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The understorey of gorgonian forests in mesophotic temperate reefs

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1 **The understory of gorgonian forests in mesophotic temperate reefs**

2

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19

20 **Abstract**

- 21 1. In the Mediterranean Sea, dense populations of the gorgonian *Paramuricea clavata* shape  
22 marine animal forests characterizing the seascapes of coralligenous habitats. Despite the  
23 concerns for its health, due to several anthropogenic threats and recent mass mortality  
24 events mainly triggered by thermal anomalies, the understory of its forests and the  
25 ecological processes they promote are still little known. Here, the abundance and  
26 composition of epibenthic assemblages inside and outside *P. clavata* forests were  
27 investigated across the central and western Mediterranean Sea, by applying a  
28 multifactorial sampling design.
- 29 2. In spite of the large variability in the structures of epibenthic assemblages at local and  
30 regional scales, the gorgonian understoreys share some common features, such as higher  
31 abundances of calcareous builder organisms and a reduced invasion by the non-  
32 indigenous alga *Caulerpa cylindracea*, compared to the adjacent unforested rocky  
33 bottoms. *P. clavata* showed non-linear density-dependent relationships with algal turfs  
34 and non-encrusting algae belonging to the genus *Peyssonnelia*. Moreover, by entrapping  
35 benthic mucilaginous aggregates with their branches, these gorgonians risk topical  
36 necrotic lesions but may reduce the suffocation risks for understory organisms.
- 37 3. Overall, *P. clavata* forests may enhance bioconstruction processes and increase resistance  
38 and resilience of the benthic assemblages in the Mediterranean coralligenous habitats.  
39 This species and its forests, together with their understoreys, should be considered as  
40 essential elements of the Mediterranean Sea ecology, and therefore worthy of specific and  
41 effective protection measures.
- 42 4. Conservation strategies should reduce the risk of mechanical damage by regulating fishing  
43 activities, anchorages and scuba diving where gorgonian forests are present. Moreover,

44 when evident alterations are documented restoration actions should be implemented to  
45 recover gorgonian forests integrity.

46

47 **Keywords:** alien species, benthos, biodiversity, climate change, endangered species,

48 invertebrates, subtidal

## 49 **1 Introduction**

50 In many marine habitats erect organisms may form dense populations resembling small  
51 terrestrial forests. They include canopy-forming algae (e.g. kelps, fucoïds), but also branched  
52 sessile invertebrates (e.g. sponges, cnidarians, bryozoans) able to form dense mono- or pluri-  
53 specific “animal forests” (*sensu* Rossi, Bramanti, Gori, & Orejas Saco del Valle, 2017).  
54 Forests forming species directly or indirectly affect availability of abiotic and biotic resources  
55 by structural changes and therefore may be considered ecosystem engineers (Jones, Lawton,  
56 & Shachak, 1994; reviewed in Romero, Gonçalves-Souza, Vieira, & Koricheva, 2015).  
57 Terrestrial forest trees control the understorey by providing favourable microclimates, with  
58 less fluctuations of environmental variables (e.g. humidity, temperature, organic matter,  
59 nutrient, shading) compared to habitats outside tree assemblages, and by driving interactions  
60 among animals and plants (Wright, 2002). In the marine environment, kelp forests and the  
61 multitude of species interactions that they support may control ecosystem structure and  
62 functioning, mitigating environmental stress and enhancing resistance towards habitat loss or  
63 fragmentation (e.g. Bennett et al., 2015; Steneck et al., 2002). In kelp forests, sedimentation  
64 and accumulation of detritus (Airoldi, 2003; Duggins & Eckman, 1994) are considered key  
65 features in structuring benthic assemblages. Moreover, shading effects (Arkema, Reed, &  
66 Schroeter, 2009; Clark, Edwards, & Foster, 2004) and depth gradient (Graham, 2004;  
67 Rodgers & Shears, 2016) control their food webs, driven by the primary production provided  
68 by kelps and their epiphytes.

69 Ecological processes in terrestrial and kelp forests have been extensively investigated,  
70 while little is known about marine animal forests. Marine animal forests are made by dense  
71 assemblages of benthic suspension-feeders, filtering large quantities of seston and  
72 substantially contributing to the benthic-pelagic coupling (Gili, Coma, Orejas, López-  
73 González, & Zabala, 2001; Gili & Coma, 1998). They include sponge gardens (Marliave,

74 Conway, Gibbs, Lamb, & Gibbs, 2009), mono-specific forests of hydroids (Di Camillo et al.,  
75 2013; Rossi, Bramanti, Broglio, & Gili, 2012), black corals (e.g. Bo, Canese, & Bavestrello,  
76 2014; Ingrassia et al., 2016), mesophotic zoantharians (e.g. gold coral) and gorgonians  
77 (Cartes, LoIacono, Mamouridis, Lopez-Perez, & Rodriguez, 2013; Cerrano et al., 2010). One  
78 of the most peculiar elements characterizing Mediterranean coralligenous habitats  
79 (mesophotic biogenic reefs, sensu Ballesteros, 2006) are the forests of the gorgonian  
80 *Paramuricea clavata* (Risso 1826) (Musard et al., 2014). *P. clavata* is a long-lived, slow-  
81 growing species (Linares, Doak, Coma, Díaz, & Zabala, 2007). Colonies, irregularly branched  
82 and purple/yellow in colour, may be more than 1.5 m in height and over 100 years old  
83 (Linares, Doak, Coma, Díaz, & Zabala, 2007). Pristine forests may reach densities of greater  
84 than 50 colonies m<sup>-2</sup> and dry masses greater than 1,700 g m<sup>-2</sup> (Coma, Ribes, Zabala, & Gili,  
85 1998; Linares, Coma, Garrabou, Díaz, & Zabala, 2008). Biology and ecology of this species  
86 have been well studied: geographic and bathymetric distributions (Boavida, Assis, Silva, &  
87 Serrão, 2016; Di Camillo, Ponti, Bavestrello, Krzelj, & Cerrano, 2017; Gori et al., 2011;  
88 Kipson et al., 2015; see also Supplementary Material S1, Figure S1.1 and Figure S1.2),  
89 reproduction, growth, secondary production and survivorship (Coma, Ribes, Zabala, & Gili,  
90 1998; Cupido et al., 2012; Cupido, Cocito, Sgorbini, Bordone, & Santangelo, 2008; Fava,  
91 Bavestrello, Valisano, & Cerrano, 2010; Linares, Coma, & Zabala, 2008; Linares, Doak,  
92 Coma, Díaz, & Zabala, 2007; Mistri & Ceccherelli, 1994; Santangelo et al., 2015), feeding  
93 ecology (Cocito et al., 2013; Coma, Gili, Zabala, & Riera, 1994; Ribes, Coma, & Gili, 1999),  
94 respiration rate (Coma, Ribes, Gili, & Zabala, 2002; Previati, Scinto, Cerrano, & Osinga,  
95 2010), and population genetic structure (Mokhtar-Jamai et al., 2011; Perez-Portela et al.,  
96 2016; Pilczynska, Cocito, Boavida, Serrao, & Queiroga, 2016).

97 Integrity of *P. clavata* forests, however, is threatened by fishing lines and nets,  
98 anchorages and recreational divers causing mechanical damage (Bavestrello, Cerrano, Zanzi,

99 & Cattaneo-Vietti, 1997; Linares & Doak, 2010; Markantonatou, Marconi, & Cerrano, 2016;  
100 Tsounis et al., 2012), suffocation by mucilaginous benthic aggregates (Giuliani, Virno  
101 Lamberti, Sonni, & Pellegrini, 2005; Mistri & Ceccherelli, 1996a), invasion from non-  
102 indigenous species (Cebrian, Linares, Marschal, & Garrabou, 2012), and increase in water  
103 turbidity and sedimentation rates due to run-off as a result of bad land management (Mateos-  
104 Molina et al., 2015). Moreover, gorgonian forests are threatened by global climate change-  
105 related disturbances such as increased frequency of exceptional storms (Teixido, Casas,  
106 Cebrian, Linares, & Garrabou, 2013) and thermal anomalies (Cerrano & Bavestrello, 2008;  
107 Linares, Coma, Garrabou, Díaz, & Zabala, 2008) that may induce physiological stress and  
108 increase their susceptibility to pathogens (Calvo et al., 2011; Rivetti, Frascchetti, Lionello,  
109 Zambianchi, & Boero, 2014; Vezzulli, Pezzati, Huete-Stauffer, Pruzzo, & Cerrano, 2013).  
110 The latter, coupled with reduced food availability due to the stratification of the water column  
111 in summer, seem to lie at the basis of the gorgonian mass mortality events recorded in recent  
112 decades in the north-western Mediterranean Sea (Calvo et al., 2011; Cerrano et al., 2000;  
113 Crisci, Bensoussan, Romano, & Garrabou, 2011; Garrabou et al., 2009; Huete-Stauffer et al.,  
114 2011; Linares et al., 2005; Martin, Bonnefort, & Chancerelle, 2002).

115         Currently, many *P. clavata* forests are fragmented in patches and considered in strong  
116 regression as a result of mass mortality events that repeatedly affected this long-lived, slow  
117 growing and low resilient species (Cerrano et al., 2005; Cupido et al., 2009; Linares et al.,  
118 2005). Concerns for gorgonian forests, and for the consequences of their loss on the  
119 associated assemblages and on the ecological processes occurring in the understory are  
120 rising, even if little is known on the structure, diversity and abundances of the benthic  
121 assemblages associated to *P. clavata* forest. Manipulative experiments have highlighted that  
122 *P. clavata* forests significantly affect the early-stage recruitment of sessile epibenthic



123 assemblages, although effects may vary across sites exposed to different environmental  
124 conditions (Ponti et al., 2014).

125 The aims of the present study were to explore spatial patterns of epibenthic  
126 assemblages inhabiting the understory of Mediterranean *P. clavata* forests, compared to  
127 adjacent not forested rocky areas, and to shed light on the conservation needs of this habitat-  
128 forming species to preserve biodiversity of coralligenous habitats.

129

## 130 **2 Materials and methods**

### 131 **2.1 Sampling design and survey method**

132 Epibenthic sessile assemblages inside and outside *Paramuricea clavata* forests were  
133 investigated by applying a multifactorial sampling design. Nine sites were randomly selected  
134 among those with a high abundance of *P. clavata*, as reported in the Reef Check database  
135 (Cerrano, Milanese, & Ponti, 2017; see Supplementary Material S1, Figure S1.1) (Figure 1).  
136 At each site four areas inside and four outside *P. clavata* forests, having similar orientation,  
137 inclination and depth ( $\pm 3$  m), were randomly selected. Four photographic samples ( $21 \times 28$   
138 cm) were collected within each area (Figure 2a) using either a Canon PowerShot G12 or a  
139 Canon PowerShot G15 digital cameras (10 to 12 Mpixel, respectively) equipped with an  
140 aluminium underwater case, S-TTL strobe (Inon D-2000) and a custom stainless steel frame.  
141 Inside gorgonian forests height and percentage cover of *P. clavata* colonies were measured in  
142 the field and by photographic samples ( $50 \times 50$  cm), respectively (Figure 2b).

143 Percentage cover of sessile organisms was quantified by superimposing a grid of 400  
144 equal-sized squares, using the software PhotoQuad (Trygonis & Sini, 2012). Although several  
145 software are available to estimate the abundance of organisms in photographic samples, such  
146 as SeaScape, based on picture segmentation (Teixido et al., 2011), and CPCe, based on  
147 random points count (Kohler & Gill, 2006), PhotoQuad was chosen because it allows to

148 define the accuracy of the percentage cover estimation, based on the number of cells in the  
149 superimposed grid, and does not set limits to the maximum number of identifiable species, as  
150 occurs counting a set of random points. Percentage cover was related to the total readable area  
151 of each image, obtained by subtracting dark and blurred zones or portions covered by motile  
152 organisms as in Ponti, Fava, & Abbiati (2011). Organisms were identified to the lowest  
153 possible taxonomic level, by comparisons to close-up photos and voucher specimens collected  
154 in previous studies (e.g. Ponti, Fava, & Abbiati, 2011; Ponti et al., 2014), and grouped into  
155 morpho-functional groups (modified from Casas-Güell, Teixidó, Garrabou, & Cebrian, 2015;  
156 Garrabou, Ballesteros, & Zabala, 2002; Teixido, Garrabou, & Harmelin, 2011). All calcifying  
157 taxa were also included in the builder group.

158

## 159 **2.2 Data analysis**

160 Differences in height and percentage cover of *Paramuricea clavata* forests between sites were  
161 assessed by one-way Analysis of Variance (ANOVA,  $\alpha = 0.05$ ; Underwood, 1997).

162 Benthic assemblage similarities were calculated for each pair of samples using the  
163 Bray-Curtis coefficient applied to square root-transformed percentage cover data and  
164 excluding *P. clavata* from the analysis (Clarke, 1993). Similarity patterns of benthic  
165 assemblage inside and outside gorgonian forest and among sites were represented by both  
166 unconstrained ordination plot, using the Principal Coordinate Analysis (PCoA; Gower, 1966),  
167 and constrained ordination plot, using the Canonical Analysis of Principal coordinates (CAP;  
168 Anderson & Willis, 2003), calculated on the centroids of similarities among replicates from  
169 the same sampling area. CAP detects the axis that best discriminate between the two *a priori*  
170 groups, i.e. benthic assemblages inside and outside gorgonian forest.

171 The possible relationship between the similarity patterns of the benthic assemblages  
172 and environmental conditions and geographical locations (see Supplementary Material S2,

173 Figure S2.1, Table S2.2) were investigated by multivariate multiple regression using the  
174 DistLM procedure that provides a step-wise conditional selection of predictor variables  
175 significantly correlated with the obtained similarity patterns (McArdle & Anderson, 2001).  
176 These relationships were graphically represented by vectors superimposed on the PCoA plot.

177 Differences in assemblage structures inside and outside gorgonian forest (Go: 2 levels,  
178 fixed), among sites (Si: 9 levels, random), in the interaction (Go  $\times$  Si), and among areas  
179 nested in this interaction (Area(Go  $\times$  Si)) were assessed by permutational multivariate  
180 analysis of variance (PERMANOVA,  $\alpha = 0.05$ ; Anderson & ter Braak, 2003). When less than  
181 999 unique values in the permutation distributions were available, asymptotical Monte Carlo  
182  $p$ -values ( $p_{MC}$ ) were used instead of permutational  $p$ -values. Results of the PERMANOVA  
183 test were reported along with the estimated component of variation, in percentage of the total,  
184 allowing to compare the relative importance of different terms in the model (Anderson,  
185 Gorley, & Clarke, 2008).

186 Species richness (as number of species,  $S$ ), species diversity (as Hill's diversity  
187 number  $NI = \text{Exp } H'$ , where  $H'$  is the Shannon's index based on natural logarithm) and the  
188 corresponding evenness component (as  $NI0 = NI/S$ ) were calculated for each sample  
189 (Magurran, 2004).  $NI$  represent the 'effective number of species' of an assemblage, i.e. the  
190 species richness of a perfectly even assemblage (all species equally common) with the same  
191 diversity as the original assemblage (Hill, 1973).

192 Differences in single species percentage cover, morpho-functional groups percentage  
193 cover and species diversity indices were assessed by mixed multifactorial ANOVA ( $\alpha = 0.05$ )  
194 following the same design adopted for PERMANOVA. Cochran's  $C$  test was used to check  
195 the assumption of homogeneity of variances and, when necessary, data transformations were  
196 applied. If variances were slightly heterogeneous even after transformations (Cochran's  $C$  test  
197  $0.05 > p > 0.01$ ), the analyses were run at  $\alpha = 0.01$  for significance test, while when variances

198 were highly heterogeneous (Cochran's C test  $p < 0.01$ ), the analyses were conservatively run  
199 at  $\alpha = 0.001$  (Underwood, 1997). In the ANOVA, when the term  $Go \times Si$  was not significant  
200 ( $p > 0.25$ ) it was pooled with the term  $Area(Go \times Si)$  (Underwood, 1997). When the term  $Go$   
201  $\times Si$  was significant, the Student–Newman–Keuls (SNK) method was used for the *post-hoc*  
202 comparisons.

203 Possible relations between the percentage cover of *P. clavata* and those of other taxa  
204 were explored by local polynomial regression fitting (LOESS), which is a smoothing method  
205 that summarizes the association between variables by fitting a multitude of regression models  
206 to adjacent subsets of the data (Cleveland & Devlin, 1988). For this purpose, percentage cover  
207 data inside gorgonian forests were averaged by area (i.e. 4 areas per site).

208 Multivariate analyses were performed using PRIMER 6 with PERMANOVA+ add-on  
209 package (Anderson, Gorley, & Clarke, 2008). LOESS and univariate analyses were made in R  
210 (R Core Team, 2017) with GAD, a specific package for General ANOVA Designs (Sandrini-  
211 Neto & Camargo, 2012). Mean values were always reported along with their standard errors  
212 (s.e.).

213

## 214 **3 Results**

### 215 **3.1 The investigated gorgonian forests**

216 The study sites were located over a wide geographical area, which spans  $5.6^\circ$  in latitude and  
217  $8.2^\circ$  in longitude, from the north-western Mediterranean Sea (P.te Causinière at Cap Ferrat,  
218 Villefranche-sur-Mer and Colombara at Portofino, in the Ligurian Sea, Punta delle Cannelle,  
219 Capo Calvo, Picchi di Pablo and Scoglio del Remaiolo at Elba Island in the central  
220 Tyrrhenian Sea) to the central Mediterranean (Punta San Paolo at Ustica Island) and to the  
221 northern Adriatic Sea (Zverinac Južni Rt and Rivanjski Kanal in Croatia). At study sites,  
222 gorgonian forests occur at different depths, with upper limits from 22 to 40 m, either on

223 vertical or horizontal substrates, with different orientations. Geological and environmental  
224 features at each site were reported in the Supplementary Material (S2, Figure S2.1, Table S2.1  
225 and S2.2).

226 Gorgonian forests significantly differed between study sites both in terms of colony  
227 height ( $F_{8,27} = 6.38$ ,  $p = 0.0001$ ) and percentage cover ( $F_{8,27} = 2.48$ ,  $p = 0.037$ ). The mean  
228 gorgonian height ranges from  $25.4 \pm 4.3$  cm to  $122.1 \pm 22.6$  cm; while their mean percentage  
229 cover ranges from  $22.3 \pm 5.1$  % to  $56.8 \pm 7.4$  % (Figure 2c,d; Figure 3).

230

### 231 **3.2 Epibenthic assemblages inside and outside gorgonian forests**

232 Besides *Paramuricea clavata*, 97 taxa were recorded and quantified, of which 45 were  
233 identified to species level. The allocation of taxa to morpho-functional groups has been  
234 reported in the Supplementary Material (S3, Table S3.1).

235 The most abundant and widely distributed taxa were encrusting calcareous  
236 rhodophytes belonging to Corallinaceae and Peyssonneliaceae families, and erect algae such  
237 as *Flabellia petiolata* (Turra) Nizamuddin 1987, *Pseudochlorodesmis furcellata* (Zanardini)  
238 Børgesen 1925 and *Halimeda tuna* (J.Ellis & Solander) J.V.Lamouroux 1816. Some species,  
239 though locally abundant, were found only in nearby sites. It was the case of the colonial  
240 ascidians *Polycitor adriaticus* (Drasche 1883) and *Aplidium conicum* (Olivi 1792) that were  
241 recorded only in the northern Adriatic Sea (Figure 2c), and of the invasive alga *Caulerpa*  
242 *cylindracea* Sonder 1845 that was found at Elba Island (Figure 2e).

243 Benthic assemblages showed a large variability among sampling areas (i.e. local  
244 scale), which accounts for 19.7% of the total observed variation, and among sites (28.1% of  
245 the total variation). Significant differences were also found in relation to the presence of  
246 gorgonian forest across sites (19.0% of the total variation; Table 1). The variability of the  
247 benthic assemblages associated with the presence/absence of the gorgonian per se,

248 independently from the geographical location, accounts for the 9.4% of the total observed  
249 variation. Patterns of similarity among assemblages were strongly affected by differences  
250 among sites rather than inside and outside gorgonian forests, as it is well represented in the  
251 PCoA ordination plot (Figure 4a). In the unconstrained plot, the data cloud is driven by the  
252 large geographical differences in assemblage structures, represented by the correlation vector  
253 of the longitude, as well as by depth and substrate inclination. Inclination, depth and latitude  
254 were selected by the DistLM step-wise procedure as the best combination of variables  
255 significantly correlated to the obtained similarity pattern and together explain 46.8% of the  
256 total variation in benthic assemblages. The variability among sites tends to mask the effects of  
257 the presence of gorgonians, however detected by PERMANOVA test (Table 1). Conversely,  
258 the constrained ordination plot, obtained by CAP, revealed a clear differentiation between  
259 assemblages inside and outside gorgonian forest, with a large canonical correlation of 0.87  
260 (Figure 4b).

261 Few species, individually analysed, showed a clear pattern in relation to the  
262 occurrence of gorgonian forest. The green algae *Codium bursa* (Olivi) C.Agardh 1817 was  
263 found at five sites out of nine, and always only outside *P. clavata* forest. The yellow  
264 gorgonian *Eunicella cavolini* (Koch 1887) was found at six sites out of nine, and at five of  
265 these was present only inside *P. clavata* forest. However, ANOVA tests failed to detect a  
266 significant effect of the gorgonian forest on the abundance of *C. bursa* and *E. cavolini* due to  
267 the paucity of data and heterogeneity of variances (Table 2). Overall, the percentage covers of  
268 encrusting sponges (from zero to  $9.9 \pm 1.6\%$ ) and encrusting bryozoans (from zero to  $6.1 \pm$   
269  $1.5\%$ ) were very variable at the local and regional scales, i.e. among areas and sites, and in  
270 both cases they were significantly more abundant inside the gorgonian forests (Table 2,  
271 Figure 5a,b). The percentage covers of erect bryozoans varied from  $0.03 \pm 0.03\%$  to  $6.1 \pm$   
272  $3.0\%$  and showed a less clear pattern with a large variability at the local scale. Their

273 abundance inside and outside gorgonian forests was not consistent across sites (Table 2). The  
274 SNK test revealed that their percentage covers were significantly higher inside the gorgonian  
275 forests at three sites, while at the six other sites no differences were detected (Figure 5c).  
276 Mixed turf, which includes many filamentous algae and hydroids, showed percentage covers  
277 ranging from  $6.6 \pm 3.3\%$  and  $52.6 \pm 4.7\%$  with significant variability at local scale (Table 2).  
278 Its abundance inside and outside gorgonian forests was not consistent across sites. In this  
279 case, the SNK test revealed that its percentage covers were significantly higher outside the  
280 gorgonian forests at seven sites, while at the two remaining sites no differences were detected  
281 (Figure 5d). Percentage cover of the encrusting calcareous rhodophytes (ECR), ranging from  
282  $1.3 \pm 0.6\%$  to  $26.7 \pm 3.2\%$ , significantly varied among sites and showed higher values inside  
283 gorgonian forest (Table 2, Figure 5e). Similar results were obtained by summing encrusting  
284 calcareous rhodophytes with all the other builder organisms that may contribute to the  
285 coralligenous framework (Table 2, Figure 5f).

286 Percentage covers of green algal turfs and non-encrusting algae belonging to the genus  
287 *Peyssonnelia*, although not significantly different between inside and outside the gorgonian  
288 forests, showed a peculiar pattern in relation to the cover of *P. clavata* inside the forests. At  
289 low gorgonian cover (up to 30%), green algal turfs seemed to be facilitated by *P. clavata*,  
290 while *Peyssonnelia* spp. were not affected (Figure 6a,b). At higher gorgonian cover, the  
291 percentage covers of both algal groups decreased dramatically, down to about 10%. The non-  
292 indigenous alga *Caulerpa cylindracea* was found only at three sites located at Elba Island. At  
293 these three sites, the percentage cover of *C. cylindracea* showed large variability at the local  
294 scale (i.e. significant differences among areas) and significantly lower values inside the  
295 gorgonian forests (Table 2, Figure 7a). Mucilaginous aggregates were found at only three  
296 sites: Colombara at Portofino, Punta San Paolo at Ustica Island and Picchi di Pablo at Elba  
297 Island (Figure 2f). At these three sites, the percentage cover of these aggregates showed large

298 variability at the local scale and a significant variation across sites and inside *vs* outside  
299 gorgonian forest (Table 2). The SNK test revealed that percentage covers were significantly  
300 higher outside the gorgonian forests at two sites out of three sites (Figure 7b).

301 All the species diversity indices (*S*, *NI* and *NIO*) showed significant variability at local  
302 scale, i.e. among areas within the interaction between site and gorgonian forest. Species  
303 richness (*S*) and evenness (*NIO*) significantly differed among sites. Overall, all indices were  
304 significantly higher inside the gorgonian forests (Table 2, Figure 8).

305

#### 306 **4 Discussion**

307 This study compared the epibenthic assemblages inside and outside gorgonian forests  
308 across a broad range of central and western Mediterranean coralligenous habitats, differing in  
309 environmental conditions and belonging to different biogeographic sectors (sensu Bianchi &  
310 Morri, 2000). Gorgonian forests vary in colony density, and dwell on rocky substrates  
311 differing in inclination, orientation and depth. Overall, understory assemblages of these  
312 animal forests showed a large variability at different spatial scales. The percentages of  
313 component of variation of benthic assemblage structures at local (i.e. areas) and regional (i.e.  
314 sites) scales were comparable to those obtained in a previous study carried out by means of  
315 photographic samples inside *P. clavata* forests in the NW Mediterranean Sea (Casas-Güell,  
316 Teixidó, Garrabou, & Cebrian, 2015). None of the species found in this study are exclusive of  
317 either forested or not forested habitats, nor closely associated with the presence of *P. clavata*.  
318 Nevertheless, at the local scale, the structures of the epibenthic assemblages significantly  
319 differed between inside and outside the gorgonian forests.

320 The Mediterranean yellow gorgonian *Eunicella cavolini* is often associated with the *P.*  
321 *clavata* forests. Interspersion between colonies of *E. cavolini* and *P. clavata*, as observed in  
322 the present study, is a common finding through all the Mediterranean Sea (Di Camillo, Ponti,



323 Bavestrello, Krzelj, & Cerrano, 2017). This suggests a large overlap in their ecological niche  
324 and limited interspecific competition, at least at low colony densities. *E. cavolini* colonies are  
325 smaller in size, have a slower growth rate, an higher P/B ratio, and a lower turnover rate  
326 compared to *P. clavata* (Coma, Ribes, Zabala, & Gili, 1998 and references therein). These  
327 two gorgonians are affected by the same local and global threats (Cerrano et al., 2000;  
328 Garrabou et al., 2009; Sini, Kipson, Linares, Koutsoubas, & Garrabou, 2015), although *E.*  
329 *cavolini*, in a field experiment, showed greater resistance to thermal stress, with a lower  
330 mortality and a higher recovery capacity compared to *P. clavata* (Fava, Bavestrello, Valisano,  
331 & Cerrano, 2010). Forests of *P. clavata* being larger in size may protect *E. cavolini* and other  
332 fragile species, such as erect bryozoans, from mechanical damage (e.g. fishing lines, nets and  
333 divers), as already documented for *Pentapora fascialis* (Pallas 1766) by Garrabou, Sala,  
334 Arcas, & Zabala (1998).

335         Compared to the unforested rocky bottoms, the understory of *P. clavata* forests host  
336 higher percentage covers of encrusting sponges, encrusting bryozoans and encrusting  
337 calcareous rhodophytes. All of them are relevant components of the Mediterranean  
338 coralligenous habitats and contribute to their frameworks (Ballesteros, 2006). Recruitment of  
339 encrusting sponges and encrusting bryozoans may be facilitated by the presence of *P. clavata*,  
340 as consistently observed in early-stage recruitment experiments carried out in the Ligurian  
341 and the Tyrrhenian Sea (Ponti et al., 2014). The reduction of light intensity and sediment  
342 accumulation induced by gorgonian branches may favour the competitive success of  
343 encrusting calcareous rhodophytes, as observed under canopies of marine plant and  
344 demonstrated by manipulating this physical factors in subtidal rocky habitats (Airoldi, 2003;  
345 Connell, 2005; Connell, 2003; Irving & Connell, 2002).

346         Overall, by summing all organisms able to deposit calcium carbonate it turns out that  
347 these forests support higher abundances of builder organisms. These findings suggest that

348 gorgonian forests may largely contribute to maintaining and developing coralligenous  
349 biogenic habitats. On the contrary, mixed turfs of filamentous algae and hydroids, which  
350 normally tend to compete for space with encrusting sponges, encrusting bryozoans and  
351 encrusting calcareous rhodophytes, were often more abundant outside the gorgonian forests.

352 *Codium bursa*, was found only outside the forests. The growth of this long-lived and  
353 slow-growing alga, is generally limited by nutrient availability (especially phosphorus), rather  
354 than by light (Vidondo & Duarte, 1995). This suggests that the limiting effect of *P. clavata*  
355 towards this seaweed go well beyond the simple shading and likely acts at the early  
356 recruitment stage.

357 At high gorgonian density, edaphic conditions (e.g. physical factors such as light,  
358 currents, sedimentation rates) may be strongly modified, increasing habitat complexity that  
359 supporting many necto-benthic organisms (Cerrano et al., 2010; Ponti et al., 2016; Valisano,  
360 Notari, Mori, & Cerrano, 2016). This study highlighted that the direct or indirect effects of the  
361 gorgonians on the abundance of other species, as green algal turfs and non-encrusting  
362 peyssonneliacean algae, may vary by gorgonians density, in terms of percentage cover.  
363 Indeed, the effects of gorgonians on erect and filamentous algae could vary with colony  
364 densities, sites and depths, as observed in the early-stage recruitment experiments (Ponti et  
365 al., 2014). The reduction in the abundance of some algal species seems to occur when the  
366 gorgonian cover exceeds 30%. This value could be considered a threshold to detect a shading  
367 effect and therefore a reference value in the assessment of the health status of the forests.  
368 However, density-dependent interactions in marine animal forests are far from being  
369 understood and deserve further investigations.

370 Higher values of species diversity indices were found inside gorgonian forests,  
371 compared to surrounding rocky bottoms. This trend is consistent across the investigated

372 geographical area, corroborating the hypothesis of a positive relationship between three-  
373 dimensional habitat complexity and species diversity (Kovalenko, Thomaz, & Warfe, 2012).

374

#### 375 **4.1 A focus on the non-indigenous species *Caulerpa cylindracea***

376 Non-indigenous species (NIS) have been recognized as a threat to the integrity of  
377 Mediterranean native communities. Establishment of NIS can drastically change the structure  
378 of marine communities, affecting species growth rates, survival and reproduction (Butchart et  
379 al., 2010; Occhipinti-Ambrogi, 2007). The green alga *Caulerpa cylindracea* is listed among  
380 the most threatening Mediterranean invaders (Streftaris & Zenetos, 2006), and represents one  
381 of the major concerns for the coralligenous habitats (Piazzi, Balata, & Cinelli, 2007; Piazzi,  
382 Gennaro, & Balata, 2012). Manipulative experiments showed that the presence of *C.*  
383 *cylindracea* negatively affects the *Paramuricea clavata* fitness by increasing the percentage  
384 of necrosis and lowering biomass and survivorship (Cebrian, Linares, Marschal, & Garrabou,  
385 2012). However, the role of gorgonian forests in preventing the settlement and invasion of *C.*  
386 *cylindracea* has never been investigated. At all sites where it occurred *C. cylindracea* was  
387 significantly less abundant inside gorgonian forests. The result seems fairly robust and  
388 suggests a resistance of the gorgonians to the invasion of this seaweed. Piazzi, Balata, Bulleri,  
389 Gennaro, & Ceccherelli (2016), in a recent review on biotic and abiotic interactions of *C.*  
390 *cylindracea* in the Mediterranean Sea, suggested that canopy-forming algae and seagrasses  
391 may limit the spread of *C. cylindracea* by reducing photosynthetic performance by shading.  
392 Gorgonian forests may cause similar shadow effects. Moreover, *P. clavata* may directly or  
393 indirectly reduce the recruitment of *C. cylindracea* by releasing allelochemicals (Rodriguez,  
394 1995) or limiting the abundance of algal turfs, which may enhance the spread of the invader  
395 (Piazzi, Balata, Bulleri, Gennaro, & Ceccherelli, 2016 and references therein).

396

## 397 **4.2 Entrapment of mucilaginous aggregates**

398           Developments of mucilaginous aggregates are recurrent events in the Mediterranean  
399 Sea (Rinaldi, Vollenweider, Montanari, Ferrari, & Ghetti, 1995; Sartoni et al., 2008).  
400 Deposition of mucilaginous aggregates on the seabed may cause severe damage to many  
401 benthic organisms, by reducing light availability, suffocating sessile invertebrates and  
402 establishing anoxic conditions (Schiaparelli, Castellano, Povero, Sartoni, & Cattaneo-Vietti,  
403 2007). Gorgonians are very sensitive to mucilage, which can cause necrosis of coenenchyme  
404 and leave portions of axial skeleton bare (Giuliani, Virno Lamberti, Sonni, & Pellegrini,  
405 2005; Mistri & Ceccherelli, 1996a). *Paramuricea clavata* colonies may recover from damage  
406 caused by mucilage in a few years through recruiting juvenile colonies (Mistri & Ceccherelli,  
407 1996b). The present study shows that gorgonians may reduce the accumulation in the  
408 understory by trapping the mucilaginous aggregates with their branches. Gorgonian forests,  
409 although at expense to themselves, may therefore limit the damage from suffocation to many  
410 associated benthic invertebrates.

411

## 412 **5 Conclusions**

413 The ecological role played by habitat-forming species cannot be easily disentangled, either  
414 from a physical or biological perspective. Generally, increased habitat complexity leads to  
415 higher species diversity in the associated assemblages, by increasing the available space and  
416 the number of microhabitats (Kovalenko, Thomaz, & Warfe, 2012). Moreover, the habitat  
417 complexity built up by ecosystem engineers induces physical changes, but may also modify  
418 many biological processes, with unpredictable ecological effects (Kelaher, 2003). Although  
419 the mechanisms underlying these processes are still not well known, forests of *Paramuricea*  
420 *clavata*, besides modifying microscale hydrodynamics, may provide additional food  
421 resources, being an effective suspension feeder able to modify littoral marine food webs

422 (Coma, Gili, Zabala, & Riera, 1994; Gili & Coma, 1998), increase refuges and available  
423 surface area (Ponti et al., 2016; Valisano, Notari, Mori, & Cerrano, 2016), as well as affect  
424 recruitment processes (Ponti et al., 2014). According to the present results, these animal  
425 forests are supporting high species diversity and promote bioconstruction processes in their  
426 understory. Presence of long-lived gorgonians may contribute to reducing the temporal  
427 variability of epibenthic assemblages, as already reported for Mediterranean coralligenous  
428 habitats (Casas-Güell, Teixidó, Garrabou, & Cebrian, 2015; Teixido, Garrabou, & Harmelin,  
429 2011). Indeed, healthy gorgonian forests may also oppose to the spread of non-indigenous  
430 species and mitigate the effects of adverse events, like mucilage formations. Gorgonian  
431 species play an ecological role that goes well beyond the aesthetic value, which attracts a  
432 large number of recreational divers (Musard et al., 2014). The obtained results support the  
433 concern raised by several scientists about the loss of habitat complexity caused by extensive  
434 mass mortalities of Mediterranean gorgonians (Cerrano & Bavestrello, 2008). The  
435 fragmentation and the local disappearance of gorgonian forests could cause severe and sudden  
436 modifications of associated epibenthic communities. It may lower species diversity, alter  
437 ecosystem functioning, and reduce the resistance and resilience of the assemblages with  
438 concomitant losses of ecological goods and services, over different spatial and temporal  
439 scales. *Paramuricea clavata* is considered a "vulnerable" species according to the  
440 Mediterranean Red List (ver. 3.1) provided by IUCN, mainly because of its low recruitment  
441 rate, and the *facies* with *P. clavata* is listed in the habitats that deserve special protection  
442 under the Barcelona Convention (RAC/SPA, Tunis). Evidence from this and many other  
443 studies strongly suggest the need to consider the health status of this species and of the forests  
444 it shapes, threatened by several anthropogenic disturbance and by the global climate changes,  
445 as essential elements of the ecological dynamics of the Mediterranean Sea, and therefore  
446 worthy of specific and effective transboundary protection measures. The European Marine

447 Strategy Framework Directive (2008/56/EC), the environmental pillar of the Blue Growth  
448 strategy, defines the need of each member state to reach Good Environmental Status (GES) of  
449 their marine waters. This achievement should require an urgent regulation of fishing activity,  
450 anchorages and scuba diving where gorgonian forests are present and restoration activities  
451 when evident alterations are documented. The results here presented clearly indicate that *P.*  
452 *clavata* represent a key species to maintain the GES of the Mediterranean temperate reefs, the  
453 coralligenous habitats.

454 Our results suggest that the health status of *P. clavata* forests could be monitored by using  
455 physical and structural descriptors, related to the magnitude of their positive effects on the  
456 complexity of benthic assemblages. The descriptors should include depth (range or upper  
457 limit of the forest), bottom inclination and orientation, mean colony height and percentage  
458 cover of the colonies. Furthermore, the percentage cover of bioconstructors in the understory  
459 could be considered as a proxy of the effectiveness protection offered by gorgonians to the  
460 benthic community. Bioconstructors are a key component in maintaining coralligenous  
461 habitats and their species diversity. Other important aspects that should be monitored are the  
462 degree of fragmentation of the forest, the extent of bare skeletons and necrotic portions of  
463 coenenchyme. Human impacts on gorgonian forest could be quantified by measuring the  
464 amount of fishing lines and nets entangled in colonies, which may cause lesions, while the  
465 quantity of epibionts may provide information on how long they have been damaged by  
466 humans or by natural events.

467 Several actions should be undertaken to protect gorgonian forests starting from the reduction  
468 of local human disturbances (both at the coast and inland; Mateos-Molina et al., 2015),  
469 establishing and enforcing properly designed and regulated marine protected areas  
470 (Arizmendi-Mejía et al., 2015; Coma, Pola, Ribes, & Zabala, 2004; Linares & Doak, 2010),  
471 and considering the aesthetic values of seascapes in conservation policies (Chimienti et al.,

472 2017). However, while much can be done for the conservation of healthy marine animal  
473 forests, methodologies for the maintenance and restoration, that have been successfully  
474 applied in coral reefs (e.g. Epstein, Bak, & Rinkevich, 2001; Jaap, 2000; Rinkevich, 2005;  
475 Young, Schopmeyer, & Lirman, 2012), are not yet available for temperate gorgonian forests.  
476 Maintenance actions may consist in removing fishing lines and nets that have a prolonged  
477 action over time (Bavestrello, Cerrano, Zanzi, & Cattaneo-Vietti, 1997) and pruning the top  
478 of branches in order to remove lesioned and compromised parts, allowing for regrowth  
479 (Previati et al., 2011; Sánchez-Tocino, De La Linde Rubio, Lizana Rosas, Pérez Guerra, &  
480 Tierno De Figueroa, 2018). Transplantation techniques are under development (Fava,  
481 Bavestrello, Valisano, & Cerrano, 2010; Linares, Coma, & Zabala, 2008; Montero-Serra et  
482 al., 2018) and could be effective in order to restore lost and damaged forests. Owing to the  
483 continuous risks of thermal anomalies due to climate change, these restoring approaches  
484 should be addressed below the average depth of the summer thermocline. These approaches  
485 are very promising, especially if chronic and persistent human disturbances are removed  
486 before interventions. Integration of biological experiments with the eco-engineering  
487 approaches has been proved to be successful in restoration of coastal ecosystems and the  
488 possibilities to use it also on temperate mesophotic biogenic reefs should be properly  
489 explored.

490

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510

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846

847

848 **TABLE 1** PERMANOVA test on differences of epibenthic assemblage structures between  
 849 inside and outside gorgonian forest (Go: 2 levels, fixed), among sites (Si: 9 levels, random),  
 850 their interaction (Go  $\times$  Si) and among areas within this interaction (Area(Go  $\times$  Si)) (square  
 851 root-transformed percentage cover data, Bray-Curtis coefficient). Estimated component of  
 852 variation, in percentage of the total (CV%), was reported for each term of the model.

Source	df	SS	MS	Pseudo- <i>F</i>	<i>p</i>	Unique perms	CV%
Gorgonian forest (Go)	1	22,252	22,252.00	2.61	0.0280	9944	9.4
Site (Si)	8	235,020	29,378.00	12.89	0.0001	9856	28.1
Go $\times$ Si	8	68,109	8,513.60	3.74	0.0001	9823	19.0
Area (Si $\times$ Go)	54	123,080	2,279.20	3.76	0.0001	9539	19.7
Residual	216	130,930	606.16				23.7
Total	287	579,390					

853

854

855 **TABLE 2** Summary of ANOVA tests. Data transformation: sqrt = square root; frt = four root. Degrees of freedom of numerator and denominator are  
 856 given in parentheses. Significant levels were indicated by the following symbols: ns = not significant; \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ .

	Cochran's C test	Gorgonian forest (Go)			Site (Si)			Go × Si			Area (Go × Si)			Res
	Transf.	MS	F	p	MS	F	p	MS	F	p	MS	F	p	MS
<i>Codium bursa</i>	none	18.39	4.69	0.062	3.92	0.88	0.540	3.92	0.88	0.540	4.45	0.97	0.542	4.60
	$p < 0.01$		(1,8)			(8,54)			(8,54)			(54,216)		
<i>Eunicella cavolini</i>	none	92.35	6.66	0.033 *	16.98	2.01	0.063	13.87	1.64	0.135	8.46	1.41	0.047 *	6.02
	$p < 0.01$		(1,8)			(8,54)			(8,54)			(54,216)		
Encrusting sponges	frt	7.56	8.04	0.022 *	4.18	8.33	0.000 ***	0.94	1.88	0.083	0.50	2.25	0.000 ***	0.22
	$p$ ns		(1,8)			(8,54)			(8,54)			(54,216)		
Encrusting bryozoans	frt	9.48	12.48	0.008 **	4.11	10.25	0.000 ***	0.76	1.89	0.080	0.40	2.14	0.000 ***	0.19
	$p$ ns		(1,8)			(8,54)			(8,54)			(54,216)		
Erected bryozoans	frt	16.72	16.58	0.004 **	2.20	4.66	0.000 ***	1.01	2.14	0.048 *	0.47	2.21	0.000 ***	0.21
	$p$ ns		(1,8)			(8,54)			(8,54)			(54,216)		
Mixed turf	none	26'978.40	21.70	0.002 **	1'987.70	5.92	0.000 ***	1'243.00	3.70	0.002 **	336.00	3.70	0.000 ***	90.90
	$p$ ns		(1,8)			(8,54)			(8,54)			(54,216)		
ECR	none	3'228.50	684.92	0.000 ***	1'779.10	377.43	0.000 ***	Pooled with			4.71	0.10	1.000	47.30
	$p < 0.01$		(1,62)			(8,62)		Area (Go × Si)				(62,216)		
Builder organisms	sqrt	134.31	28.49	0.000 ***	33.15	7.03	0.000 ***	Pooled with			4.71	4.50	0.000 ***	1.05
	$p < 0.01$		(1,62)			(8,62)		Area (Go × Si)				(62,216)		
<i>Caulerpa cylindracea</i>	none	1'193.70	6.71	0.017 *	282.70	1.59	0.229	Pooled with			177.85	4.62	0.000 ***	38.50
	$p$ ns		(1,20)			(2,20)		Area (Go × Si)				(20,72)		
Mucilaginous algae	sqrt	169.09	5.08	0.153	26.59	4.09	0.034 *	33.290	5.13	0.017 *	6.49	5.27	0.000 ***	1.23
	$p$ ns		(1,2)			(2,2)			(2,18)			(18,72)		
<i>S</i>	none	308.35	14.90	0.005 **	61.88	5.68	0.000 ***	20.70	1.90	0.079	10.89	1.96	0.000 ***	5.55
	$p$ ns		(1,8)			(8,54)			(8,54)			(54,216)		
<i>NI</i>	frt	0.77	20.74	0 **	0.04	2.56	0.02 *	0.04	2.4	0.03 *	0.02	1.69	0.01 **	0.01
	$p < 0.05$		(1,8)			(8,54)			(8,54)			(54,216)		
<i>NI0</i>	none	0.14	6.79	0.031 *	0.10	6.77	0.000 ***	0.02	1.45	0.197	0.01	1.66	0.006 **	0.01
	$p$ ns		(1,8)			(8,54)			(8,54)			(54,216)		

857



858 **Figures legends**

859

860 **FIGURE 1** Study area and study sites (circles): 1, P.te Causinière; 2, Colombara; 3, Punta  
861 delle Cannelle; 4, Capo Calvo; 5, Picchi di Pablo; 6, Scoglio del Remaiolo; 7, Punta San  
862 Paolo; 8, Zverinac Južni Rt; 9, Rivanjski Kanal (Mercator Projection, Datum WGS 84).

863

864 **FIGURE 2** Photographic sampling method (a, courtesy of Adelmo Sorci); a sampled area  
865 inside a gorgonian forest at Punta San Paolo, Ustica Island (b); benthic assemblages at  
866 Rivanjski Kanal, northern Adriatic (c); a dense gorgonian forest in the Tyrrhenian Sea (d);  
867 some thalli of *Caulerpa cylindracea* at the basis of *Paramuricea clavata* at Punta delle  
868 Cannelle, Elba Island (e); mucilaginous aggregates entrapped by gorgonian branches (f).

869

870 **FIGURE 3** Mean ( $\pm$  s.e.) height (a) and percentage cover (b) of *Paramuricea clavata* inside  
871 the gorgonian forest at each study site.

872

873 **FIGURE 4** Unconstrained (a; PCoA) and constrained (b; CAP) ordination plots of benthic  
874 assemblage data from inside and outside forests of the gorgonian *Paramuricea clavata* at 9  
875 sites in the Mediterranean Sea. Each symbol represents the centroid of 4 areas with 4  
876 replicated samples each. Vectors superimposed to plot (a) represent the correlations of  
877 substrate inclination, site depth and longitude with the PCoA axes.

878

879 **FIGURE 5** Mean ( $\pm$  s.e.) percentage covers of encrusting sponges (a), encrusting bryozoans  
880 (b), erect bryozoans (c), mixed turf (d), encrusting calcareous rhodophytes (ECR, e) and all  
881 builder organisms together (f), inside and outside forests of the gorgonian *Paramuricea*  
882 *clavata* at 9 sites in the Mediterranean Sea. Significant levels in SNK tests inside vs. outside

883 gorgonian forests within sites were indicated by the following symbols: \* =  $p < 0.05$ ; \*\* =  $p <$   
884  $0.01$ ; \*\*\* =  $p < 0.001$ .

885

886 **FIGURE 6** Polynomial regression fitting (LOESS) between percentage cover of *Paramuricea*  
887 *clavata* and percentage cover of green algal turf (a) and non-encrusting algae of the genus  
888 *Peyssonnelia* (b). The dashed lines delimit the confidence intervals at 95%.

889

890 **FIGURE 7** Mean ( $\pm$  s.e.) percentage covers of *Caulerpa cylindracea* (a) and mucilaginous  
891 aggregates (b), inside and outside forests of the gorgonian *Paramuricea clavata* at 3 sites in  
892 the Mediterranean Sea. Significant levels in SNK tests inside vs. outside gorgonian forests  
893 within sites were indicated by the following symbols: \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p <$   
894  $0.001$ .

895

896 **FIGURE 8** Mean ( $\pm$  s.e.) species richness ( $S$ , a), species diversity in terms of effective  
897 number of species ( $NI$ , b) and the corresponding evenness component ( $NI0$ , c), inside and  
898 outside forests of the gorgonian *Paramuricea clavata* at 9 sites in the Mediterranean Sea.

899