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

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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 Puellas 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

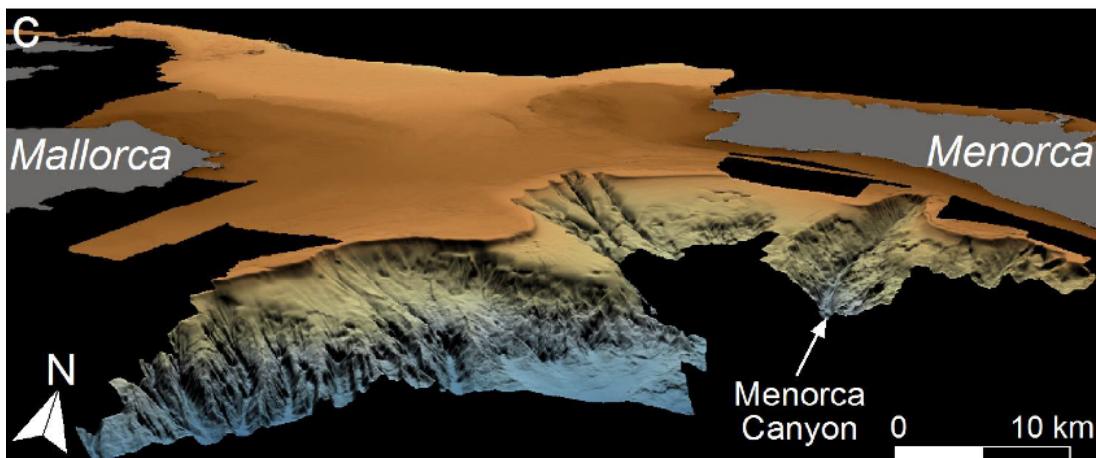
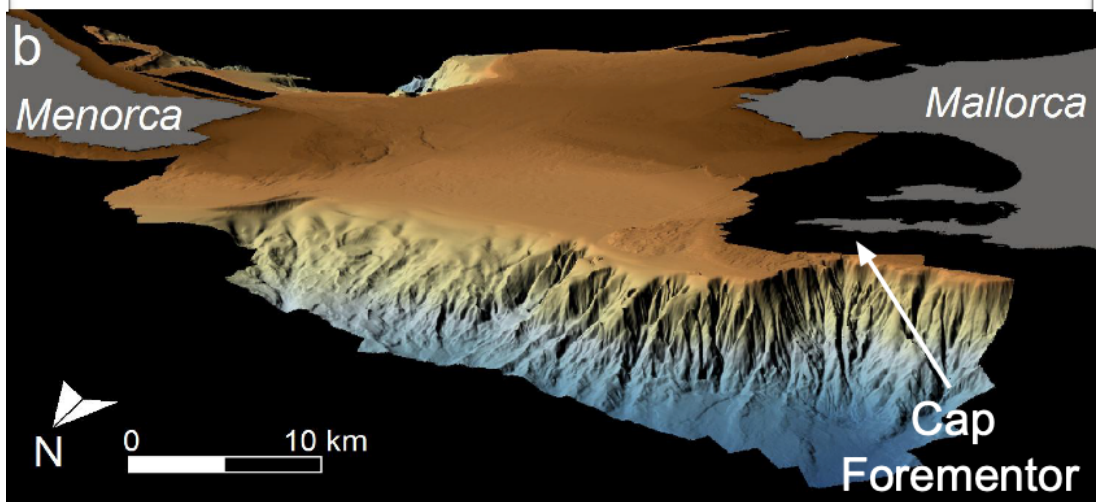
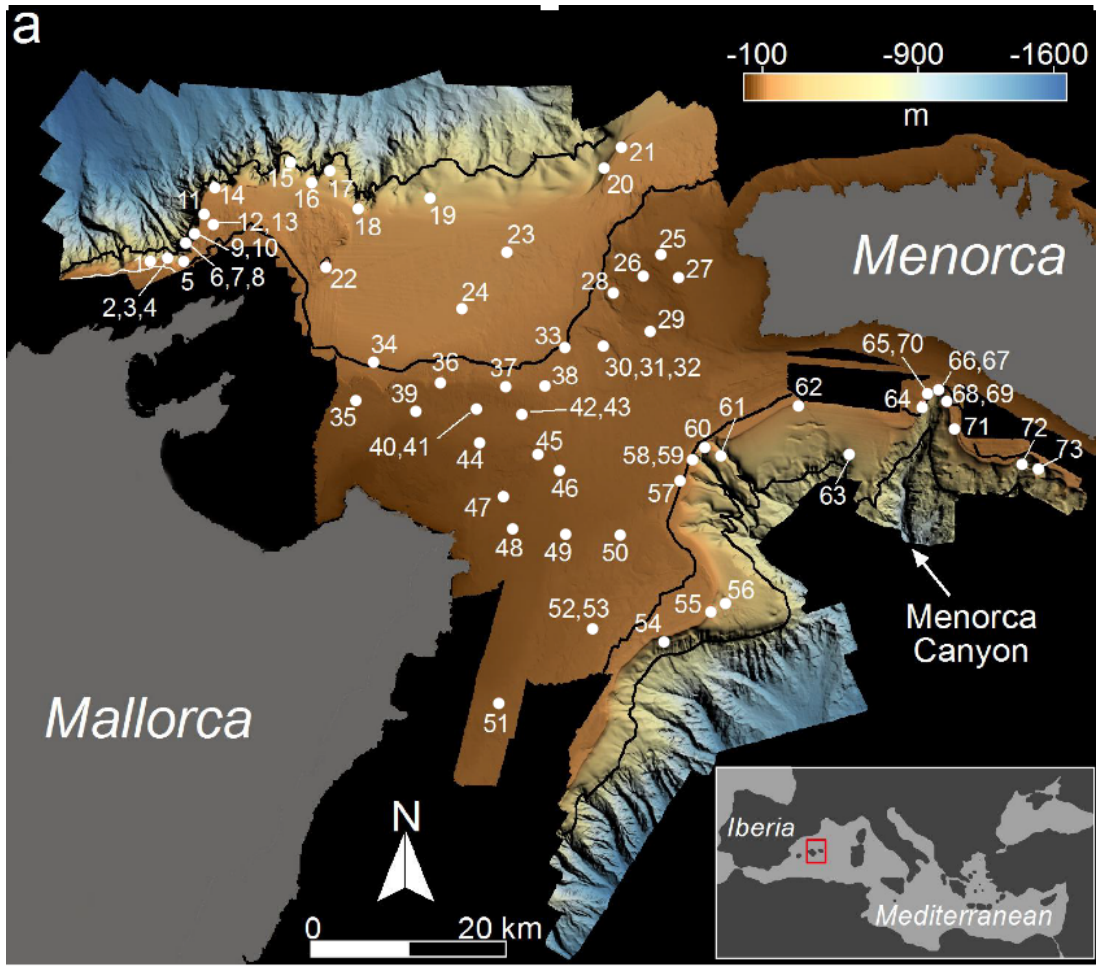
127 2.1 Study area

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 m² (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 km². 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

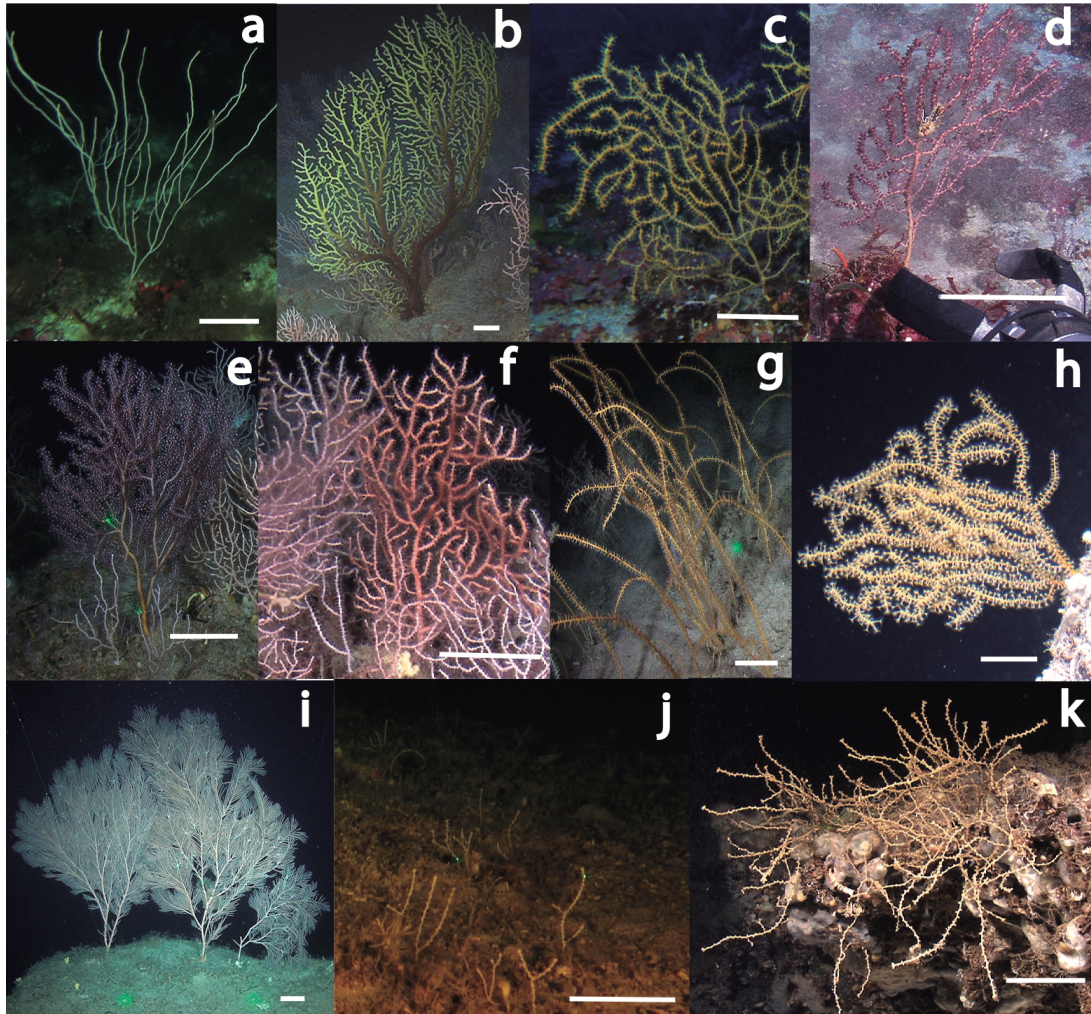
319

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

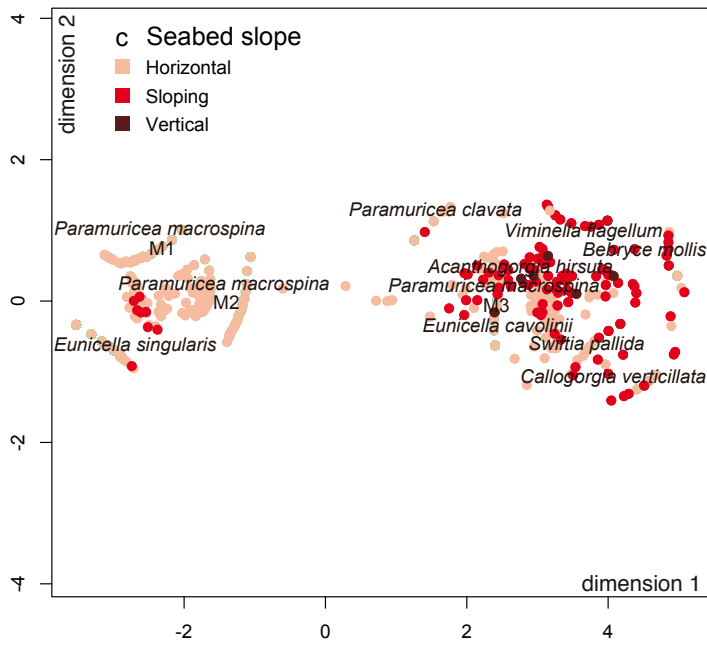
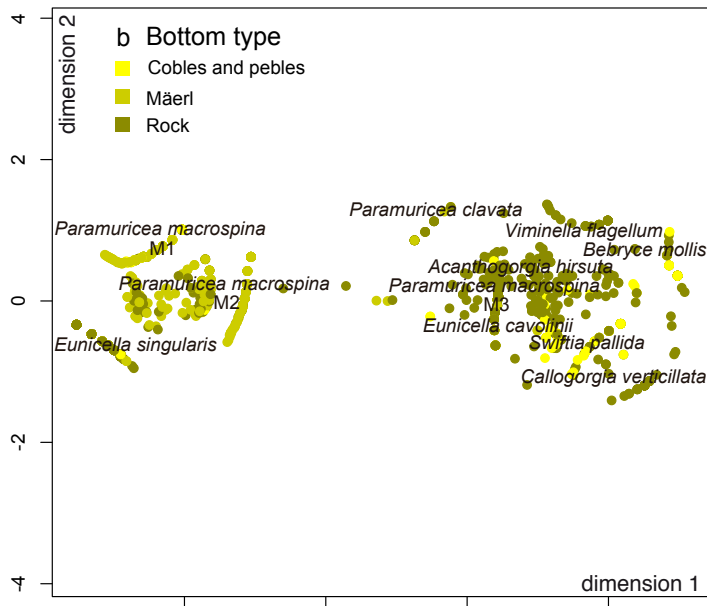
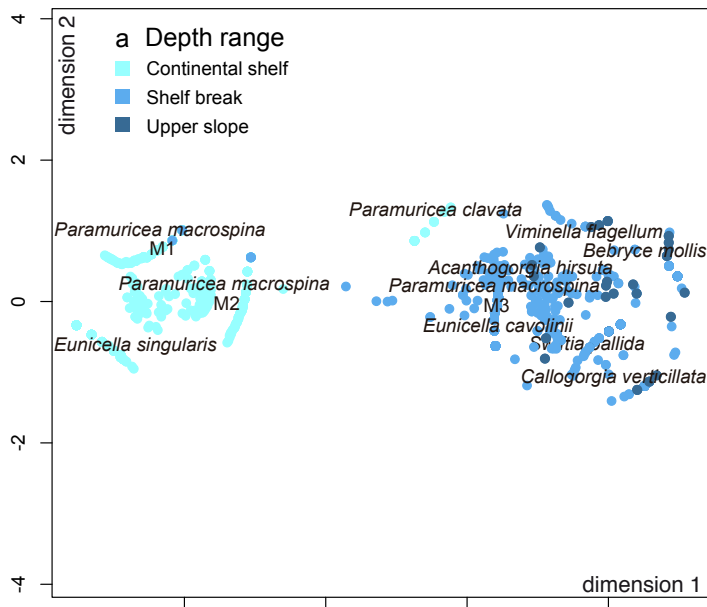
Depth-range	Sampling Units			Species	Occupancy		Abundance		Mean density \pm SD (colonies \cdot m ⁻²)	Max density (colonies \cdot m ⁻²)
	Number	with gorgonians	(%)		Number	(%)	Number	(%)		
Continental shelf (40 - 100 m)	2723	735	(27)	<i>E. singularis</i>	357	(48.5)	966	(23.0)	1.2 \pm 1	7.5
				<i>P. clavata</i>	22	(3.1)	48	(1.1)	1.1 \pm 0.8	3
				<i>P. macrospina M1</i>	292	(39.7)	1899	(44.0)	3.2 \pm 5	33
				<i>P. macrospina M2</i>	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 M1</i>	3	(0.4)	4	(0.1)	0.7 \pm 0.3	1.0
				<i>P. macrospina M2</i>	7	(0.9)	11	(0.3)	0.8 \pm 0.7	2.5
				<i>P. macrospina M3</i>	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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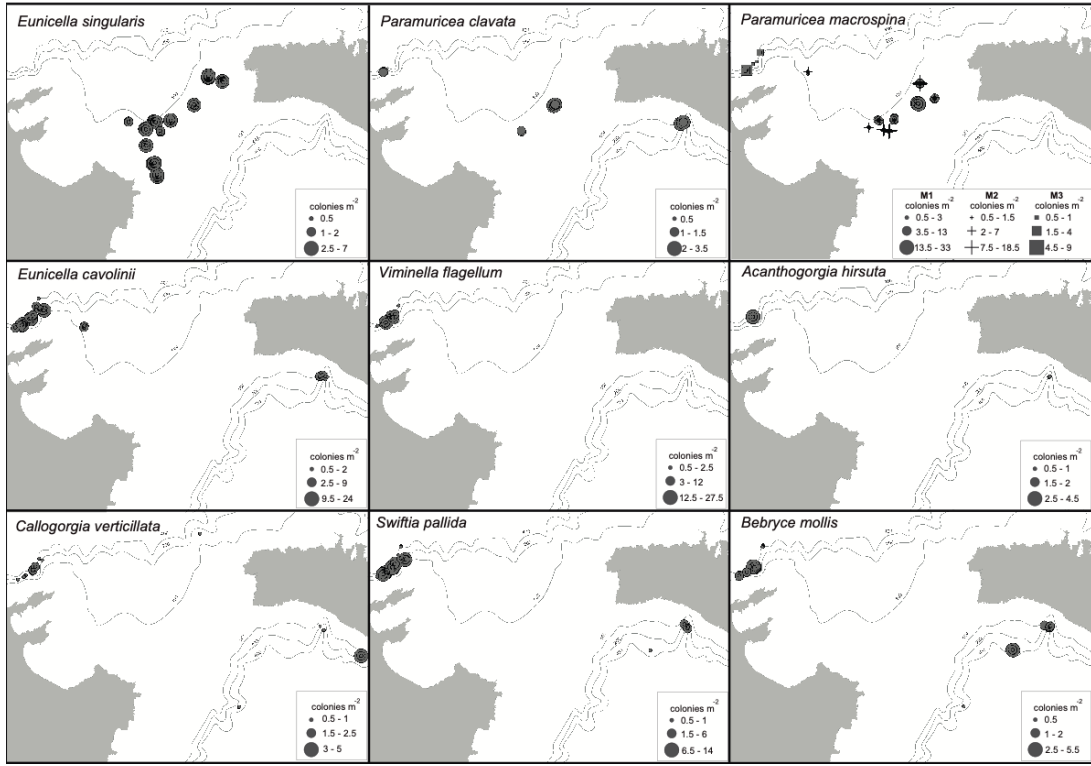
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Depth range	Sim/SD	Contribution%	Cum. Contribution%
Continental shelf: 22.43%			
<i>E. singularis</i>	0.48	60.33	60.33
<i>P. macrospina</i> M1	0.34	24.59	84.92
<i>P. macrospina</i> M2	0.25	14.86	99.79
Shelf edge: 21.45%			
<i>E. cavolinii</i>	0.65	78.43	78.43
<i>S. pallida</i>	0.25	14.70	93.14
Upper slope: 17.89%			
<i>B. mollis</i>	0.33	38.55	38.55
<i>C. verticillata</i>	0.26	24.83	63.38
<i>S. pallida</i>	0.27	23.30	86.68
<i>V. flagellum</i>	0.21	12.13	98.81
Bottom type			
Rock: 18.63%			
<i>E. singularis</i>	0.37	54.89	54.89
<i>E. cavolinii</i>	0.33	32.61	87.50
<i>S. pallida</i>	0.12	3.68	91.19
Cobbles & pebbles: 17.67%			
<i>S. pallida</i>	0.42	60.77	60.77
<i>E. cavolinii</i>	0.21	14.08	74.85
<i>P. macrospina</i> M1	0.16	10.86	85.70
<i>B. mollis</i>	0.15	9.93	95.64
Maërl: 28.68%			
<i>P. macrospina</i> M1	0.62	60.20	60.20
<i>P. macrospina</i> M2	0.42	33.55	93.75
Seabed Slope			
Horizontal: 18.11%			
<i>E. singularis</i>	0.35	49.09	49.09
<i>P. macrospina</i> M1	0.28	25.11	74.19
<i>P. macrospina</i> M2	0.29	14.93	89.13
<i>E. cavolinii</i>	0.15	7.12	96.25
Slopping: 19.66%			
<i>E. cavolinii</i>	0.50	66.28	66.28
<i>B. mollis</i>	0.17	9.94	76.22
<i>S. pallida</i>	0.17	9.26	85.48
<i>V. flagellum</i>	0.17	7.03	92.51
Vertical: 31.68%			
<i>E. cavolinii</i>	0.56	53.09	53.09
<i>V. flagellum</i>	0.51	44.75	97.84

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.

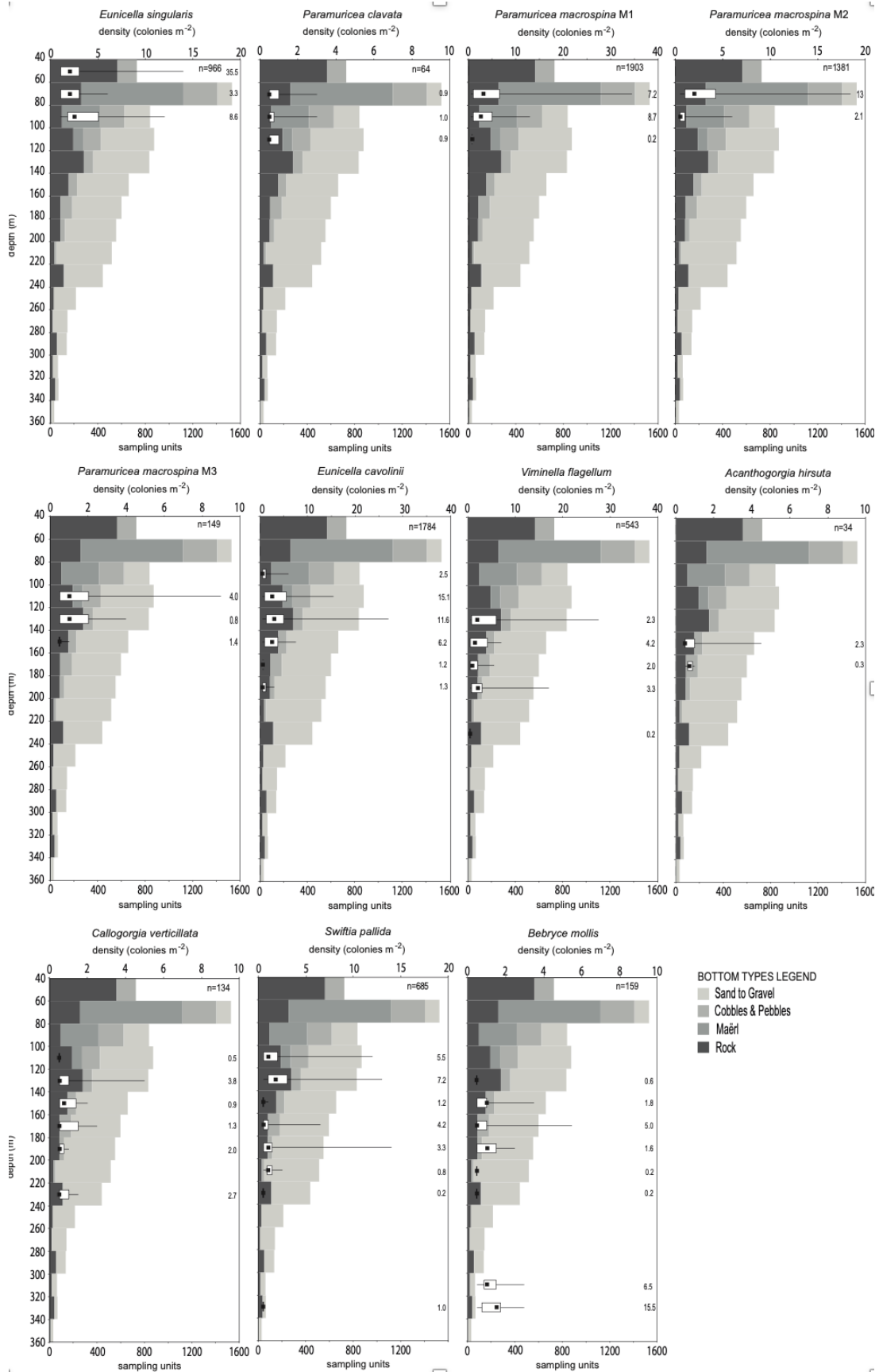


431

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.

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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).

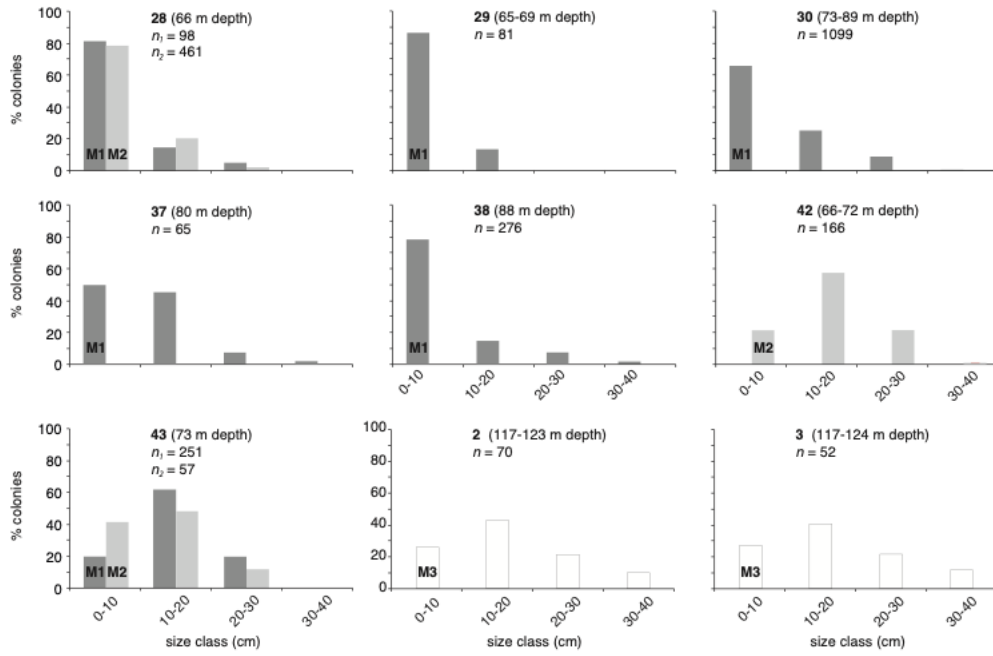
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	Transect	Colonies	Mean	SD	Height (cm)			Skewness		Kurtosis	
					Max	Skew	p-value	Sig.	Kurt	p-value	Sig.
<i>E. singularis</i>	37	169	25.3	10.35	55.1	0.541	0.062		2.708	0.497	
	47	45	8.86	4.58	23	0.066	0.209		3.216	0.449	
<i>P. macrospina</i> (M1)	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	

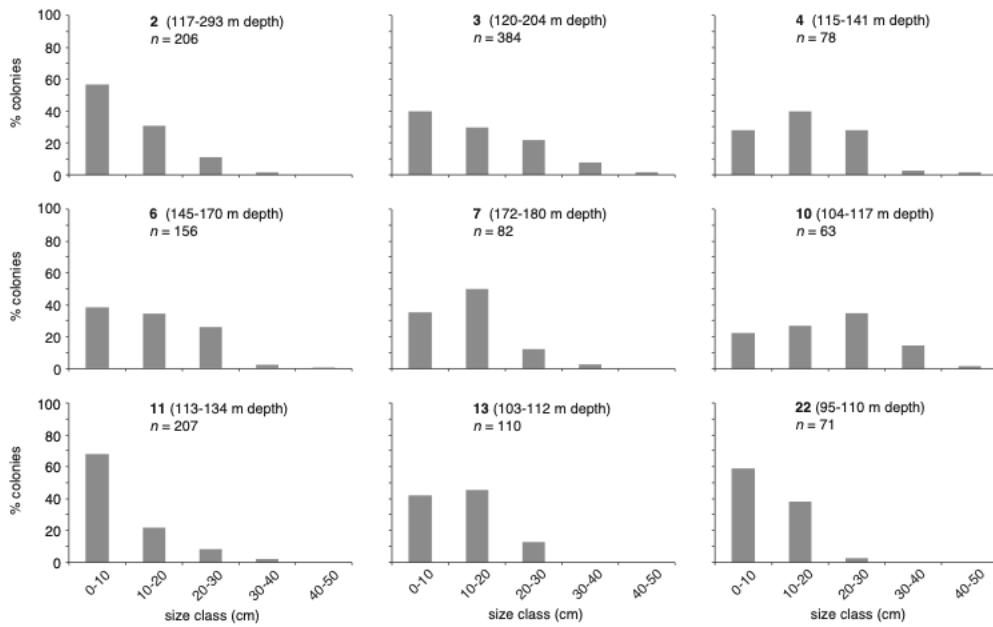
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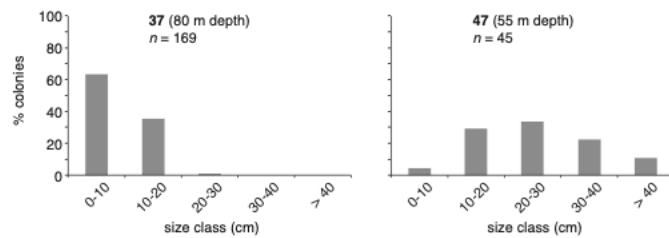
Paramuricea macrospina



Eunicella cavolinii



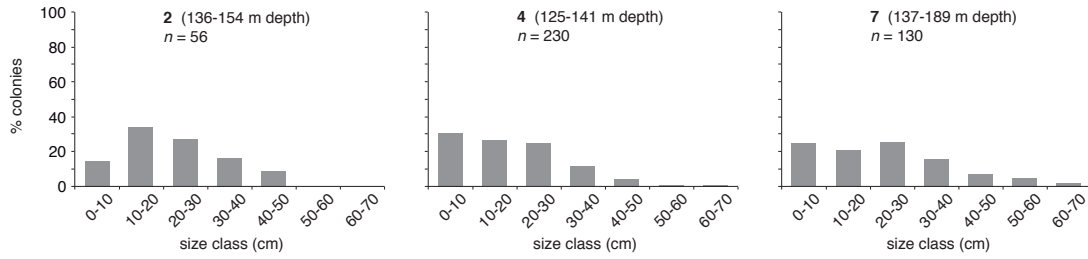
Eunicella singularis



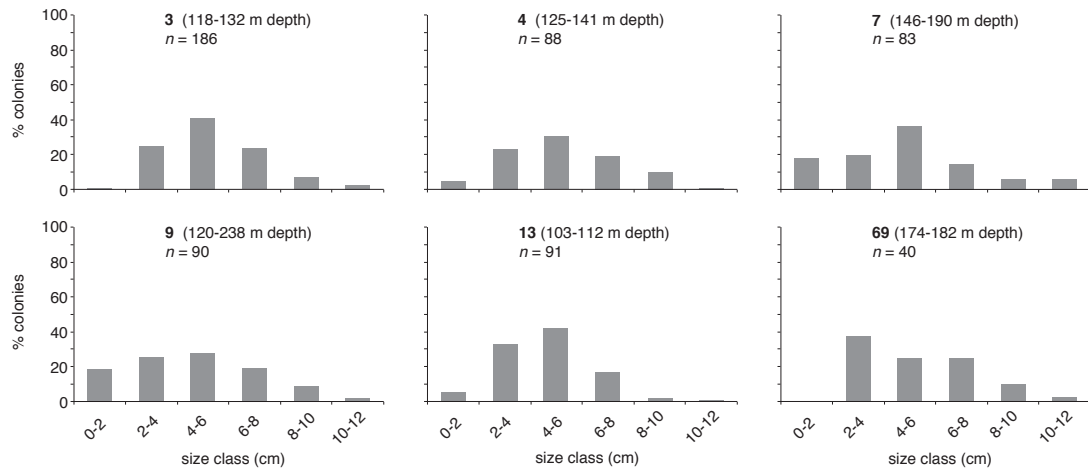
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473 **Fig. 6a.** *P. macrospina* (M1, M2, M3), *E. cavolinii* and *E. singularis* population size frequency
 474 distribution (transect number as in Fig. 1 and Table 3, depth range, n = number of colonies).

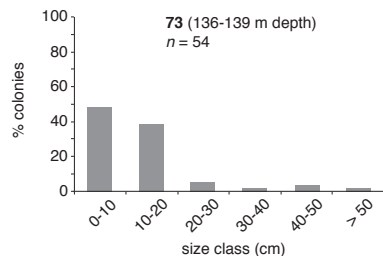
Viminella flagellum



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).

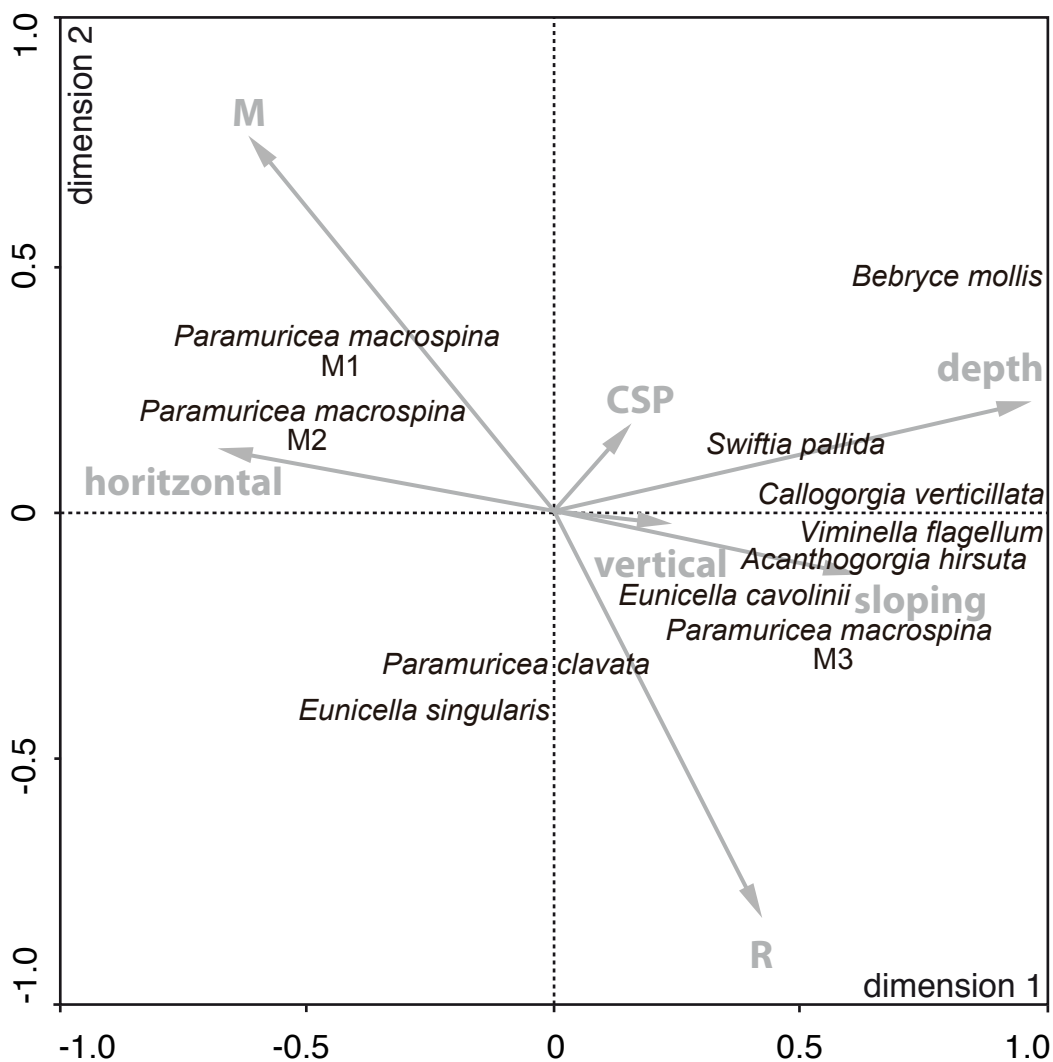
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480 3.4 Relationship with environmental features

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).



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 497

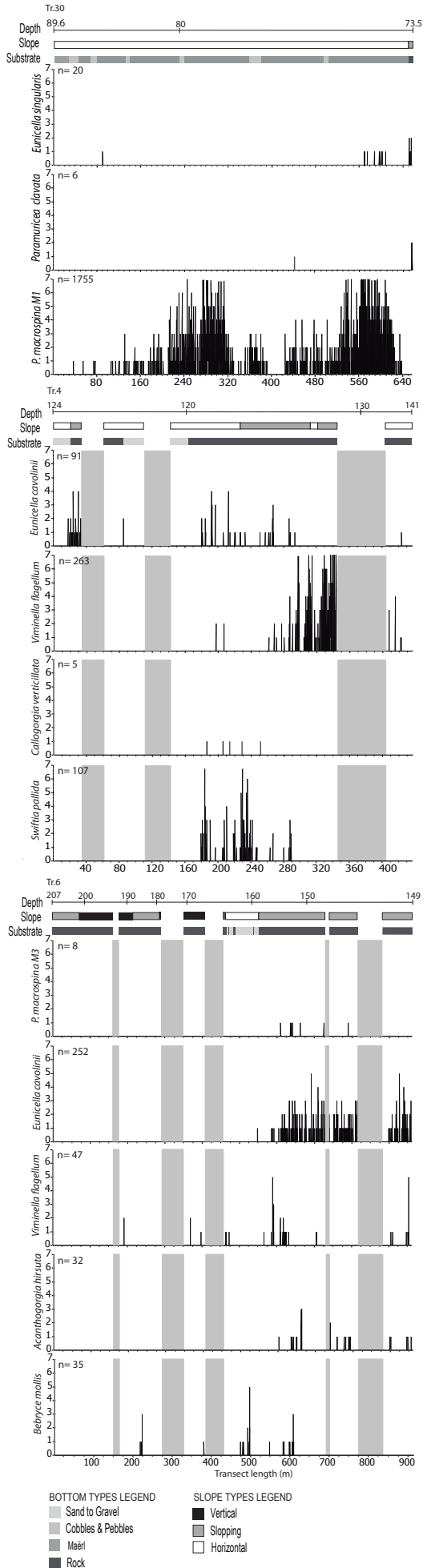
498 **Fig. 7.** Canonical correspondence analysis (CCA): biplot showing the ordination of gorgonian species
499 and the roles of the significant environmental variables. M: maërl, CSP: cobbles and pebbles and R:
500 rocky substrates.

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⁻²) 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 ± 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⁻², 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).