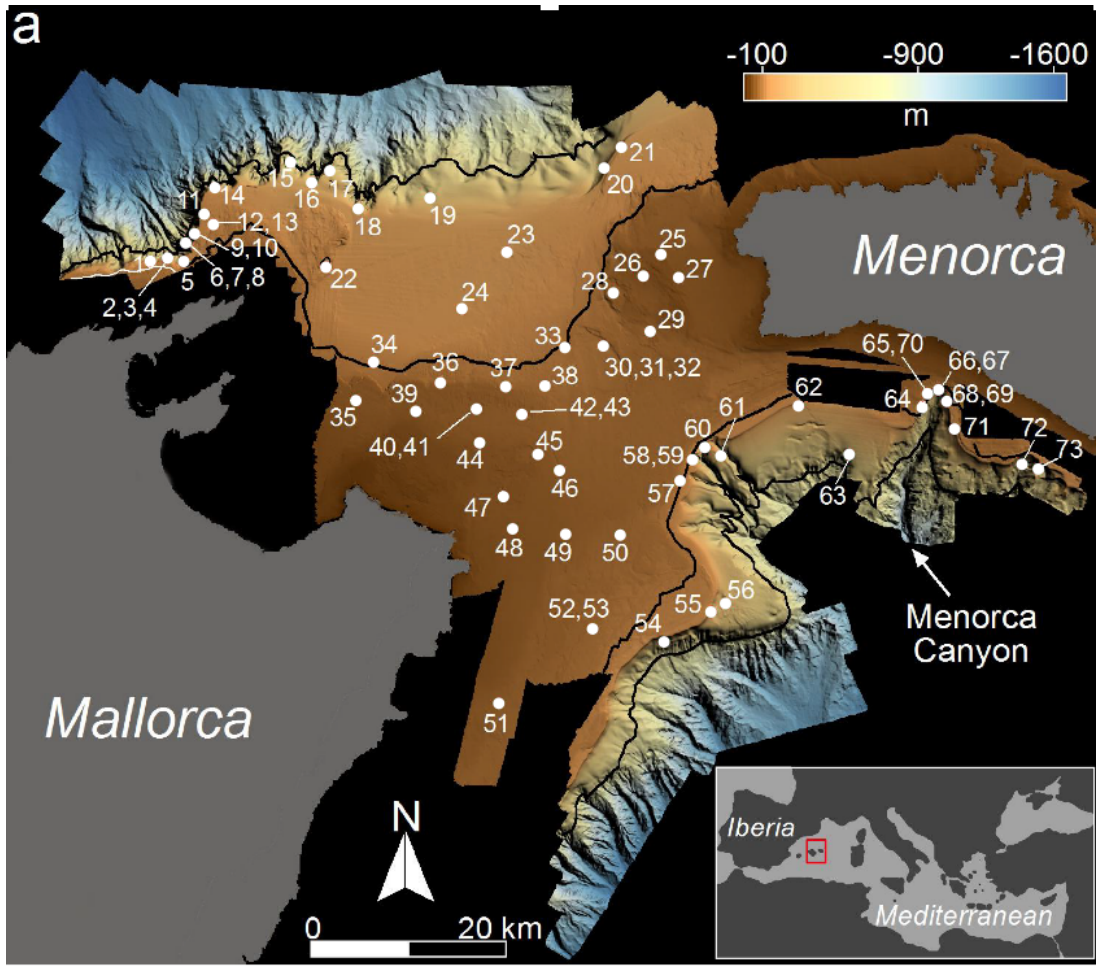
### 127 2.1 Study area

128

129 The Menorca Channel is located in the Western Mediterranean Sea between Mallorca  
130 and Menorca Islands (39° 53' 0.73" N, 3° 29' 51.16" E) (Fig. 1a), as part of the Balearic  
131 Promontory (Acosta et al., 2002). The continental shelf in this area extends between  
132 40 and ~110 m depth, and is largely covered by maërl alternating with patches of  
133 coastal detritic sediments and coralligenous outcrops (Barberá et al., 2012).  
134 Conversely, smooth reliefs and large extensions of detritic sediments with few isolated  
135 patches of outcropping rocks characterize most of the shelf edge and continental slope.

136 Only near Cap Formentor (Fig. 1b) and in the Menorca Canyon (Fig. 1c) sharply  
137 edged rock outcroppings and rocky vertical walls are the dominant substrates.

138         The northern shelf edge and continental slope of the study area is mainly  
139 influenced by the Balearic Current (Balbín et al., 2012) and its associated front (Ruiz  
140 et al., 2009), which originates from a branch of the Liguro-Provençal-Catalan current,  
141 flowing northward over the continental slope of the Balearic archipelago at ~200 m  
142 depth (López García et al., 1994; Ruiz et al., 2009). Secondary currents flow  
143 northward from the Algerian subbasin entering the Balearic subbasin and feed the  
144 Balearic current (Alemany et al., 2006; Amores et al., 2013). Conversely, the southern  
145 shelf edge and upper slope is not influenced by a steady current (Amores and  
146 Montserrat, 2014), but by the sporadic arrival of mesoscale structures detached from  
147 the Algerian Current and the Almería-Oran front (Millot, 1987; García et al., 2005).





149 **Fig. 1.** The study area. (a) Three-dimensional bathymetry of the Menorca Channel: the map shows the  
150 location of the video transects (1 to 73) and the location of the study area in the western Mediterranean.  
151 Detail of the (b) northern and (c) southern subareas.

152

153

## 154 2.2 Sampling procedure

155

156 A total of 73 video transects (Fig. 1a, Supplementary material 1) were recorded during  
157 five surveys conducted on board of the R/V “Garcia del Cid” (September 2010, April  
158 2011, October 2011, June 2012) and the R/V “Miguel Oliver” (August 2011). During  
159 the first two surveys, 20 video transects were recorded with the manned submersible  
160 JAGO (IFM-GEOMAR), whereas 53 video transects were recorded with the ROV  
161 NEMO (Gavin Newman) during the last three campaigns. Both instruments were  
162 equipped with a 1080 horizontal line resolution camera, a grabber and two parallel  
163 laser beams which provided a scale to define a fixed width of the transects (0.3 m)  
164 during the subsequent video analysis. Transects were recorded in a close-zoom (~0.5  
165 - 1.5 m width of view) and in a digital format. Positioning of JAGO and NEMO was  
166 achieved with underwater acoustic positioning system (LinkQuest TrackLink 1500  
167 HA). Both JAGO and NEMO moved at a constant speed of ~0.3 knots, and transect  
168 lengths ranged between 309 and 2375 m, over depths ranging from 52 to 347 m.  
169 Transects were haphazardly located in order to cover the whole study area, but areas  
170 showing morphological features possibly related to the presence of rocky bottoms  
171 were explored more intensively (Fig. 1 and Supplementary material 1). Overall, a total  
172 of 57.8 km was video recorded along the seabed.

173 In order to confirm the taxonomic identification of the species observed in the  
174 video-transects, voucher colonies of gorgonian species observed along the transects

175 were also collected (Supplementary material 2). Colonies were fixed and preserved in  
176 10% formalin until analyzed in the laboratory.

177

### 178 2.3 Video analysis

179

180 Quantitative video analysis was performed according to the methodology described  
181 in Gori et al. (2011a) using Apple's Final Cut Pro software. All the pauses in the  
182 movement of the JAGO or NEMO were removed from the footage, in order to  
183 correctly estimate the length in each transect, and those sequences with poor image  
184 quality or too far away from the seafloor were considered unsuitable for analysis. The  
185 remaining useful sequences comprised 94.6% of the total recorded material and  
186 corresponded to a total distance of 54.7 km. Every gorgonian observed within a width  
187 of 0.3 m (based on the laser beams) along each video transect was identified with a  
188 time reference derived from the time elapsed since the beginning of the video transect  
189 to the crossing of the laser beams with the base of the colony (Gori et al., 2011a). This  
190 time reference was posteriorly converted into position along the transect according to  
191 known velocity ( $P = t \cdot v$ , where  $t$  is the time reference expressed in seconds, and  $v$   
192 is the velocity expressed in meters per second). A similar procedure was used to  
193 characterize seabed substrate types and slope along every transect, within the same  
194 width of 0.3 m. Seabed substrate type was classified (based on the Wentworth scale)  
195 into four categories: sand to gravel, cobbles and pebbles, maërl, and rock. Seabed  
196 slope was classified into three categories: horizontal (0°–30°), sloping (30°–80°) and  
197 vertical (80°–90°); slope was estimated from the video by looking at the two parallel  
198 laser beams and the depth sensor (Gori et al., 2011a; Ambroso et al., 2013).

199 To study population size structure, the maximum height of each observed  
200 gorgonian colony was measured using the Macnification 2.0.1 software (Schols and  
201 Lorson, 2008) on still images extracted from recorded footage. The distance from the

202 two lasers beams was used to calibrate the images. Measurements were done on still  
203 images in which the colony base was in the same plane as the laser beams, while the  
204 colony lied perpendicular to the video (Gori et al., 2011b). This methodological  
205 constraint entails that only a subsample of observed gorgonians could be measured for  
206 the study of population size structure (81% of the total observed colonies, 63%–100%  
207 of the colonies in each transect).

208

## 209 2.4 Species identification

210

211 Identification of the observed species was based on the existing taxonomic works on  
212 Atlanto-Mediterranean gorgonians (Carpine and Grasshoff, 1975; Grasshoff, 1992),  
213 and confirmed by the examination of the voucher specimen collected (see section 2.2),  
214 looking at the colonial branching pattern, the distribution and shape of calyces and  
215 polyps along branches, as well as the shape and size of sclerites. For this purpose,  
216 small fractions of the sampled colonies were placed in a sodium hypochlorite solution  
217 until organic matter was dissolved and sclerites disaggregated. Sclerites were rinsed  
218 with distilled water, and observed under a stereoscope (Olympus SZ-60). Three  
219 *Paramuricea macropsina* (Koch, 1882) morphotypes were differentiated in the video,  
220 two chromatic morphotypes on the continental shelf (M1, M2) and a third one on the  
221 shelf edge (M3) (more details in Grinyó et al. submitted) (Figs. 2c, d and e).

222

## 223 2.5 Data treatment

224

### 225 2.5.1 Gorgonian occupancy and abundance

226

227 To quantify gorgonian occupancy (frequency of occurrence in the set of sampling

228 units) and abundance (number of colonies per sampling unit), and examine the species  
229 composition of gorgonian assemblages within the study area, each transect track was  
230 divided into a string of 2 m<sup>2</sup> (0.3 m width and 6.66 m long) sampling units, using  
231 ArcMap 10.1 software (ESRI ArcGIS ArcInfo v10). Such sampling unit size was  
232 chosen as representative of Mediterranean octocorals on rocky substrate (based on  
233 Weinberg, 1978), as well as to allow a comparison with previous studies on shallow  
234 gorgonian and coral species (Gori et al., 2011a; Ambroso et al., 2013). A total of 8221  
235 sampling units were obtained from the 73 transects, corresponding to a total area of  
236 0.016 km<sup>2</sup>. Each sampling unit was characterized by the number of colonies of each  
237 gorgonian species, as well as by its depth and coverage percentage for each substrate  
238 and slope type. For each gorgonian species, occupancy and abundance were  
239 quantified. Gorgonian assemblages were assessed based on species composition using  
240 a non-metric multidimensional scaling ordination (nMDS) of the sampling units, with  
241 gorgonian abundances square root transformed, and ordination by a Bray-Curtis  
242 similarity matrix. Adonis permutation multivariate analysis of variance and  
243 subsequent pairwise tests were used to test for significance of differences in gorgonian  
244 assemblages based on depth: continental shelf (40–100 m depth), shelf edge (100–180  
245 m depth), upper slope (180–360 m depth), as well as substrate type (sand to gravel,  
246 cobbles and pebbles, maërl and rock), and slope (horizontal, sloping and vertical).  
247 Dominant substrate and slope type was assigned to each sampling unit for this  
248 analysis. Ordination and permutation multivariate analysis of variance and subsequent  
249 pairwise tests were performed using the r-language functions metaMDS and adonis,  
250 respectively, which are available in the vegan library of the R software platform (R  
251 Core Team 2014). The adonis test was performed considering depth, substrate and  
252 slope simultaneously. Additionally, a similarity percentage procedure analysis  
253 (SIMPER, Clarke and Warwick, 1994) was performed to identify which gorgonian  
254 species contributed the most to the different assemblages considering the previously

255 mentioned environmental features using the software PRIMER v6 (Clarke and  
256 Warwick, 2001).

257

## 258 2.5.2 Geographical and vertical distribution

259

260 Geographical distribution of each species in the study area was studied by mapping  
261 the observed density on a geographically referenced map using GIS (ESRI ArcGIS  
262 ArcInfo v10). Vertical distribution of each species was studied grouping sampling  
263 units in 20 m depth intervals (based on their depth), and estimating the median (first  
264 and third quartile, and the range between minimum and maximum values) of  
265 gorgonian density in each depth interval.

266

## 267 2.5.3 Population size structure

268

269 Size structure of gorgonian populations was analyzed in terms of descriptive statistics  
270 using distribution parameters such as skewness and kurtosis. Skewness is a measure  
271 of the symmetry of a distribution using its mean, reflecting the proportion of small  
272 versus large colonies in a gorgonian population. If skewness is significant ( $p < 0.05$ )  
273 population size structure is asymmetrical. Positive skewness denotes the prevalence  
274 of small size colonies, while negative skewness denotes the dominance of large size  
275 colonies in the population. Kurtosis is a measure of the peakedness of a distribution  
276 near its central mode. A significant kurtosis value ( $p < 0.05$ ) indicates longer tails than  
277 would be expected for a normal distribution, and therefore a particular colony size  
278 prevails in the population. Skewness and kurtosis were calculated by means of the R-  
279 language functions `agostino.test` (Komsta and Novomestky, 2012) and `anscombe.test`  
280 (Anscombe and Glynn, 1983), which are available in the moments library of the R  
281 software platform. Only populations with more than 40 colonies were studied for their

282 population size structure in order to perform meaningful skewness and kurtosis  
283 estimates.

284

#### 285 2.5.4 Relationship with environmental features

286

287 Relationships between gorgonian abundances and depth, substrate type and slope  
288 were explored by means of canonical correspondence analysis (CCA), using the  
289 ordination software Canoco 4.5 (ter Braak and Smilauer, 2002). For this analysis, each  
290 sampling unit was characterized by its depth and the percentage coverage of each  
291 substrate and slope type. Gorgonian's abundance was log transformed, and the  
292 statistical significance of the species-environment relationship was evaluated using  
293 Monte Carlo permutation test using 999 unrestricted permutations.

294

#### 295 2.5.5 Spatial structure

296

297 Finally, spatial structure in the distribution of one gorgonian species respect to the  
298 others was analyzed along 3 of the video transects, chosen in order to be representative  
299 of the assemblages identified in the study area. Abundance of each gorgonian species  
300 along the transects was displayed in density plots, obtained by transforming each  
301 transect into a string of contiguous quadrats (0.2 x 0.3 m) and counting the number of  
302 colonies of each species inside each quadrat. Spatial covariance between pairs of  
303 species was analyzed with the Three-Term Local Quadrat Covariance (3TLQC)  
304 function, using the Passage 2.0 software (Rosenberg, 2008). In the 3TLQC, the  
305 variance as a function of block size for species A (Var A), specie B (Var B), and the  
306 combined number (Var A+B) ( $Cov = Var A + B - Var A - Var B$ ) is examined (Dale,  
307 1999). To test the null hypothesis of an independent distribution of one species with  
308 respect to the other along each transect, randomized transects were generated for

309 comparison by randomly permuting the “labels” (species A or B) of all the observed  
310 colonies along each transect. For statistical significance (95% confidence interval) the  
311 values at the limit of 2.5% tails of 999 of these randomizations was used. In the  
312 produced plots of covariance as a function of block size, position of a significantly  
313 positive deviated sample statistic from the bounds of the confidence interval (peaks)  
314 indicates the scale of any positive association (attraction) between species, whereas  
315 significant negative deviations (valleys) indicate the scale of any negative association  
316 (repulsion) (Dale, 1999).

317

### 318 3 Results

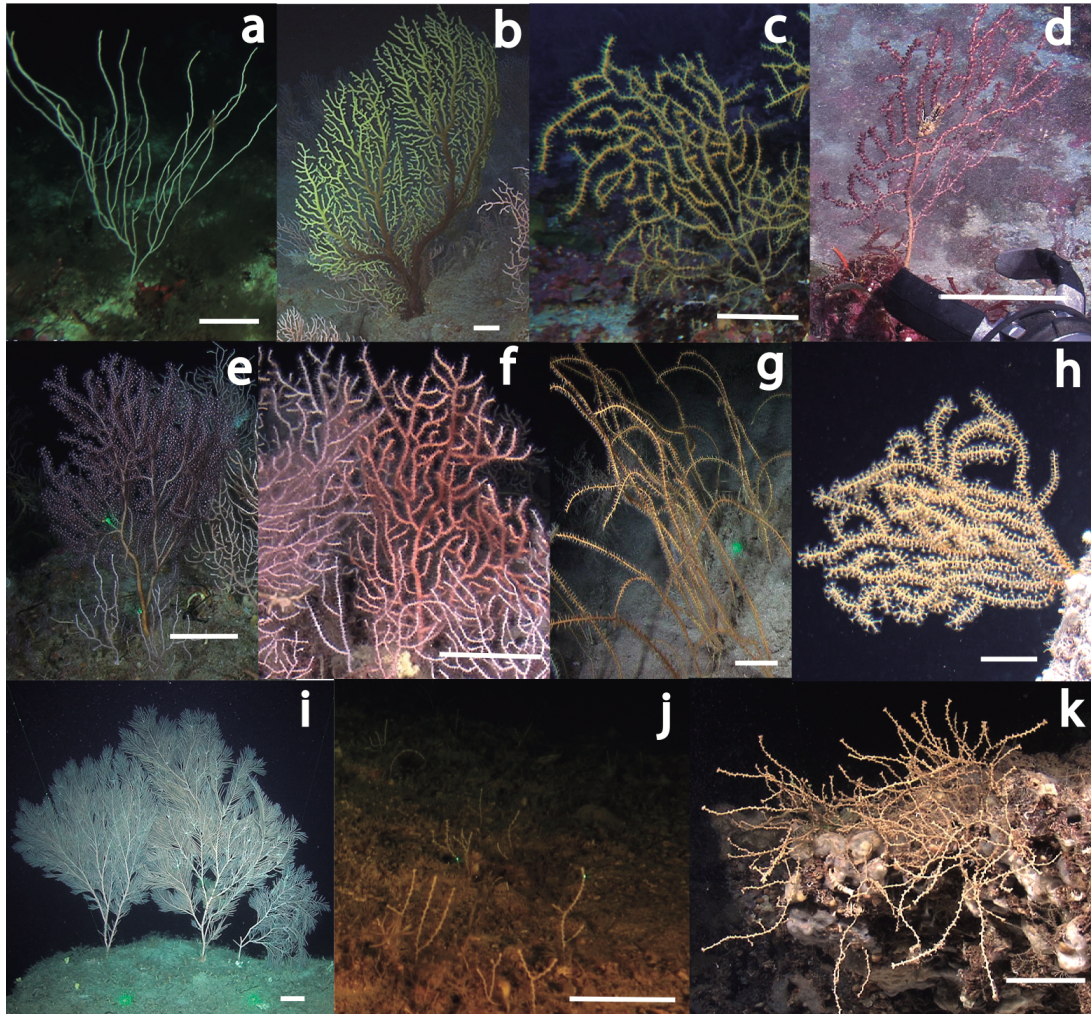
319

#### 320 3.1 Gorgonian occupancy and abundance

321

322 A total of 7802 colonies of nine gorgonian species (Fig. 2) were observed along all  
323 transects (Table 1), occurring in 18.9% of the 8220 sampling units. Overall, *P.*  
324 *macrospina* was the most abundant and frequent species, with its three morphotypes  
325 representing 44% of observed colonies present in 6.8% of the sampling units.  
326 *Eunicella cavolinii* (Koch, 1887) was the second most abundant and the third most  
327 frequent species, whereas *Eunicella singularis* (Esper, 1791) was the third most  
328 abundant and the second most frequent species. *Swiftia pallida* Madsen, 1970 and  
329 *Viminella flagellum* (Johnson, 1863) were the fourth and fifth most abundant and  
330 frequent species. The other species accounted for less than 2% of the observed  
331 colonies, occurring in less than 1% of the sampling units.

332



333

334 **Fig. 2.** Studied species images. (a) *Eunicella singularis*, (b) *Paramuricea clavata*, (c) *Paramuricea*  
 335 *macrospina* morphotypes (M1), (d) M2, (e) M3, (f) *Eunicella cavolinii*, (g) *Viminella flagellum*, (h)  
 336 *Acanthogorgia hirsuta*, (i) *Callogorgia verticillata*, (j) *Swiftia pallida*, (k) *Bebryce mollis*.

337 Scale Bar: 10 cm.

338

339 **Table 1** Gorgonian occupancy and abundance in the study area. Occupancy (frequency of occurrence  
 340 in the set of sampling units) is given for each bathymetric range and species; abundance (number of  
 341 colonies); mean and maximum density of each species is given per each bathymetric range.

342



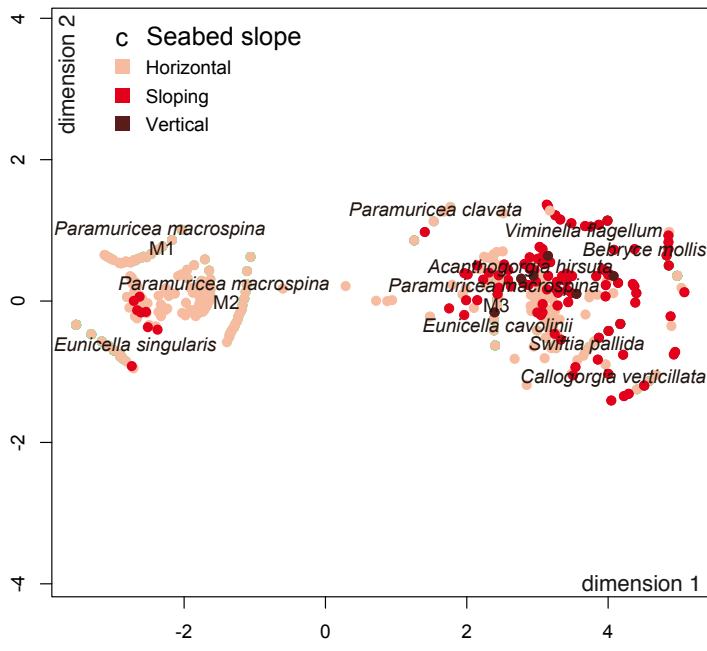
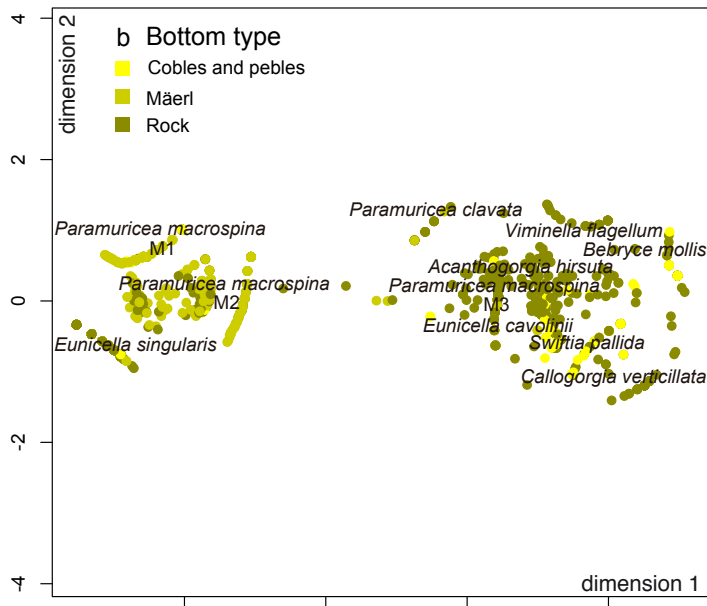
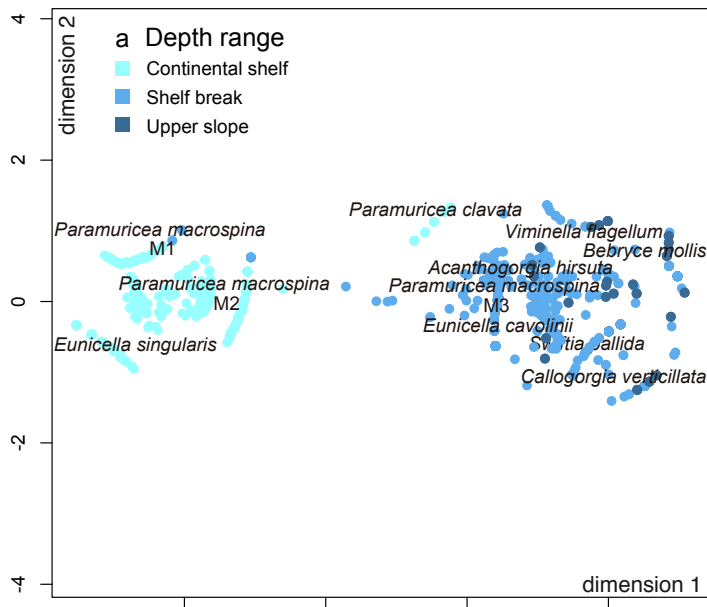
Depth-range	Sampling Units			Species	Occupancy		Abundance		Mean density $\pm$ SD (colonies $\cdot$ m <sup>-2</sup> )	Max density (colonies $\cdot$ m <sup>-2</sup> )
	Number	with gorgonians	(%)		Number	(%)	Number	(%)		
Continental shelf (40 - 100 m)	2723	735	(27)	<i>E. singularis</i>	357	(48.5)	966	(23.0)	1.2 $\pm$ 1	7.5
				<i>P. clavata</i>	22	(3.1)	48	(1.1)	1.1 $\pm$ 0.8	3
				<i>P. macrospina</i> M1	292	(39.7)	1899	(44.0)	3.2 $\pm$ 5	33
				<i>P. macrospina</i> M2	208	(29.0)	1370	(32.0)	3.6 $\pm$ 3.9	18.5
Shelf edge (100 - 180 m)	3338	751	(22.5)	<i>P. clavata</i>	10	(1.3)	16	(0.5)	1.2 $\pm$ 1	3.0
				<i>P. macrospina</i> M1	3	(0.4)	4	(0.1)	0.7 $\pm$ 0.3	1.0
				<i>P. macrospina</i> M2	7	(0.9)	11	(0.3)	0.8 $\pm$ 0.7	2.5
				<i>P. macrospina</i> M3	51	(6.8)	149	(4.6)	1.5 $\pm$ 1.7	9.0
				<i>E. cavolinii</i>	308	(41.0)	1768	(55.1)	2.9 $\pm$ 2.7	24
				<i>V. flagellum</i>	65	(8.7)	425	(13.2)	3.2 $\pm$ 5.4	27.5
				<i>A. hirsuta</i>	17	(2.3)	34	(1.1)	1.0 $\pm$ 1.0	4.5
				<i>C. verticillata</i>	102	(13.6)	102	(3.2)	1.0 $\pm$ 0.9	5
				<i>S. pallida</i>	141	(18.8)	606	(18.9)	2.1 $\pm$ 2.6	13
<i>B. mollis</i>	47	(6.3)	93	(2.9)	1.0 $\pm$ 1.0	5.5				
Upper slope (180 - 360 m)	2159	75	(3.5)	<i>E. cavolinii</i>	8	(10.6)	16	(5.1)	1.0 $\pm$ 0.9	3
				<i>V. flagellum</i>	19	(25.3)	118	(37.9)	3.1 $\pm$ 4.5	17
				<i>C. verticillata</i>	23	(30.7)	32	(10.3)	0.7 $\pm$ 0.3	1.5
				<i>S. pallida</i>	23	(30.7)	79	(25.4)	1.6 $\pm$ 2.8	14
				<i>B. mollis</i>	26	(34.2)	66	(21.2)	1.2 $\pm$ 0.8	3

343

344

345

346 Two major groups could be identified in the nMDS, one represented by sampling  
347 units from the continental shelf covered by rock and maërl and presenting an  
348 horizontal inclination, and a second one formed by sampling units on the shelf edge  
349 and upper slope mostly covered by rock and presenting a flat or sloping inclination  
350 (Fig. 3).



352 **Fig. 3.** Non-metric multidimensional scaling (nMDS) ordination plot. Gorgonian abundance was  
353 square root transformed and analysis performed on Bray-Curtis dissimilarity matrix. Sampling units  
354 (n= 1562) containing gorgonians are represented considering (a) depth range, (b) bottom type and (c)  
355 seabed slope. A stress estimate of 0.025 was obtained.

356

357 Permutation multivariate analysis of variance and subsequent pairwise test revealed  
358 that for all environmental categorizations gorgonian assemblages were significantly  
359 different ( $p < 0.001$ ) from one another. The SIMPER analysis showed an average  
360 similarity in species composition that ranged from 17.89% to 31.68% (Table 2). The  
361 number of species contributing up to 90% of the similarity varied between two to four  
362 (Table 2). *E. singularis* dominated assemblages located on the continental shelf as  
363 well as those located on rocky and horizontal sampling units (Table 2). *E. cavolinii*  
364 was especially relevant on assemblages located on the shelf edge as well as on sloping  
365 and vertical rocky outcrops (Table 2). *Bebryce mollis* Phillipi, 1842 dominated  
366 assemblages located in the upper slope, whereas *P. macrospina* M1 on those located  
367 on maërl beds, and *V. flagellum* dominate in vertical rocky bottoms (Table 2).

368

369 **Table 2** SIMPER analysis. Species that belong to the similarity group of 90% of cumulative  
370 contribution are present. Percentages in bold letters are the average similarity values for each category.

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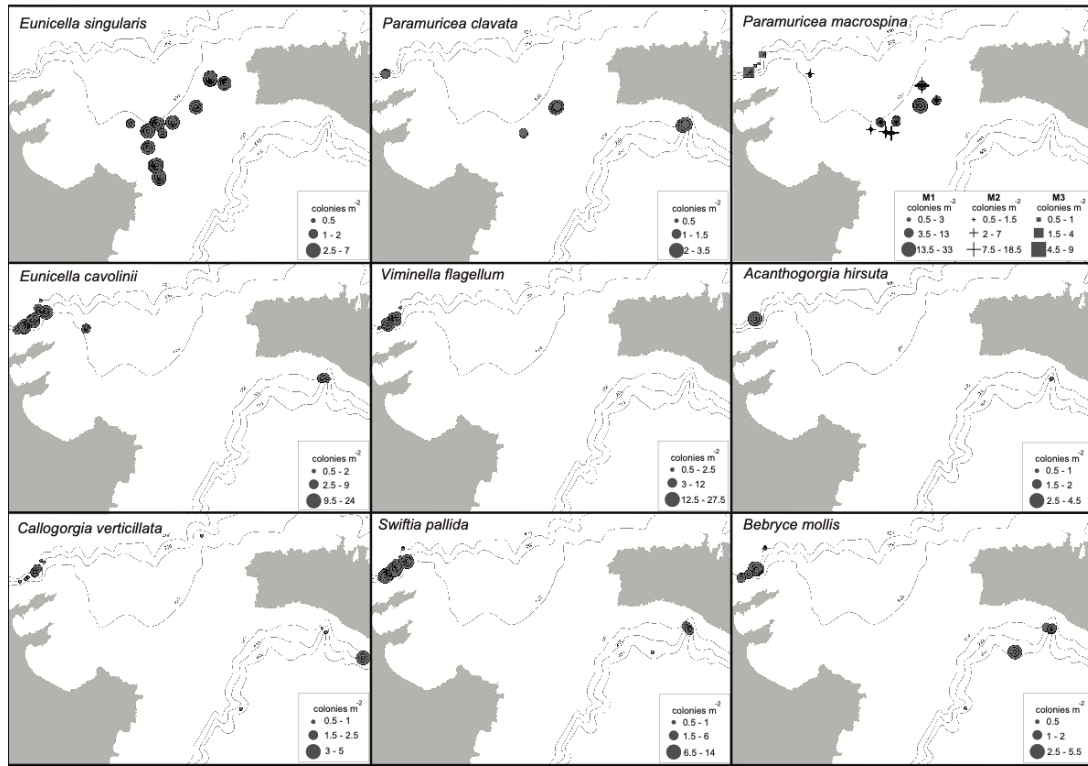
377

	<b>Depth range</b>	<b>Sim/SD</b>	<b>Contribution%</b>	<b>Cum. Contribution%</b>
378				
379	<b>Continental shelf: 22.43%</b>			
380	<i>E. singularis</i>	0.48	60.33	60.33
	<i>P. macrospina</i> M1	0.34	24.59	84.92
381	<i>P. macrospina</i> M2	0.25	14.86	99.79
382	<b>Shelf edge: 21.45%</b>			
	<i>E. cavolinii</i>	0.65	78.43	78.43
383	<i>S. pallida</i>	0.25	14.70	93.14
384	<b>Upper slope: 17.89%</b>			
	<i>B. mollis</i>	0.33	38.55	38.55
385	<i>C. verticillata</i>	0.26	24.83	63.38
	<i>S. pallida</i>	0.27	23.30	86.68
386	<i>V. flagellum</i>	0.21	12.13	98.81
387	<b>Bottom type</b>			
	<b>Rock: 18.63%</b>			
388	<i>E. singularis</i>	0.37	54.89	54.89
	<i>E. cavolinii</i>	0.33	32.61	87.50
389	<i>S. pallida</i>	0.12	3.68	91.19
390	<b>Cobbles &amp; pebbles: 17.67%</b>			
	<i>S. pallida</i>	0.42	60.77	60.77
391	<i>E. cavolinii</i>	0.21	14.08	74.85
392	<i>P. macrospina</i> M1	0.16	10.86	85.70
	<i>B. mollis</i>	0.15	9.93	95.64
393	<b>Maërl: 28.68%</b>			
	<i>P. macrospina</i> M1	0.62	60.20	60.20
394	<i>P. macrospina</i> M2	0.42	33.55	93.75
395	<b>Seabed Slope</b>			
	<b>Horizontal: 18.11%</b>			
396	<i>E. singularis</i>	0.35	49.09	49.09
397	<i>P. macrospina</i> M1	0.28	25.11	74.19
	<i>P. macrospina</i> M2	0.29	14.93	89.13
398	<i>E. cavolinii</i>	0.15	7.12	96.25
399	<b>Slopping: 19.66%</b>			
	<i>E. cavolinii</i>	0.50	66.28	66.28
400	<i>B. mollis</i>	0.17	9.94	76.22
	<i>S. pallida</i>	0.17	9.26	85.48
401	<i>V. flagellum</i>	0.17	7.03	92.51
402	<b>Vertical: 31.68%</b>			
	<i>E. cavolinii</i>	0.56	53.09	53.09
403	<i>V. flagellum</i>	0.51	44.75	97.84
404				

### 405 3.2 Geographic and vertical distribution

406

407 Only three species were observed on the continental shelf of the study area, *P.*  
408 *macrospina* (M1, M2), *E. singularis* and *Paramuricea clavata* (Risso, 1826) (Fig. 4,  
409 Table 1). *P. macrospina* (M1, M2) and *E. singularis* were the most frequent species  
410 scattered over the continental shelf (Fig. 4) at 65–100 m and 52–88 m depth,  
411 respectively (Fig. 5). Both morphotypes of *P. macrospina* were much more abundant  
412 in terms of colony number than *E. singularis* (Table 1). Conversely, *P. clavata* was  
413 only found on the continental shelf in two low-density patches on coralligenous banks  
414 at 67–92 m depth, and few colonies on the shelf edge at 109–120 m depth (Figs. 4 and  
415 5). The shelf edge and upper slope were much more diverse than the continental shelf  
416 in terms of species richness. In this depth range, gorgonian assemblages were highly  
417 localized in the areas dominated by rocky outcrops and vertical walls near Cap  
418 Formentor and in the Menorca Canyon (Fig. 4). *E. cavolinii* was the most frequent  
419 and abundant species of the shelf edge, with the highest abundances concentrated at  
420 100–160 m depth, together with *P. macrospina* M3 (Figs. 4 and 5). *V. flagellum*, *S.*  
421 *pallida*, *C. verticillata* were also abundant on the shelf edge, but extended their  
422 distribution beyond 240 m depth, with one colony of *S. pallida* observed at 324 m  
423 (Figs. 4 and 5). *Acanthogorgia hirsuta* Gray, 1857 was the species showing the most  
424 restricted distribution, occurring in few locations of the shelf edge at 149–176 m depth  
425 (Fig. 5). *B. mollis* extended its distribution from the shelf edge to the upper slope,  
426 where it was the most frequent species, followed by *C. verticillata* and *V. flagellum*  
427 (Table 1). *V. flagellum* was the most abundant species in the upper slope, followed by  
428 *S. pallida*, *B. mollis* and *C. verticillata* (Table 1). Finally, some colonies (~20) of the  
429 precious coral, *Corallium rubrum*, were observed at 80–120 m depth, whereas only  
430 few isolated colonies were seen below 150 m depth.

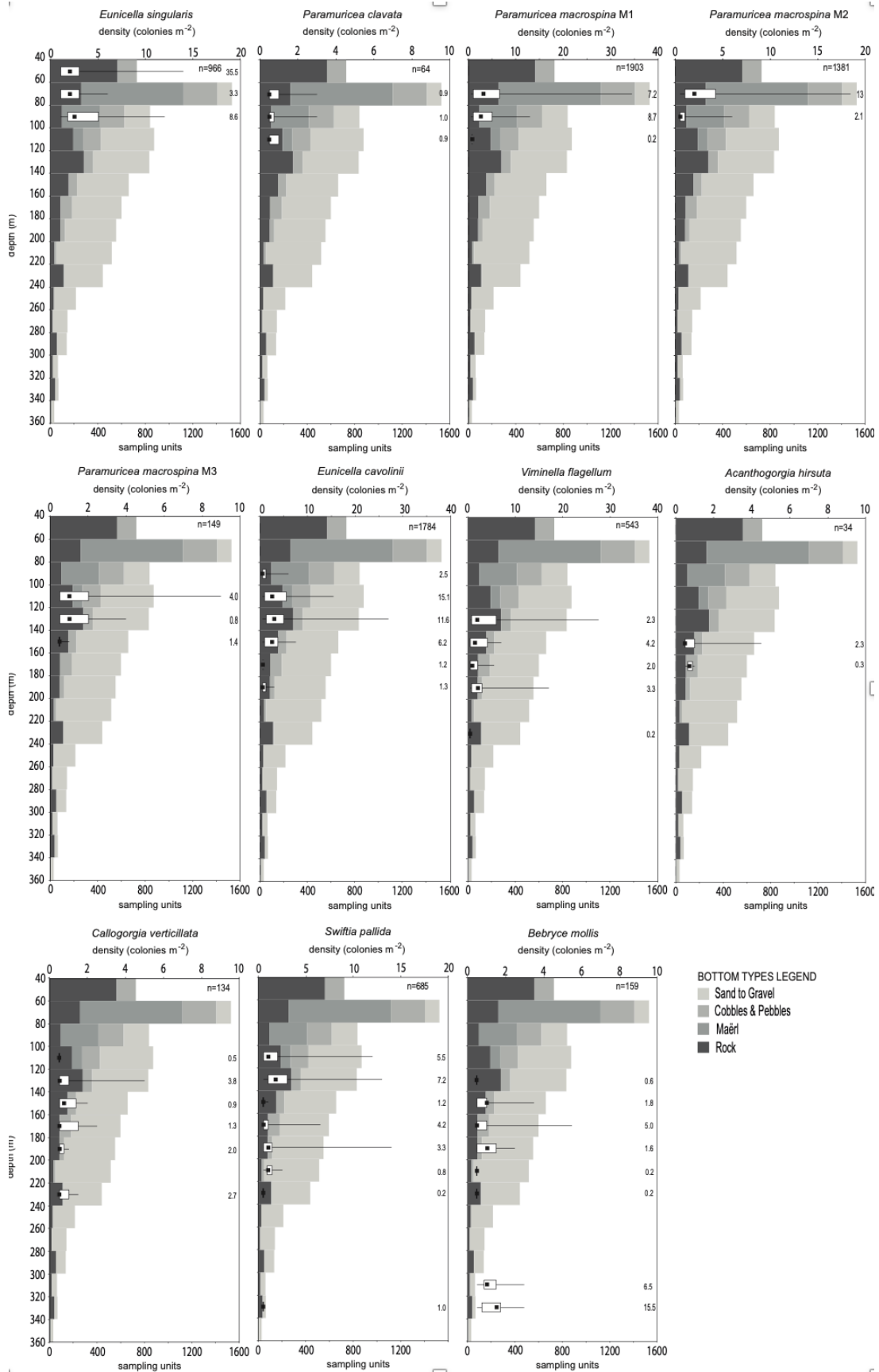


431

432 **Fig. 4.** Geographical distribution. *E. singularis*, *P. clavata*, *P. macrospina* (M1, M2, M3), *E. cavolinii*,  
 433 *V. flagellum*, *A. hirsuta*, *C. verticillata*, *S. pallida*, and *B. mollis* distribution is represented on the study  
 434 area based on sampling unit density. Species have been displayed from shallowest to deepest  
 435 distribution.

436

437



438

439

440

**Fig. 5.** Vertical distribution. *E. singularis*, *P. clavata*, *P. macrospina* (M1, M2, M3), *E. cavolinii*, *V.*

441

*flagellum*, *A. hirsuta*, *C. verticillata*, *S. pallida*, and *B. mollis* distribution is represented along the

442

studied bathymetric range based on sampling unit density. Black square indicates the median value; the

443 box indicates the first and third quartiles; and the line indicates the range between minimum and  
444 maximum values. Gray-scale histograms represent the total number of sampling units for each substrate  
445 type (see legend) over the studied bathymetric range. The numbers on the right indicate the percentage  
446 of sampling units with a certain species presence (n = number of colonies).

447

### 448 3.3 Population size structure

449

450 Overall, the maximum height of 81% of all the observed colonies was measured (63-  
451 100% of the colonies in each transect). All the analyzed populations, indistinctively  
452 of the species, were unimodal (Figs. 6a and b). Most populations of *P. macrospina*  
453 M1, *V. flagellum* and the only analyzed population of *C. verticillata* were positively  
454 skewed, indicating the dominance of small colonies (Figs. 6a, b and Table 3).  
455 Conversely, most population of *P. macrospina* M2, *E. cavolinii*, *S. pallida* and all the  
456 *E. singularis* populations were not skewed, being dominated by medium sized  
457 colonies (Figs. 6a, b and Table 3). One of the two-studied populations of *P.*  
458 *macrospina* M3 was positively skewed (Fig. 6b, Table 3). All the *P. macrospina* M1  
459 populations showed significant kurtosis (Table 3), indicating that they were slightly  
460 more peaked or over-centralized than normal distributions; conversely, only a few  
461 populations showed significant kurtosis in the other species (Table 3). The shrub like  
462 morphology, and the densely intertwined branches of *B. mollis* did not allow the study  
463 of population size structure in this species.

464

465

466 **Table 3** Size structure characteristics of the studied morphotypes and species: colony height, skewness  
467 and kurtosis. Significant skewness or kurtosis are indicated with one (p-value <0.05) two (p-value <  
468 0.01), or three asterisks (p-value < 0.001).

469

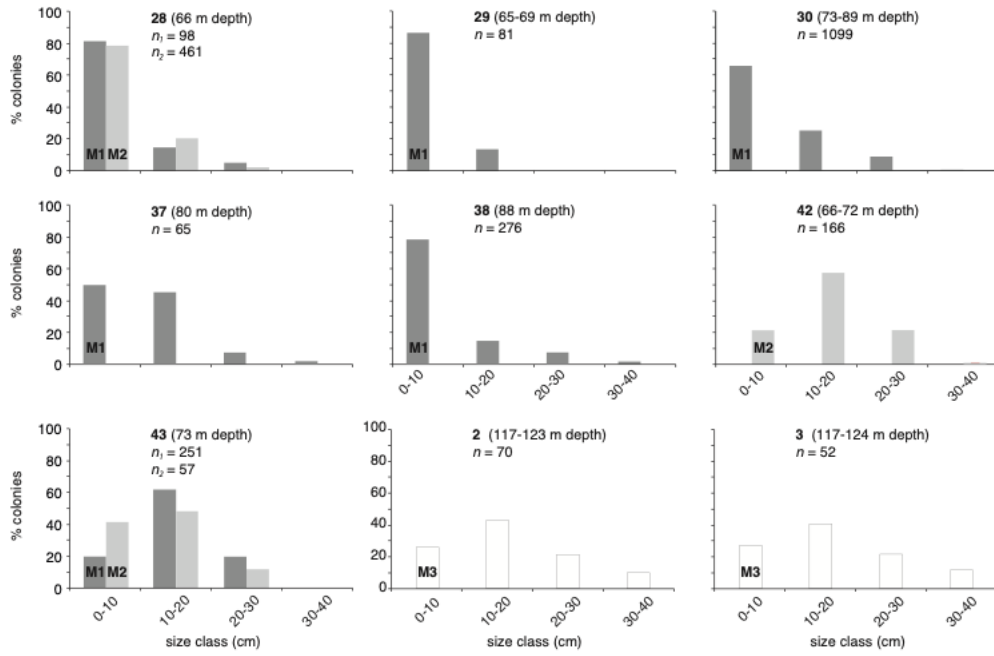


	Transect	Colonies	Mean	SD	Height (cm)			Skewness		Kurtosis	
					Max	Skew	p-value	Sig.	Kurt	p-value	Sig.
<i>E. singularis</i>	37	169	25.3	10.35	55.1	0.541	0.062		2.708	0.497	
	47	45	8.86	4.58	23	0.066	0.209		3.216	0.449	
<i>P. macrospina</i> (M1)	28	98	6.26	5.83	29.4	1.775	< 0.001	***	5.870	< 0.001	***
	29	81	5.90	3.36	18.4	1.377	0.004	**	4.939	0.008	**
	30	1099	8.72	6.9	33.1	1.056	< 0.001	***	3.335	0.037	*
	37	65	10.82	6.1	33.8	0.829	0.075		4.550	0.027	*
	38	276	8.24	6.17	41.9	2.013	< 0.001	***	7.596	< 0.001	***
<i>P. macrospina</i> (M2)	43	251	12.1	6.24	29.4	0.185	0.421		2.247	< 0.001	***
	28	461	6.82	5.13	30.1	1.302	< 0.001	***	4.415	< 0.001	***
	42	166	15.05	5.75	31.35	0.346	0.222		2.570	0.222	
<i>P. macrospina</i> (M3)	43	57	14.52	5.61	25.1	-0.242	0.590		2.366	0.286	
	2	70	17.22	9.07	41.31	0.784	0.086		2.831	0.967	
<i>E. cavolinii</i>	3	52	17.95	11.43	55.65	13.566	0.018	*	4.037	0.272	
	2	206	10.55	7.43	35.63	0.985	< 0.001	***	3.205	0.417	
	3	384	15.16	10.06	50.45	0.739	< 0.001	***	2.912	0.843	
	4	78	16.03	7.98	43.51	0.081	0.059		3.621	0.177	
	6	156	14.59	8.77	47.15	0.579	0.056		2.909	0.990	
	7	82	13.03	6.65	31.94	0.694	0.092		3.136	0.542	
	10	63	19.07	9.83	47.65	0.276	0.524		2.775	0.950	
	11	207	9.08	7.3	38.55	1.492	< 0.001	***	4.940	< 0.001	***
	13	110	11.93	6.93	29.75	0.442	0.202		2.468	0.198	
	22	71	9.81	4.92	22.42	0.686	0.116		2.703	0.785	
<i>V. flagellum</i>	2	56	42.35	22.2	96.41	0.308	0.500		2.558	0.606	
	4	230	38.19	25.14	148.3	1.045	< 0.001	***	4.721	< 0.001	***
	7	130	46	30.86	136.6	0.740	0.0300	*	3.045	0.689	
<i>C. verticillata</i>	73	54	26.43	21.52	115.3	2.513	< 0.001	***	9.467	< 0.001	***
<i>S. pallida</i>	3	186	5.35	1.98	13.54	0.932	< 0.001	***	4.452	< 0.001	***
	4	88	7.12	2.12	12.17	0.224	0.548		2.655	0.615	
	7	83	6.83	2.71	13.96	0.753	0.069		3.190	0.480	
	9	90	6.66	2.81	17.46	1.061	0.013	*	5.329	0.002	**
	13	91	4.62	1.75	10.47	0.552	0.151		3.641	0.156	
	69	40	5.32	1.99	10.39	0.439	0.408		2.571	0.759	

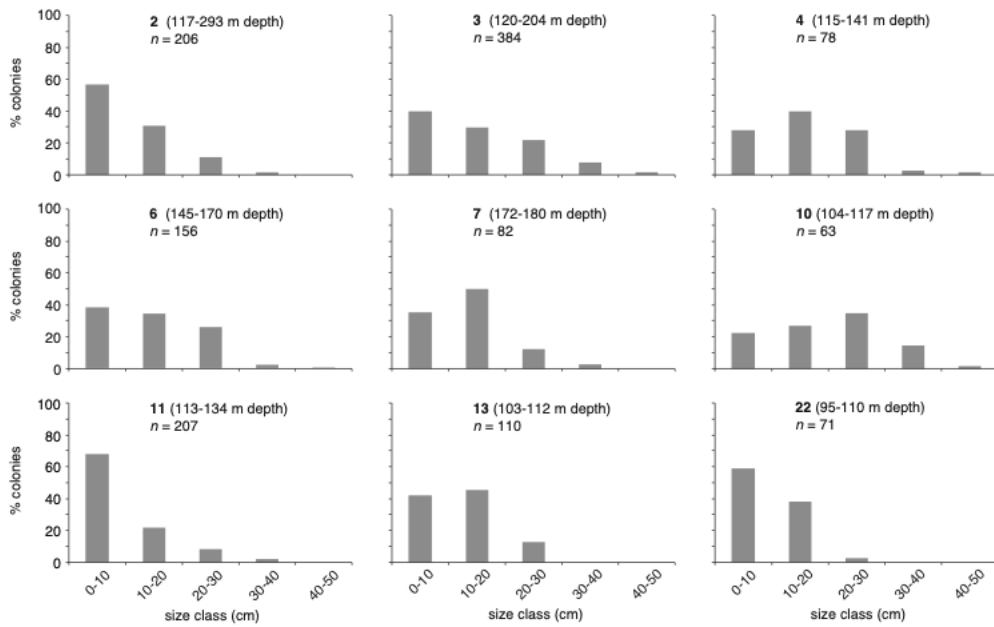
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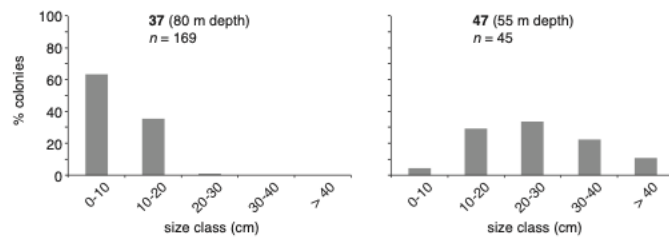
*Paramuricea macrospina*



*Eunicella cavolinii*



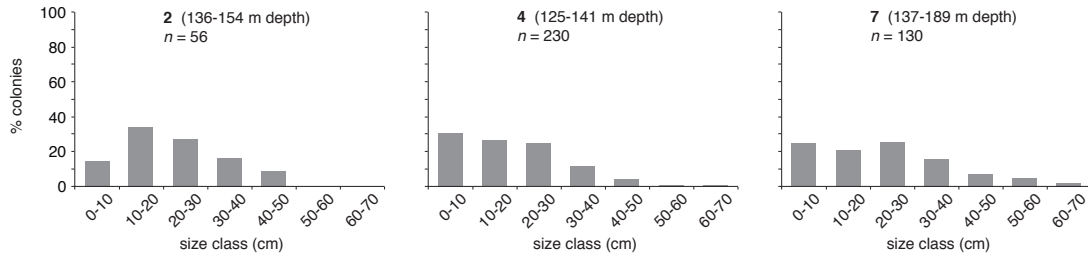
*Eunicella singularis*



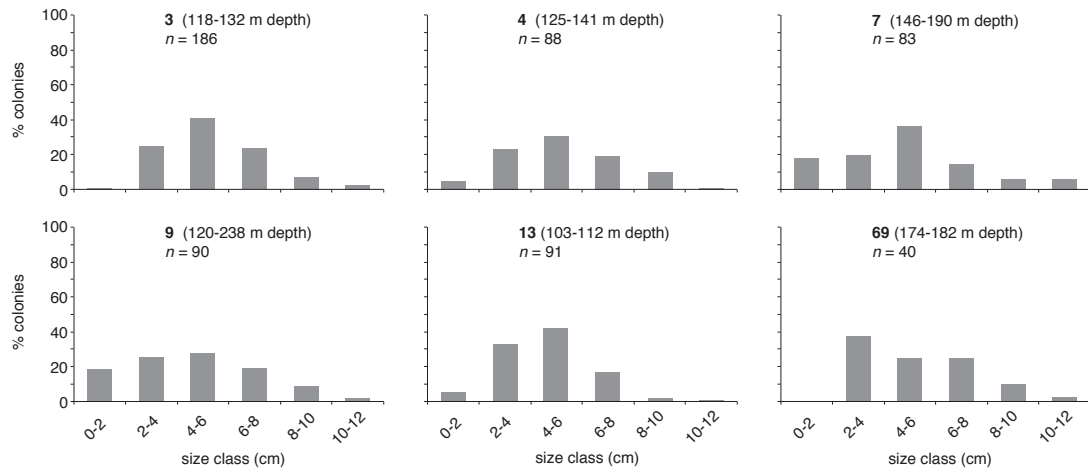
472

473 **Fig. 6a.** *P. macrospina* (M1, M2, M3), *E. cavolinii* and *E. singularis* population size frequency  
 474 distribution (transect number as in Fig. 1 and Table 3, depth range, n = number of colonies).

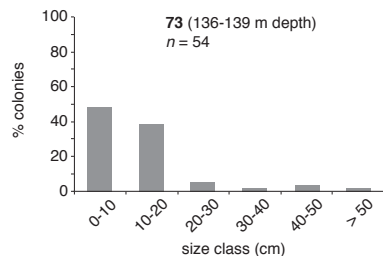
*Viminella flagellum*



*Swiftia pallida*



*Callogorgia verticillata*



476

477 **Fig. 6b.** *V. flagellum*, *S. pallida* and *C. verticillata* population size frequency distribution (transect  
 478 number as in Fig. 1 and Table 3, depth range, n = number of colonies).

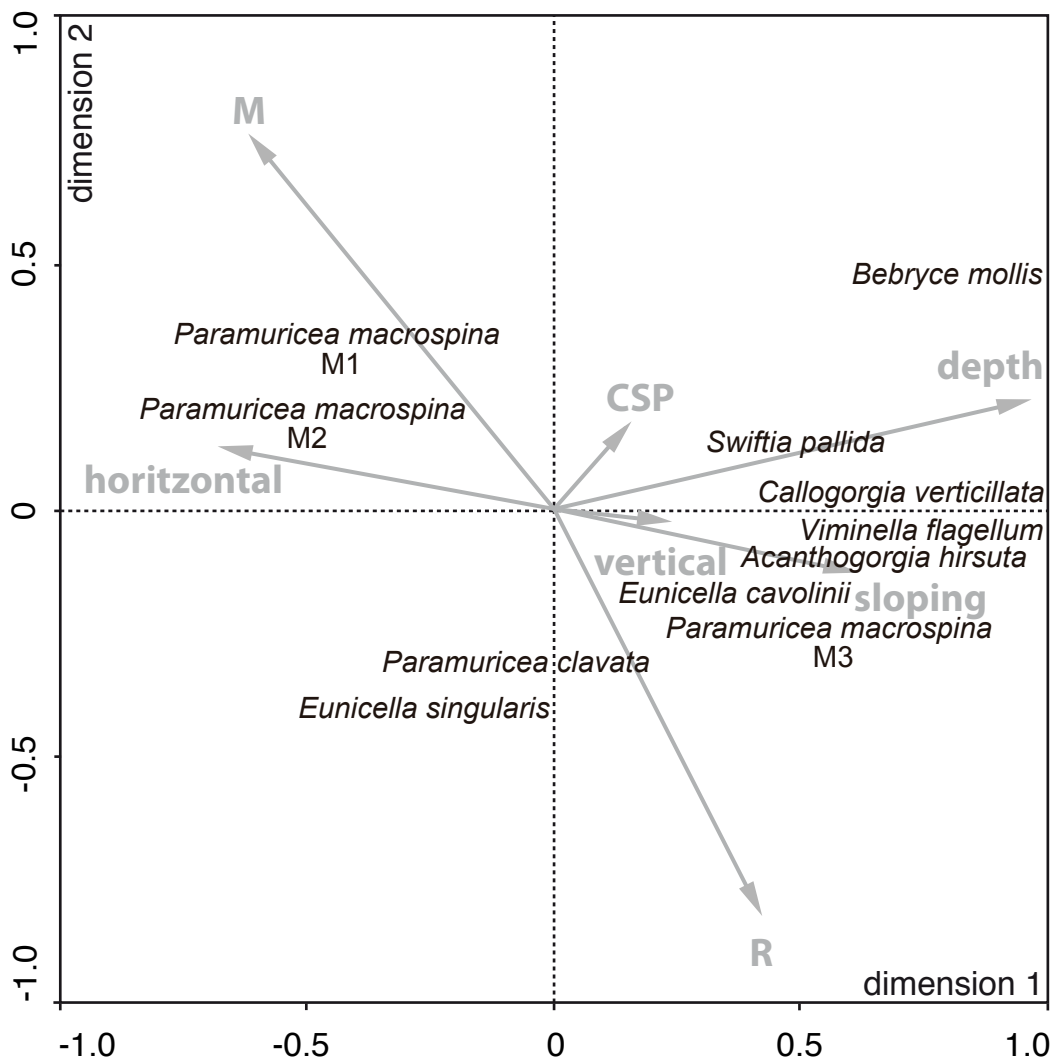
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480 3.4 Relationship with environmental features

481

482 Depth, substrate and slope explained ~20.8% of the total inertia (i.e. explained  
 483 variation of the data) in the CCA, with the first two axis accumulating 17.1% of the  
 484 species variances, and 82.3% of the species-environment relation variance (Fig. 7).

485 According to the Monte Carlo permutation test, the three factors contributed  
 486 significantly ( $p < 0.001$ ) to the ordination. Depth clearly segregates gorgonians found  
 487 on the continental shelf (*P. macrospina* M1 and M2, *E. singularis*, *P. clavata*) from  
 488 those from the shelf edge and continental slope (*P. macrospina* M3, *V. flagellum*, *E.*  
 489 *cavolinii*, *S. pallida*, *B. mollis*, *C. verticillata*, and *A. hirsuta*). On the continental shelf,  
 490 *P. macrospina* M1 and M2 were mainly associated with horizontal maërl beds,  
 491 whereas *E. singularis* and *P. clavata* with rocky bottoms (Fig. 7). On the shelf edge  
 492 and continental slope, *E. cavolinii* and *P. macrospina* M3 were mainly associated with  
 493 sloping rocky bottoms. At increasing depth *V. flagellum*, *S. pallida*, *C. verticillata*,  
 494 and *A. hirsuta* were also mainly associated with sloping bottoms (Fig. 7). Finally, *B.*  
 495 *mollis* was the species most strongly associated with highest depths (Fig. 7).



496  
 497

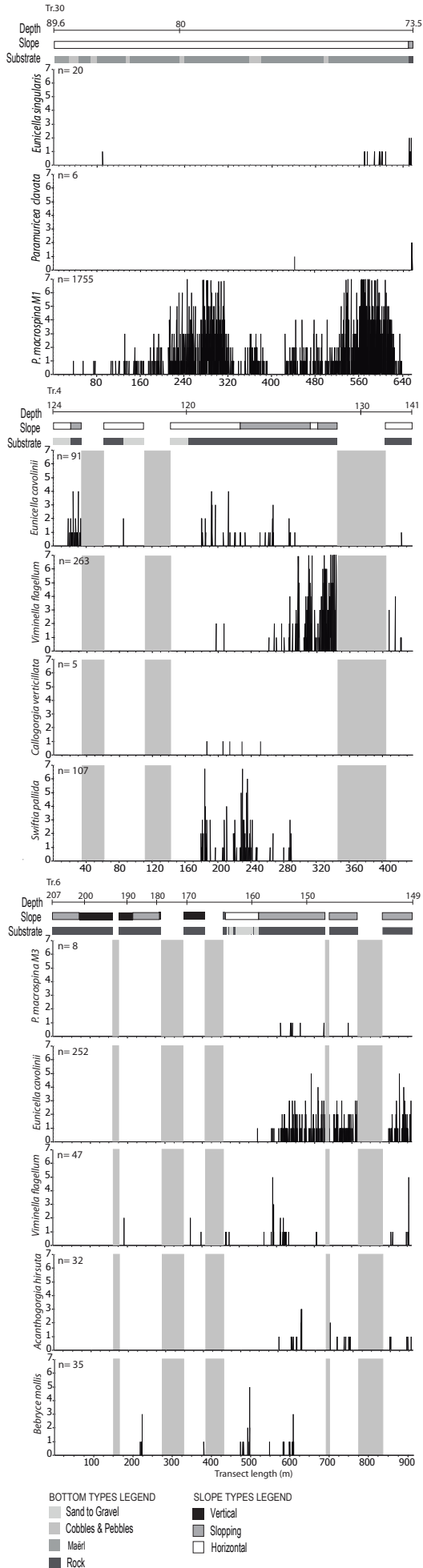
498 **Fig. 7.** Canonical correspondence analysis (CCA): biplot showing the ordination of gorgonian species  
499 and the roles of the significant environmental variables. M: maërl, CSP: cobbles and pebbles and R:  
500 rocky substrates.

501

### 502 3.5 Spatial structure

503

504 Spatial structure of gorgonian distribution was analyzed along three of the video  
505 transects (Fig. 8), representative of the continental shelf (transect 30) and slope  
506 (transects 4 and 6). On the continental shelf, *E. singularis* was positively associated  
507 with *P. macrospina* M1 at large spatial scales (more than 30 m), whereas they were  
508 independently distributed at smaller scales (Fig. 8, Table 4). *E. singularis* was  
509 negatively associated to *P. clavata* at small scales (less than 5 m) and tended to be  
510 independently distributed at large and intermediate scale. *P. clavata* was  
511 independently distributed with respect to *P. macrospina* at all scales (Fig. 8 and Table  
512 4). On the continental slope, in transect 4, all species were independently distributed  
513 at small and medium scales (few to tens of meters) (Fig. 8 and Table 4). At larger  
514 spatial scales (more than 30 m), *C. verticillata*, *S. pallida* and *E. cavolinii* were  
515 positively associated, whereas *V. flagellum* occurred in exclusion to the other species  
516 (Fig. 8, Table 4). In transect 6, *E. cavolinii*, *P. macrospina* M3, *V. flagellum* and *B.*  
517 *mollis* were positively associated at large spatial scales (more than 30 m) (Fig. 8 and  
518 Table 4). *A. hirsuta* tended to be independently distributed at small (less than 30 m)  
519 and large spatial scale (more than 30 m) (Fig. 8 and Table 4). *E. cavolinii* presented  
520 no association with *B. mollis* and *V. flagellum*, and the same situation was found for  
521 *P. macrospina* M3 when compared to *A. hirsuta*.



523

524 **Fig. 8.** Density plots. Species densities are plotted along representative transects from the continental  
 525 shelf (transect 30) continental shelf edge and slope (transect 4 and 6, respectively). Bottom type and  
 526 seabed slope are indicated (see legend). Vertical gray rectangles indicate invalid sequences for the  
 527 analysis (Tr = transect, n = number of colonies).

528

529 **Table 4** Summary of the three-term local quadrat covariance (3TLQC). Significant spatial covariance  
 530 between pairs of species along the three analyzed transects.

Transect Number	Compared species	Negative	Random	Positive
30	<i>P. macrospina</i> M1 vs. <i>E. singularis</i>		0-30 // 55-75	30-55 // > 75
	<i>P. macrospina</i> M1 vs. <i>P. clavata</i>			All transect
	<i>P. clavata</i> vs. <i>E. singularis</i>	2-5	>5	
4	<i>C. verticillata</i> vs. <i>E. cavolinii</i>		0-50	>50
	<i>C. verticillata</i> vs. <i>S. pallida</i>		0-5	>5
	<i>C. verticillata</i> vs. <i>V. flagellum</i>	>55	0-55	
	<i>E. cavolinii</i> vs. <i>S. pallida</i>		0-50	>50
	<i>E. cavolinii</i> vs. <i>V. flagellum</i>	>34	0-34	
	<i>S. pallida</i> vs. <i>V. flagellum</i>	>48	0-48	
6	<i>A. hirsuta</i> vs. <i>B. mollis</i>	30-60	0-30 // >60	
	<i>A. hirsuta</i> vs. <i>E. cavolinii</i>	11-20	0-11 // 20-40	>40
	<i>A. hirsuta</i> vs. <i>P. macrospina</i> M3		All transect	
	<i>A. hirsuta</i> vs. <i>V. flagellum</i>	30-65	0-30 // >65	
	<i>B. mollis</i> vs. <i>E. cavolinii</i>		All transect	
	<i>B. mollis</i> vs. <i>P. macrospina</i> M3		20-30	0-20 // >30
	<i>B. mollis</i> vs. <i>V. flagellum</i>	11-20	0-11 // 20-32	>32
	<i>E. cavolinii</i> vs. <i>P. macrospina</i> M3		0-35	>35
	<i>E. cavolinii</i> vs. <i>V. flagellum</i>		All transect	
<i>P. macrospina</i> M3 vs. <i>V. flagellum</i>	12-22	0-12 // 22-60	> 60	

531

#### 532 4. Discussion

533

534 The diversity of the studied deep gorgonian assemblages was much higher than in  
 535 shallow Mediterranean coastal areas (Weinberg, 1978; Linares et al., 2008; Gori et  
 536 al., 2011a). Nine species were observed to dwell between 40 and 360 m depth within  
 537 the study area, while only 4–5 species are commonly present in littoral areas  
 538 (Velimirov, 1973; Gori et al., 2011a; Garrabou et al., 2001). Gorgonian diversity  
 539 resembled that reported of Atlantic coastal areas (Cúrdia et al., 2013), subtropical

540 areas (Opresko, 1973) and similar depth ranges in the Aleutian Islands (Stone, 2006),  
541 compared to Mediterranean coastal bottoms (Gori et al., 2011a). Conversely,  
542 gorgonian density observed in these deep multispecific assemblages reached high  
543 values (~20 colonies m<sup>-2</sup>) comparable to those reported for Mediterranean coastal  
544 species (Weinbauer and Velimirov, 1996; Linares et al., 2008; Gori et al., 2011a).  
545 These high density values are similar to those found in temperate (Grigg, 1975; 1977;  
546 Cúdira et al., 2013) and tropical (Lasker and Coffroth, 1983; Yoshioka and Yoshioka,  
547 1989) coastal gorgonian assemblages, and clearly exceed those found at similar depths  
548 (180–500 m) in the North Atlantic (Mortensen and Buhl-Mortensen, 2004; Buhl-  
549 Mortensen et al., 2014), and polar continental shelves and slopes (Orejas et al., 2002;  
550 Miller et al., 2012).

551         However, the observed high gorgonian diversity was mainly concentrated on  
552 the shelf edge (100–180 m depth). A clear vertical zonation can be established  
553 regarding species distribution: (1) coastal species extending their distribution to deep  
554 coralligenous banks (*E. singularis* and *P. clavata*); (2) dominance of one single  
555 species on the continental shelf (*P. macrospina*); (3) concentration of several  
556 gorgonian species on the shelf edge (*E. cavolinii*, *P. macrospina*, *S. pallida*, *A. hirsuta*,  
557 *V. flagellum*, *B. mollis* and *C. verticillata*); and (4) species extending their distribution  
558 deeper into the upper slope (*B. mollis*, *C. verticillata*, *V. flagellum* and *S. pallida*).

559         The common Mediterranean coastal species *E. singularis* and *P. clavata* were  
560 found on deep coralligenous banks on the continental shelf of the studied area (45–  
561 100 m depth). The high water transparency allows a very deep distribution of  
562 coralligenous banks (Ballesteros and Zabala, 1993), which in turns could explain the  
563 deep distribution of *E. singularis* within the study area (down to 100 m depth). In  
564 coastal environments characterized by high water turbidity, this species is limited to  
565 70 m depth (Gori et al., 2011a). In the study area continental shelf both species' density  
566 was much lower than that reported in shallow coastal environments (Linares et al.



567 2008; Gori et al., 2011a). This could indicate that these species' deep bathymetric limit  
568 lies around this depth, according to our data. Interestingly, the observed colonies of  
569 *E. singularis* presented the same morphology as the deep asymbiotic morphotype  
570 reported in coastal environments below 40 m depth (Théodor, 1969; Gori et al., 2012).  
571 These populations were dominated by medium sized colonies, corresponding to what  
572 has been observed in deep coastal environments (60 m depth) (Gori et al., 2011b).  
573 Conversely, in shallow coastal environments (20 m depth) these species populations  
574 are mainly composed of small colonies (Linares et al., 2008). Populations of *P. clavata*  
575 extending beyond 40 m have also been reported in several coastal areas (Gori et al.,  
576 2011a; Angiolillo et al., 2015), as well as on top of seamounts (Bo et al., 2011) and  
577 on rocky bottoms of the continental shelf and slope (Bo et al., 2012, 2014). In these  
578 deep environments, *P. clavata* colonies generally achieve larger sizes ( $50 \pm 15$  cm  
579 (mean  $\pm$  SD), min = 25 cm, max = 90 cm) than in shallower environments (Linares et  
580 al., 2008), as a possible consequence of the higher environmental stability of deeper  
581 areas (Grigg, 1975). Deep populations of *E. singularis* and *P. clavata* are probably  
582 protected from high hydrodynamic processes (Teixidó et al., 2013) as well as from  
583 unusually high-temperature conditions associated to mass mortality events in shallow  
584 benthic communities (Garrabou et al., 2009).

585 Maërl beds on the continental shelf of the studied area are covered by very  
586 high abundances of *P. macrospina* (M1 and M2) (Supplementary material 3). In this  
587 environment this species presents high frequency of occurrence over large areas (Fig.  
588 4 and 8) and can reach densities of up to 33 colonies m<sup>-2</sup>, which is at odds with  
589 previous data on this species, having been only reported on rocky substrates and never  
590 as a dominant species (Bo et al., 2011; Topçu and Öztürk, 2015). Preservation of these  
591 *P. macrospina* populations may be a consequence of low trawling pressure over large  
592 areas of the continental shelf (Moranta et al., 2014), as well as the habit of local  
593 artisanal fishermen to clean their nets *in situ* (Díaz et al., 2015). This habit consists of

594 releasing by-catch over the same fishing grounds. This practice might result in partial  
595 damage of entangled colonies of *P. macrospina*, but as long as their holdfast remains  
596 attached to the maërl rodholite, their survival might be favored (Díaz et al., 2015).  
597 Population size structures of *P. macrospina* were mostly asymmetrical and positively  
598 skewed (Table 4), suggesting high recruitment rates (Linares et al., 2008) and  
599 implying that maërl beds are particularly suitable habitats for this species. However,  
600 unlike *E. singularis* and *P. clavata* that occur on coralligenous banks, the structural  
601 instability of maërl may limit the presence of large colonies of *P. macrospina* in the  
602 continental shelf (Tunncliffe et al., 1983). Furthermore, fishing activities might be  
603 particularly detrimental to large colonies, which are probably more susceptible than  
604 smaller colonies to get entangled and broken by nets used by artisanal fishermen in  
605 the area. Indeed, populations dominated by small colonies have been reported in  
606 intensely fished areas (Althaus et al., 2009).

607         Highest gorgonian diversity was concentrated on the rocky bottoms of the  
608 shelf edge (at 100–180 m depth). In this environment, gorgonian assemblages were  
609 mostly multispecific (92% of occupied sampling units contained several species)  
610 (Supplementary material 4) and included seven of the nine observed species (Fig. 4  
611 and 5). This diversity is probably influenced by the joint effect of habitat heterogeneity  
612 and hydrodynamic stability. In the study area's shelf edge, boulders, slaps and vertical  
613 walls alternate over short distances. Shelf edge are mainly influenced by steady flow  
614 currents and stable hydrodynamic conditions (e.g. Puig et al., 2000), such as the  
615 Balearic current associated with the Balearic front, which flows from south to north  
616 along the western shelf edge of the Balearic Promontory (Ruiz et al., 2009). Stable  
617 hydrodynamic conditions, together with the hydrodynamic processes that increase  
618 particle suspension in the near-bottom water layers, may also suppose enhanced food  
619 availability for gorgonians on the shelf edge (Thiem et al. 2006). Finally, the observed  
620 increase in gorgonian diversity on the shelf edge could also results from the merging

621 of species with shallower and deeper distributions, causing a mid-domain effect  
622 (Colwell and Lees 2000), as previously suggested for deep coral diversity in other  
623 locations (Stone, 2006; Matsumoto et al., 2007). Most gorgonian populations located  
624 on the shelf edge had a bell-shaped, unimodal size structure dominated by medium  
625 sized colonies (Fig. 6a and b). *P. macrospina* (M3) populations on the shelf edge were  
626 bell-shaped, in contrast to its populations on the continental shelf (M1 and M2) that  
627 were mostly dominated by small size colonies. When compared to maërl, rocky  
628 substrates provide higher structural stability allowing colonies to achieve larger sizes.  
629 In these multispecific gorgonian assemblages of the shelf edge, the fine scale spatial  
630 covariance of species appears to be related to the combined effect of density,  
631 occupancy, and colony size. When a large species such as *V. flagellum* achieves high-  
632 densities over extended areas, it tends to exclude any other species (Fig. 8).  
633 Conversely, coexistence is observed at low and intermediate densities among large  
634 (*C. verticillata*), medium (*E. cavolinii*) and small sized species (*S. pallida*). This could  
635 indicate that differences in size may reduce interspecific competition for space and  
636 food (Schoener, 1974). Species with similar size probably feed on the food particles  
637 that are transported by the same water layer, with a potential competition for food  
638 (Kim and Lasker, 1997). Conversely, species with different size are probably feeding  
639 on different water layer, thus avoiding potential shading processes. Coexistence at  
640 medium spatial scales (~30 m) may also occur at low and intermediate densities  
641 among species of similar size and morphology (*E. cavolinii* and *A. hirsuta*). In this  
642 case, however, spatial exclusion occurred at smaller scales (~10 m), suggesting that  
643 these species share the same habitat but partially compete for space. Overall, the  
644 species dwelling on the shelf edge within the study area, have been recently found  
645 with increasing frequency on rocky substrates at similar depths in other areas of the  
646 Mediterranean Sea (Bo et al., 2009; 2011; 2012; 2014), suggesting the general validity  
647 of the observed pattern of high gorgonian diversity.

648 Below the shelf edge, gorgonian abundance strongly decreases, and only *B.*  
649 *mollis*, *S. pallida*, *V. flagellum* and *C. verticillata* were observed to extend their  
650 distribution under 200 m depth (Fig. 4). Gorgonian assemblages are here mainly  
651 monospecific, (76% of occupied sampling units contained one single species) and  
652 with low densities ( $\sim 0.75 \pm 0.3$  colonies  $m^2$  (mean  $\pm$  SD)) (Supplementary material  
653 5). These species are typically found along the continental slope in other  
654 Mediterranean locations (Mytilineou et al., 2014; Deidun et al., 2014; Bo et al., 2015)  
655 where they mostly concentrate along the edges, maximizing their exposure to currents  
656 (Genin et al., 1986). On the scarce rocky substrates occurring in these deeper  
657 environments, gorgonian abundance tends to decrease with increasing depth, and  
658 antipatharians become the dominant arborescent species (Deidun et al., 2014; Bo et  
659 al., 2015). Finally, the soft sediments of these deeper environments can be colonized  
660 by the bamboo coral *Isidella elongata* (Maynou and Cartes, 2012; Bo et al., 2015),  
661 which can form extended assemblages in bathyal muds (Pérès, 1967).

662 Due to their arborescent morphology, gorgonians are especially vulnerable to  
663 fishing activities (Mytilineou et al., 2014; Bo et al., 2014), and their slow growth rate  
664 (Coma et al., 1998; Sherwood and Edinger, 2009) makes their recovery from related  
665 fishing damages very slow (Althaus et al., 2009). The high diversity and abundance  
666 of deep gorgonian assemblages in the rocky areas of the shelf edge, and the vast area  
667 covered by high densities of *P. macrospina* on the continental shelf are probably  
668 related to the low trawling pressure and the exceptional fishing practices exerted by  
669 local artisanal fishermen. This represents an example of the possibility of conserving  
670 deep gorgonian assemblages and their associated high-diverse fauna (e.g. Buhl-  
671 Mortensen and Mortensen, 2005) through better management of fishing activities.  
672 These high-density deep gorgonian assemblages may provide an approximate idea of  
673 how Mediterranean continental shelves and upper slopes stood before decades of  
674 bottom trawling.

675

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677

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1084 Supplementary material captions:

1085

1086 Supplementary material 1: Transect location, length, number of useful sampling units (USU),  
1087 percentage of gorgonian occupied sampling units (% OSU), depth (minimum and maximum depth),  
1088 main substrate (> 50% coverage of USU) (M: maërl, CSP: cobbles and pebbles, MS: medium sands,  
1089 R: rocky substrates), main slope (> 50% coverage of USU)(H: horizontal, S: slopping, V: vertical).  
1090

1091 Supplementary material 2: Number of voucher species sampled in the Menorca Channel (CS =  
1092 continental shelf, SE = shelf edge, US = upper slope, bf = branch fragment).  
1093

1094 Supplementary material 3: Population of *P. macrospina* M1 on a maërl bed located on the continental  
1095 shelf at ~78 m depth (transect 31 on Fig. 1).  
1096

1097 Supplementary material 4: Multispecific gorgonian assemblage (white and pink colonies = *E. cavolinii*,  
1098 yellow colonies = *A. hirsuta*, purple colonies = *P. macrospina* M3) on the shelf edge at ~150 m  
1099 depth. Individuals of the sponge *Poecillastra compressa* can also be seen (transect 6 on Fig. 1).  
1100

1101 Supplementary material 5: Population of *C. verticillata* on the upper slope at 237 m depth. Colonies of  
1102 the antipatharian *Leiopathes glaberrima* can also be seen (transect 56 on Fig. 1).