The understorey of gorgonian forests in mesophotic temperate reefs

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

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Abstract

1. In the Mediterranean Sea, dense populations of the gorgonian *Paramuricea clavata* shape marine animal forests characterizing the seascapes of coralligenous habitats. Despite the concerns for its health, due to several anthropogenic threats and recent mass mortality events mainly triggered by thermal anomalies, the understorey of its forests and the ecological processes they promote are still little known. Here, the abundance and composition of epibenthic assemblages inside and outside *P. clavata* forests were investigated across the central and western Mediterranean Sea, by applying a multifactorial sampling design.

2. In spite of the large variability in the structures of epibenthic assemblages at local and regional scales, the gorgonian understoreys share some common features, such as higher abundances of calcareous builder organisms and a reduced invasion by the non-indigenous alga *Caulerpa cylindracea*, compared to the adjacent unforested rocky bottoms. *P. clavata* showed non-linear density-dependent relationships with algal turfs and non-encrusting algae belonging to the genus *Peyssonnelia*. Moreover, by entrapping benthic mucilaginous aggregates with their branches, these gorgonians risk topical necrotic lesions but may reduce the suffocation risks for understorey organisms.

3. Overall, *P. clavata* forests may enhance bioconstruction processes and increase resistance and resilience of the benthic assemblages in the Mediterranean coralligenous habitats. This species and its forests, together with their understoreys, should be considered as essential elements of the Mediterranean Sea ecology, and therefore worthy of specific and effective protection measures.

4. Conservation strategies should reduce the risk of mechanical damage by regulating fishing 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.

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1 Introduction

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

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

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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^{-2} and dry masses greater than 1,700 g m^{-2} (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, Fraschetti, 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 understorey 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

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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 understorey 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 (21×28

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 (50×50 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

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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 × Si), and among areas

179   nested in this interaction (Area(Go × 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 $N1 = $ Exp H', where H' is the Shannon's index based on natural logarithm) and the

188   corresponding evenness component (as $N10 = N1/S$) were calculated for each sample

189   (Magurran, 2004). $N1$ 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

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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 × Si was not significant

200   ($p > 0.25$) it was pooled with the term Area(Go × Si) (Underwood, 1997). When the term Go

201   × 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° in latitude and

217   8.2° 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 ± 4.3 cm to 122.1 ± 22.6 cm; while their mean percentage

229 cover ranges from 22.3 ± 5.1 % to 56.8 ± 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,

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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*, *N1* and *N10*) 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 (*N10*) 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, understorey 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 understorey 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

4.2 Entrapment of mucilaginous aggregates

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

5 Conclusions

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

18

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   understorey. 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 understorey

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 al 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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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 × Si) and among areas within this interaction (Area(Go × 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-*F*	*p*	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 × Si	8	68,109	8,513.60	3.74	0.0001	9823	19.0
Area (Si × 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

TABLE 2 Summary of ANOVA tests. Data transformation: sqrt = square root; frt = four root. Degrees of freedom of numerator and denominator are 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	Transf.	Gorgonian forest (Go) MS	F	p	Site (Si) MS	F	p	Go × Si MS	F	p	Area (Go × Si) MS	F	p	Res MS
Codium bursa	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)		
Eunicella cavolini	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 Area (Go × Si)			4.71	0.10	1.000	47.30
$p <0.01$			(1,62)			(8,62)						(62,216)		
Builder organisms	sqrt	134.31	28.49	0.000 ***	33.15	7.03	0.000 ***	Pooled with Area (Go × Si)			4.71	4.50	0.000 ***	1.05
$p <0.01$			(1,62)			(8,62)						(62,216)		
Caulerpa cylindracea	none	1'193.70	6.71	0.017 *	282.70	1.59	0.229	Pooled with Area (Go × Si)			177.85	4.62	0.000 ***	38.50
p ns			(1,20)			(2,20)						(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)		
S	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)		
N1	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)		
N10	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)		

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 (± 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 (± 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 (± 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 (± s.e.) species richness (*S*, a), species diversity in terms of effective

897   number of species (*N1*, b) and the corresponding evenness component (*N10*, c), inside and

898   outside forests of the gorgonian *Paramuricea clavata* at 9 sites in the Mediterranean Sea.

899