

1 **Meiofaunal community along vermetid reefs: The role of**
2 **macroalgae in influencing distribution**

3
4
5 **F. Ape¹, M. Gristina², R. Chemello³, G. Sarà⁴, S. Mirto⁵**

6
7 ¹Institute for Coastal Marine Environment, CNR, Via del Mare, 3 - 91021 Torretta Granitola -
8 Fraz. Campobello di Mazara (TP), Italy

9 ²Institute for Coastal Marine Environment, CNR, Via L. Vaccara, 61 - 91142 Mazara del
10 Vallo (TP), Italy

11 ³Dipartimento di Scienze della Terra e del Mare, University of Palermo, via Archirafi 18,
12 90123 Palermo, Italy

13 ⁴Dipartimento di Scienze della Terra e del Mare, University of Palermo, Viale delle Scienze
14 Ed. 16, 90128 Palermo, Italy

15 ⁵Institute for Coastal Marine Environment, CNR, Via G. da Verrazzano, 17 - 91014
16 Castellammare del Golfo (TP), Italy

17
18 E-mail of communicating author: simone.mirto@iamc.cnr.it
19
20
21

22 **Keywords:** habitat complexity; biogenic constructions; meiofaunal community;
23 Mediterranean intertidal habitat
24

25 **Abstract**

26 Habitat complexity is considered an important factor in influencing the structure of
27 meiofaunal communities. In this study, we present the first dataset of meiofauna associated
28 with vermetid reefs (biogenic constructions of Mediterranean intertidal habitat) in two areas
29 along the northern coast of Sicily, Italy. The vermetid reefs are characterized by a horizontal
30 extension from the shore towards the open sea, and can be divided into three zones (the inner
31 margin, the *cuvette* zone and the outer margin) which differ in hydrodynamic features. We
32 studied the spatial distribution of meiofauna along the horizontal axis of the vermetid reefs,
33 investigating the meiofaunal communities inhabiting the sediment deposited inside *cuvettes*
34 (shallow pools inside the “*cuvette* zone”) located between the inner to the outer margin of the
35 reefs. We observed an increase in abundance from the inner to the outer part of the vermetid
36 reef. Moreover, because the macroalgae present on the vermetid reef can determine increase
37 in substrate complexity, we studied meiofaunal communities associated with the most
38 abundant macroalgae taxa (*Cystoseira* sp., *Jania rubens*, *Palisada perforata*, *Dictyota* sp. and
39 *Padina pavonica*) living on the reef, in order to investigate their role in determining the
40 distribution of meiofauna along this bioconstruction. We found that meiofauna varied in
41 abundance, in particular crustaceans and in community composition on different macroalgae,
42 showing a positive correlation with habitat size and complexity (measured as algal biomass
43 and fractal dimension). The higher algal cover and the presence of more complex macroalgae
44 (*Cystoseira* sp. and *J. rubens*) in the outer zone, rather than the inner zone, of the vermetid
45 reef may contribute to a potential gradient of structural complexity along the reef and further
46 influencing meiofauna density distribution. These results confirm that vermetid reefs, with
47 their structural complexity, may play an important role in structuring benthic fauna in
48 intertidal habitats.

49

50

51 **Introduction**

52 In marine habitats, ecosystem engineers modify the local environment both physically and
53 ecologically, creating a living three-dimensional structure (Jones et al. 1994; Dubois et al.
54 2002; Gutierrez et al. 2003; Callaway et al. 2010). Habitat complexity is considered to be an
55 important factor influencing the structure of associated communities, providing a wider range
56 of niches for a large and diverse group of associated organisms (May 1972; Atrill et al. 2000).

57 Within rocky intertidal Mediterranean habitats, vermetid reefs represent unique and highly
58 diverse biogenic constructions, structurally comparable to coral fringing reefs in tropical
59 areas (Safriel and Ben-Eliahu 1991; Antonioli et al. 1999). Vermetid reefs are intertidal
60 bioconstructions, built up by gastropod molluscs of the genus *Dendropoma* in association
61 with some coralline encrusting algae (Safriel 1966). These bioconstructions are of particular
62 ecological and conservation interest because of their broad, horizontal extension and their
63 structural role in modifying the shape and ecological characteristics of the transitional area
64 between mesolittoral and infralittoral rocky flats, creating more complex tridimensional
65 structures and promoting marine biodiversity (Consoli et al. 2008; Colombo et al. 2013;
66 Milazzo et al. 2016). Vermetid reefs can be divided into three morphological zones along a
67 horizontal axis, extending from the shore to the sea: (1) the inner margin, which correspond to
68 the terrestrial boundary; (2) the “*cuvette zone*”, the central area of the reef with shallow pools
69 named *cuvettes* located between the inner and the outer margin of the reef; and (3) the outer
70 margin, the sea boundary of the reef (Molinier and Picard 1953; Chemello and Silenzi 2011).

71 These zones differ in hydrodynamic features (such as emersion and wave exposures), creating
72 different microhabitats with distinct populations (Chemello et al. 1998; Chemello and Silenzi
73 2011; Sarà et al. 2014; Franzitta et al. 2016).

74 *Cuvettes* hold water on the flat during low tide and periods of calm seas, and are similar to
75 tidal pools in the rocky shore environment (Little et al. 2009; Colombo et al. 2013). *Cuvettes*

76 are host to macroalgae and encrusting organisms and represent a zone characterized by a high
77 level of habitat complexity and biodiversity (Milazzo et al. 2016).

78 Vermetid reefs along Sicilian coasts are characterized by several macroalgal species, the most
79 characteristic being: *Palisada perforata*, a red alga that is distributed uniformly along the reef;
80 the brown algae *Padina pavonica*, *Cystoseira* spp. and *Dictyota* spp., mainly present in the
81 “*cuvette* zone”, where we commonly found also corallinales such as *Jania rubens* (Milazzo et
82 al. 2016). The outer margin, a narrow upper infralittoral fringe, is characterized by
83 *Cystoseira*-dominated assemblages.

84 Vermetid tubes and reef crevices act as sediment and organic matter traps (Chemello and
85 Silenzi 2011), macroalgae present on the reef have the effect of buffering against wave energy
86 and increasing substrate complexity, therefore they play an additional role in providing refuge
87 and structure for meiofaunal communities (Danovaro and Fraschetti 2002; Frame et al. 2007;
88 Milazzo et al. 2016).

89 The information on benthic assemblages inhabiting vermetid reefs is still scant and many
90 references are sourced from grey literature. Until now, studies concerned with macrobenthic
91 communities such as gastropods (Chemello 1998), polychaetes (Safriel and Ben-Eliahu 1991)
92 and macroalgae (Mannino 1992) revealed high diversity and species abundance at a small
93 scale (i.e. *cuvette* scale), and different distributions across the different parts of the reef. Little
94 is known on the role of vermetid reef habitat structure in modifying and influencing the
95 distribution and community composition of benthic invertebrates; meiobenthic communities
96 in particular, have historically been completely neglected.

97 The metazoan meiofauna is a key component of the coastal benthos, contributing to the
98 energy transfer to higher trophic levels and sustaining important ecological processes
99 (Danovaro et al. 2008). The distribution and diversity of meiofauna are affected by several
100 abiotic and biotic factors (Giere 2009) and, in intertidal systems, bioengineers may represent

101 one of the most important determinants in structuring meiofaunal communities (Danovaro and
102 Frascchetti 2002; Kostylev et al. 2005; Bianchelli et al. 2013). In rocky intertidal habitats, the
103 physical structure of macroalgae favors meiofaunal settlement and distribution, reducing
104 sediment agitation, providing refuge from desiccation and increasing substrate complexity
105 (Gibbons 1988; Gee and Warwick 1994; Danovaro and Frascchetti 2002; Frame et al. 2007).
106 The complexity of the phytal habitat is associated with the small-scale variations in shape,
107 size and texture of the algal species (Gee and Warwick 1994). Abundance and diversity of
108 meiofaunal assemblages differ among macroalgal species, generally showing a positive
109 correlation with algal complexity (Gibbons 1988; Gee and Warwick 1994; Veiga et al. 2016).
110 This study aims to describe meiofaunal communities associated with vermetid reefs along the
111 northern coast of Sicily. By testing hypotheses on the differences in spatial distribution of
112 meiofauna on the vermetid reefs, we investigated the abundance, diversity (at taxa level) and
113 community composition of meiofauna inhabiting the sediment inside the *cuvettes* located in
114 different parts of the “*cuvette zone*” along the horizontal axis, from the inner to the outer
115 margin of the reefs.

116 Moreover, to test the idea that macroalgae themselves may represent an additional gradient of
117 structural complexity along the vermetid reef, we explored the differences in meiofaunal
118 community associated with macroalgae living on vermetid reefs, and investigated the
119 differences in algal architecture (habitat size and complexity), hypothesizing that complexity
120 of phytal habitat will differ among macroalgae and this should play a significant role in
121 shaping the abundance and the community structure of meiofauna living on the reef.

122

123 **Materials and Methods**

124 **Study areas and sampling**

125 The study was carried out along the northern coast of Sicily (Italy), where large vermetid
126 reefs are commonly found (Chemello and Silenzi 2011; Milazzo et al. 2016). We investigated
127 two coastal rocky areas (Fig. 1a) characterized by the presence of vermetid reefs, of
128 comparable dimensions (total horizontal width ~6-7 m; width of inner margin ~30-40 cm, and
129 few centimetres thick; outer margin width ~50-70 cm; deep of *cuvettes* ~30-40 cm;
130 Badalamenti et al. 1992; Antonioli et al. 1999; Chemello and Silenzi 2011; Balistreri et al.
131 2015). The study areas were: (1) Capo Gallo, at the westernmost limit of the Gulf of Palermo
132 (38°12'38' N; 13°17'13"E), inside the Marine Protected Area (MPA) "Capo Gallo-Isola delle
133 Femmine"; and (2) Favignana Island (37°56'50"N, 12°17'51"E) within the Marine Protected
134 Area (MPA) "Egadi Islands", where we sampled on a vermetid reef located along the northern
135 side of the island.

136 Both area are subjected to the same tidal regime and are exposed at similar winds (north and
137 north/west) and wave action (Badalamenti et al. 1992; Antonioli et al. 1999; Balistreri et al.
138 2015).

139 Sampling was carried out in October 2014, in calm water and under low tide. In each area,
140 two horizontal transects of vermetid reef were investigated to study the meiofaunal
141 communities living in the sediment deposited inside the *cuvettes* and those associated with the
142 most characteristic macroalgae taxa present on the reefs.

143

144 **Experimental assumptions and design**

145 In order to study the distribution of meiobenthic organisms along the horizontal axis (shore –
146 sea) of the vermetid reef, we sampled meiofauna inside the *cuvettes*, where fine sandy
147 sediment can be deposited (Chemello and Silenzi 2011). Sediment samples were collected in
148 the "*cuvette* zones" from *cuvettes* located: (1) close to the inner margin; (2) in the middle of
149 the "*cuvette* zone"; and (3) close to the outer margin of the vermetid reef (Fig. 1b).

150 To investigate the meiofaunal communities associated with macroalgae colonizing the
151 vermetid reef, we carried out a preliminary survey (one month before sampling) to assess the
152 coverage (%) of macroalgae colonizing the inner margin, central “*cuvette zone*” and the outer
153 margin of the selected vermetid reefs (Capo Gallo and Favignana Island). The macroalgal
154 coverage was visually estimated, using a plastic frame 20 cm x 20 cm in size (n= 5),
155 randomly placed on each sampling reefs (Di Franco et al. 2011).

156 We found similar total macroalgae coverage on the reefs of both study areas: ~ 40% on the
157 inner margin; ~ 80% on the “*cuvette zone*”; and ~ 60% on the outer margin; with the
158 remaining percentage represented by vermetid complex (*Dendropoma cristatum* and
159 *Neogoniolithon* sp.) and bare rocky substrate. Because we found that *Palisada perforata*,
160 *Padina pavonica*, *Jania rubens*, *Dyctiota* sp. and *Cystoseira* sp. were the most abundant
161 macroalgae, according with literature (Mannino 1992; Milazzo et al. 2016),
162 at the sampling time (in October), we investigated meiofaunal communities associated with
163 these macroalgal taxa. Because the coverage of the investigated macroalgae varied along the
164 vermetid reefs, we randomly sampled each macroalgae where it was more abundant and
165 formed homogeneous and single-taxa patches. Some macroalgae were sampled only in one of
166 the two vermetid horizontal transects in each areas because we have not always found
167 homogeneous and single-taxa patches. Moreover the macroalga *P. pavonica* was sampled only
168 at Favignana Island because it was not found as homogeneous patches at the Capo Gallo reefs
169 during the sampling period. Considering that the complexity of phytal habitat may differ
170 among the investigated macroalgae, and this in turn could affect the abundance and
171 community structure of the associated meiofauna (Gibbons 1988; Gee and Warwick 1994;
172 Veiga et al. 2016), we estimated algal architecture (in terms of habitat size and complexity) of
173 the five most abundant macroalgae taxa and we correlated it with meiofaunal taxa abundances.
174

175 **Sample collection**

176 Three randomly chosen sediment samples were manually collected in each *cuvette* located in
177 the three positions (3 replicates X 3 positions X 2 horizontal transects in each area; Fig. 1b),
178 scraping a thin layer of sediment (1 cm thick inside quadrates of 10 cm x 10 cm). The
179 sediment was fixed in 4% buffered formaldehyde in filtered (0.4 µm) seawater solution until
180 laboratory meiofauna analyses could be performed.

181 To analyse meiofauna associated with macroalgae taxa, macroalgal patches were entirely
182 scraped from three randomly chosen quadrates (10 cm x 10 cm) and carefully and quickly
183 placed into plastic bags to avoid the loss of organisms. These samples (3 replicates X 5
184 macroalgae taxa X 2 horizontal transects in each area) were preserved in 4% buffered
185 formaldehyde in filtered (0.4 µm) seawater solution, and were brought back to the laboratory
186 for analysis.

187

188 **Meiofauna analysis**

189 Meiofauna sediment samples were sieved through a 37 µm mesh. The fraction retained on the
190 sieve was resuspended and centrifuged three times with Ludox HS40 (diluted with water to a
191 final density of 1.18 g cm⁻³; Heip et al. 1985). The material collected was preserved in 50 ml
192 tubes with 4% buffered formalin and stained with Rose Bengal (0.5 g l⁻¹).

193 To extract meiofaunal organisms from macroalgae, the samples were washed in fresh water
194 and shaken vigorously several times to remove the meiofauna, which were extracted by
195 decantation and sieved through a 37 µm mesh (Gee and Warwick 1994). This procedure was
196 repeated ten times for each sample. The fraction retained on the sieve was preserved in 50 ml
197 tubes with 4% buffered formalin and stained with Rose Bengal (0.5 g l⁻¹). Meiobenthic
198 organisms were counted and classified at the major taxa level of taxonomic discrimination
199 using a stereomicroscope. The abundance of total meiofauna and of single taxa was reported

200 to the surface unit (10 cm x 10 cm area = 100 cm²) both for the sediment samples and for
201 macroalgae patches.

202

203 **Macroalgal architecture**

204 We measured the habitat architecture using biomass and fractal dimension of macroalgae as
205 proxies for habitat size and habitat complexity respectively (Gee and Warwick 1994; Hooper
206 and Davenport 2006; Veiga et al. 2016). Macroalgae were dried (for 48 h at 60 °C) and
207 weighed to determine the biomass in a 100 cm² area, expressed in grams of dry weight (DW).

208 To calculate the fractal dimensions, a branch (3 replicates from each quadrat) of each
209 macroalga was photographed with a Nikon Coolpix S2600 digital camera. Fractal dimensions
210 were calculated following procedures described by McAbendroth et al. (2005). Each resulting
211 TIFF image was converted to grayscale mode and threshold to produce a binary that was used
212 to quantify the fractal dimensions (i.e. complexity) of area (DA) and perimeter (DP) for each
213 image, by using the ImageJ software (Rasband 1997). The DA is an estimate of area
214 occupancy indicating how the perception of surface area might change with scale. The DP is
215 an estimate of edge complexity, relating to the nature of the gaps between the macroalgal
216 parts (McAbendroth et al. 2005; Veiga et al. 2014). Due to the small size of meiofauna
217 (ranging from 30 µm to 1 mm; Mare 1942), complexity parameters of a branch of macroalga
218 were considered an appropriate scale in structuring the physical environment at the
219 complexity perception of our target organisms (Attrill et al. 2000; Veiga et al. 2016).

220

221 **Statistical analysis**

222 To test differences along the horizontal axis of the vermetid reefs, univariate and multivariate
223 distance-based permutational nonparametric analyses of variance (PERMANOVA; Anderson
224 2001; McArdle and Anderson 2001) were performed on abundance, taxa richness and

225 communities composition of meiofauna in the sediment inside the *cuvettes*, including study
226 areas (two levels: Capo Gallo and Favignana Island) and positions in the “*cuvette zone*”
227 (three levels: Inner, Medium and Outer) as fixed factors. PERMANOVA was also performed
228 to test the hypotheses that the habitat size (biomass) and complexity (DA and DP) and
229 associated meiofauna communities (abundance, the taxa richness and the structure) differed
230 among macroalgae (fixed factor with 5 levels: *P. perforata*, *P. pavonica*, *J. rubens*, *Dictyota*
231 *sp.* and *Cystoseira sp.*), colonizing the reefs in both sampling areas (fixed factor with 2 levels:
232 Capo Gallo and Favignana Island). PERMANOVAs were based on Euclidean distance
233 matrices calculated on normalized data (biomass and fractal measures) or Bray–Curtis
234 similarity matrixes after square root transformation of the data (for meiofaunal parameters),
235 using 9999 random permutations of the appropriate units (Anderson 2001). Because of the
236 restricted number of unique permutations in the pair wise tests, p values were obtained from
237 Monte Carlo samplings (Anderson and Robinson, 2003). SIMPER analyses were performed
238 on matrices of Bray–Curtis similarities, constructed on previously square-root transformed
239 data, to assess the percentage dissimilarity in meiofaunal community composition both
240 between the three position and among different macroalgae and to identify which of the
241 investigated taxa was most responsible for the observed dissimilarities.

242 To test the hypothesis that macroalgal architecture can influence the distribution and
243 community composition of meiofauna, linear regressions (Statistica 6.0, StatSoft) between
244 habitat size and complexity of macroalgae and meiofauna abundances (square-root
245 transformed data) were tested for significance. Moreover, to assess what extent the habitat
246 architecture explained the differences in abundance, diversity and community composition of
247 meiofauna associated with macroalgae, we used DistLM analysis (distance based linear
248 models), in combination with dbRDA (distance based redundancy analysis) routine for
249 meiofaunal community, using R^2 selection criterion and on step-wise as a selection procedure;

250 they were based on the Bray-Curtis dissimilarities (McArdle and Anderson 2001). Macroalgal
251 parameters were transformed to normalize them to comparable scales and remove skewness
252 (Clarke and Warwick 1994). Statistical analyses were performed using the PRIMER v6+
253 software (Plymouth Marine Laboratory; Clarke 1993).

254

255 **Results**

256 **Meiofauna in the *cuvettes* sediments**

257 Our results showed that the meiofaunal abundance significantly varied along the horizontal
258 axis of vermetid reefs (PERMANOVA, $df = 2$, Pseudo-F = 14.1; $p < 0.001$). Pairwise
259 comparisons (ESM Table 1) revealed significant higher values of total meiofaunal abundance
260 (mean between the two reefs in each areas \pm SE; Fig. 2) inside the *cuvettes* located close to
261 the outer margin (2842.5 ± 143.5 and 2992.3 ± 512.3 ind. 100 cm^{-2} at Capo Gallo and
262 Favignana Island respectively) than those found in the other two positions (from $1807.7 \pm$
263 80.3 ind. 100 cm^{-2} in *cuvettes* close to the inner margin at Capo Gallo to 2252.2 ± 265.2 ind.
264 100 cm^{-2} in the middle *cuvettes* at Favignana Island $p < 0.05$). We also found significant
265 differences in taxa richness when comparing *cuvettes* located along the horizontal axis of the
266 reefs (PERMANOVA, $df = 2$, Pseudo-F = 6.2, $p < 0.01$), however pairwise comparison
267 showed significant differences only at Favignana, where we found significant higher values in
268 the *cuvettes* located in the middle position respect to the other two positions ($p < 0.01$; ESM
269 Table 1). The values of taxa richness and of the abundance of single meiofaunal taxon are
270 reported in Table 1.

271 In both areas, the communities were dominated by copepods (from 61% close to the inner
272 margin at Capo Gallo, to 82% close to the outer margin at Favignana Island), followed by
273 nematodes (from 8% close to the outer margin at Favignana Island to 24% close to the inner
274 margin at Capo Gallo). Following copepods and nematodes, the next most abundant taxa were

275 polychaetes, ostracods, amphipods, isopods, turbellaries and tanaids. The less abundant taxa,
276 with percentage lower than 0.5%, were pooled into a single category named ‘others’ (Fig. 3).
277 PERMANOVA showed significant differences in meiofaunal community composition among
278 the different *cuvette* positions ($df = 2$; Pseudo-F = 4.4, $p < 0.001$). SIMPER analyses revealed
279 that dissimilarity in meiofaunal communities between the three positions in the “*cuvette*
280 zone” was mostly explained by copepod abundance (from 20% to 30% of total dissimilarity;
281 Table 2). In fact, while nematodes showed no significant difference in abundance along the
282 horizontal axis of vermetid reefs (PERMANOVA, $df = 2$; Pseudo-F = 0.8, $p = ns$), total
283 crustaceans (copepods, ostracods, amphipods, isopods, and tanaids),
284 copepods in particular, showed significantly higher values inside the *cuvettes* close to the
285 outer margin than those in *cuvettes* located in the inner zone (pairwise $p < 0.01$; ESM Table 1).

286

287 **Meiofauna associated to macroalgae**

288 The abundance of meiofauna associated to the macroalgae varied significantly among the
289 different taxa (PERMANOVA, $df = 4$, Pseudo-F = 31.1, $p < 0.001$). Pairwise comparisons
290 (ESM Table 2) showed that in both investigated areas, the meiofaunal abundance (mean
291 between the two reefs in each areas \pm SE; Fig. 4) associated with *Cystoseira* sp. ($1736.8 \pm$
292 260.9 and 1758.1 ± 231.4 ind. 100 cm^{-2} at Capo Gallo and Favignana Island respectively) was
293 significantly higher with respect to the other algae (from 445.8 ± 50.8 ind. 100 cm^{-2} on *P.*
294 *perforata* at Capo Gallo to 1188.9 ± 115.4 ind. 100 cm^{-2} on *J. rubens* at Favignana Island; $p <$
295 0.01). Moreover, the abundance of meiofauna associated with *J. rubens* was significantly
296 higher with respect to those associated with *P. perforata* and *P. pavonica* (pairwise, $p < 0.05$).
297 Taxa richness showed not significant differences among macroalgal taxa (PERMANOVA; df
298 $= 4$, Pseudo-F = 1.2, $p = ns$). The values of taxa richness and of the abundance of single
299 meiofaunal taxon on the five macroalgae taxa are reported in Table 3.

300 Meiofaunal communities associated with all macroalgae, both at Capo Gallo and Favignana
301 Island, were dominated by copepods, representing more of 50% of the total abundance,
302 followed by nematodes (ranging from 19% to 32%). Following these taxa were polychaetes,
303 amphipods, acari, isopods, ostracods, gasteropods, tanaids, and “other” taxa, representing <
304 0.5% of total abundance (Fig. 5).

305 Meiofaunal community composition significantly varied among different macroalgae
306 (PERMANOVA, $df = 4$, Pseudo-F = 15.3, $p < 0.001$). We found significant differences when
307 comparing *Cystoseira* sp. with the other macroalgae taxa (pairwise, $p < 0.01$; Table 4 and
308 ESM Table 2), mostly explained by copepod abundance (SIMPER ~30% of total
309 dissimilarity). In fact we observed a significantly higher abundance of crustaceans (copepods,
310 ostracods, amphipods, isopods, and tanaids), particularly copepods, associated with
311 *Cystoseira* sp. than with other macroalgae (pairwise, $p < 0.01$; ESM Table 2). In addition, *J.*
312 *rubens* hosted a higher copepod abundance than the three remaining macroalgae, significantly
313 with respect to *P. perforata* (pairwise, $p < 0.05$).

314

315 **Macroalgal coverage and architecture**

316 During the survey we found on the inner margin only *P. perforata* ($13 \pm 1.8\%$) and *Dictyota*
317 sp. ($8 \pm 0.3\%$), while *Dictyota* sp. ($38 \pm 3.4\%$) dominated in the central “cuvette zone”
318 followed by *P. pavonica* ($18 \pm 3.1\%$), *J. rubens* ($7 \pm 1.7\%$), *P. perforata* ($5 \pm 0.9\%$) and
319 *Cystoseira* sp. ($4 \pm 0.9\%$). On the outer margin, the dominant macroalga was *Cystoseira* sp.
320 ($20 \pm 4.0\%$) followed by *Dictyota* sp. ($15 \pm 2.1\%$), *P. perforata* ($12 \pm 2.6\%$) and *J. rubens* ($2 \pm$
321 0.3%).

322 PERMANOVA analysis showed that macroalgal taxa significantly differed in both biomass
323 ($df = 4$, Pseudo-F = 50.3, $p < 0.001$) and fractal dimension ($df = 4$, Pseudo-F = 67.9, $p < 0.001$
324 for DA and $df = 4$, Pseudo-f = 88.0, $p < 0.001$ for DP) at both study areas . Pairwise

325 comparisons (ESM Table 3) showed that the biomass of *Cystoseira* sp. was significantly
326 higher ($p < 0.001$) than that of other macroalgae, followed by *J. rubens* (Table 4; $p < 0.01$).
327 Values of the macroalgal DA and DP, reported in Table 5, were significantly variable
328 (PERMANOVA, $p < 0.001$). *J. rubens* and *P. pavonica* showed significantly higher DA
329 (pairwise, $p < 0.01$), whilst *Cystoseira* sp. and *J. rubens* were more complex according to DP
330 (pairwise, $p < 0.01$).

331

332 **Relationship between macroalgal architecture and meiofauna**

333 Regression analysis showed that the meiofaunal abundance was positively correlated with the
334 different measures of habitat architecture, significantly with algal biomass and DP (Fig. 6).
335 We found that the abundance of total crustaceans, particularly copepods, and of nematodes
336 significantly increased with an increase of algal biomass (Fig. 6) and DP such as
337 polychaetes. . The DistLM procedure (ESM Table 4) indicated that the macroalgal
338 architecture significantly explained an important fraction of the variance in meiofaunal
339 communities associated with macroalgae. Habitat size (biomass) represented the most
340 important predictor variable for the abundance, taxa richness and community composition of
341 meiofauna, explaining 57%, 19% and 26% of total variance on the different macroalgae,
342 respectively. Habitat size also represented the major driver in the abundance of crustaceans,
343 namely copepods (explaining 54% of the variance) and in the abundance of nematodes and
344 polychaetes (explaining 40% and 30% of the variance, respectively). The abundance of total
345 meiofauna, crustaceans and copepods, and consequently also the community composition,
346 was also significantly explained by the complexity of macroalgal perimeter ($p < 0,01$; ESM
347 Table 4). This was evident in the dbRDA plot, showing that meiofaunal community on the
348 investigated macroalgae was driven by the vector of biomass, followed in importance by that
349 of DP. The first two axes explained 96%% of the variation of the fitted model, and up to 32%
350 of the total variation in meiofaunal communities (Fig. 7).

351

352 **Discussion**

353 Vermetid reef are biogenic constructions that, thanks to their horizontal extension (from the
354 upper mesolittoral area to the infralittoral fringe) and their spatial complexity, play a key role
355 in modulating morphological coastal processes and in structuring associated communities
356 (Chemello and Silenzi 2011; Di Franco et al. 2011; Milazzo et al. 2016).

357

358 Residual water, particulate organic matter and sediment are often trapped between the reef
359 rims and inside the *cuvettes* (Milazzo et al. 2016), making the substrate suitable for the
360 settlement of meiofaunal communities. In fact in this study we found, in the sediments
361 collected from *cuvettes* on the investigated reefs, values of meiofauna abundance comparable
362 or higher than those reported in sediments associated with coral reefs and coral colonies
363 (Logan et al. 2008; Cerrano et al. 2010). We observed a significant increase in meiofaunal
364 density inside *cuvettes*, from the inner to the outer margin of the reefs. The studies on benthic
365 assemblages inhabiting Mediterranean vermetid reefs, many of which are derived from grey
366 literature, revealed high abundance and diversity of species at a small scale (i.e. *cuvette* scale)
367 (Mannino 1992; Chemello et al. 1998; Goren and Galil 2001). Consistently with our results,
368 Chemello et al. (1998) found higher abundance and diversity (number of species) of
369 macrobenthic gastropods on the outer margin of the vermetid reefs at Capo Gallo,
370 highlighting that the distribution patterns of organisms reflected their hydrodynamic tolerance.
371 The different sections of the vermetid reef are characterized by physical and environmental
372 differences that give the microhabitat different features (Chemello and Silenzi 2011; Vizzini
373 et al. 2012). The inner margin is the zone most exposed to emersion periods during low tide,
374 desiccation and thermal stress in the warmer months, whereas the outer margin is the zone
375 most exposed to wave action and to the input of allochthonous resources from the adjoining

376 open sea (Chemello and Silenzi 2011; Vizzini et al. 2012). These physical conditions along
377 the vermetid reef could explain the higher abundance of meiofauna observed inside the
378 *cuvettes* close to the outer margins, where the organisms could find more suitable living
379 conditions with regard to water temperature and input of trophic resources (i.e. allochthonous
380 organic matter). The richness of taxa showed no significant difference along the investigated
381 reefs. We observed significant differences in meiofaunal community composition among the
382 different *cuvettes* positions and these differences were mostly explained by copepod
383 abundance. In fact, we found that crustaceans, namely copepods, were significantly more
384 abundant and more dominant in the *cuvettes* close to the outer margin than in those close to
385 the inner margin. This finding is in agreement with Donnarumma et al. (2014) who found that,
386 in a study on benthic macrofauna associated with Spanish vermetid reefs, the communities on
387 the outer margin were dominated by crustaceans.

388 Macroalgae provide a suitable habitat for a wide range of animal species and can also be
389 deemed as biological “formers” of habitat structure (Jones et al. 1994; García-Charton et al.
390 2000). At a small spatial scale of observation, marine algae promote complexity of coastal
391 rocky bottoms, providing additional resources such as surface area for attachment, shelter,
392 sediment or organic matter traps, and food items for invertebrate species (Hayward 1980;
393 Gibbons 1988). The presence of macroalgae on vermetid reef can increase the availability of
394 spatial niches for meiofaunal organisms, increasing the habitat structural complexity (Gibbons
395 1988; Chemello and Milazzo 2002; Danovaro and Fraschetti 2002).

396 Our results showed a significantly higher abundance of meiofauna on *Cystoseira* sp. than on
397 the four remaining macroalgae. Also, *J. rubens* hosted a significantly higher number of
398 meiofaunal organisms than *P. pavonica*, *Dyctiota* sp. and *P. perforata*. Other authors who
399 found similar results showed a higher number of associated organisms on these two
400 macroalgae with respect to other algal species, due to their complex structure (Russo 1997;

401 Chemello and Milazzo 2002). In particular, *Cystoseira* spp. are known to be among the most
402 important habitat-forming species of shallow Mediterranean Sea ecosystems, and are
403 responsible for the maintenance of abundant and biodiverse faunal and algal assemblages
404 (Bianchelli et al. 2016; Bulleri et al. 2002).

405 Meiofaunal communities associated with sampled macroalgae taxa were dominated by
406 copepods, followed by nematodes, in agreement with other studies (Gibbons 1988; Danovaro
407 and Fraschetti 2002; Pérez-García et al. 2015; Veiga et al. 2016). Copepods are frequently
408 associated with macroalgae, being part of the phytal meiofauna, due to a greater capacity to
409 swim and colonize macroalgae when compared to interstitial forms of meiofauna (Hicks 1986;
410 Ólafsson et al. 2001). However, we found that different macroalgae taxa showed significant
411 differences in associated community structures. In particular, we found significant
412 dissimilarities in meiofauna community structure comparing *Cystoseira* sp. and the other four
413 macroalgae taxa. These dissimilarities were mostly explained by copepods, found in
414 significantly higher abundance on *Cystoseira* sp. than the other macroalgae. Among the
415 investigated macroalgae, *J. rubens* showed the lowest dissimilarity with *Cystoseira* sp.,
416 hosting a higher copepod abundance than *P. pavonica*, *Dictyota* sp. and *P. perforata*. There is
417 evidence that different macroalgae do not support benthic fauna in the same way (Veiga et al.
418 2014, 2016), and this may depend on several factors such as life cycle, exhibition of chemical
419 defence and algal architecture (Duffy and Hay 1994; Chemello and Milazzo 2002).

420 Macroalgae with a more complex frond architecture usually offer a large number of habitats
421 for colonization of meiofauna (Gibbons 1991), good protection from predators and physical
422 stress, and have a high sediment-trapping potential (Coull and Wells 1983; Russo 1997).
423 Therefore, meiofauna associated with complex macroalgae usually shows higher abundance
424 and diversity than those associated with less complex macroalgae (Hicks 1980; Gee and
425 Warwick 1994; Frame et al. 2007; Veiga et al. 2016). The architecture of the macroalgae

426 includes measure of the complexity and the size of the habitat (Gee and Warwick 1994; Veiga
427 et al. 2014, 2016). Previous studies of macroalgae have generally included measures of the
428 habitat size (i.e. biomass, surface area, volume) (Taniguchi et al. 2003; Wernberg et al. 2004;
429 Gestoso et al. 2010), but to describe the fine structure and complexity of the habitat, it is
430 useful to estimate the complexity using measures of fractal dimension (Gee and Warwick
431 1994; McAbendroth et al. 2005; Hooper and Davenport 2006). In light of this, we investigated
432 the differences among macroalgae architecture by measuring algal biomass (used as a proxy of
433 habitat size) and the fractal dimensions of area and perimeter (used as a proxy of complexity).
434 Our results showed that the macroalgae with the highest values of structural complexity were
435 *Cystoseira* sp. and *J. rubens*, both in term of biomass and DP, confirming the high complexity
436 of these algae found by other authors (Russo 1997; Chemello and Milazzo 2002).

437 DistLM analysis showed that habitat size (biomass) was the most important factor in
438 explaining the differences in abundance and community composition of meiofauna associated
439 with the five investigated macroalgae. According to previous studies, reporting a positive
440 correlation between habitat size, estimated as biomass or surface area of macroalgae, and the
441 abundance and diversity of meiofaunal assemblages (Hicks 1980; Arroyo et al. 2004; Veiga et
442 al. 2016), we found a significant, positive correlation between algal biomass and abundance of
443 the principal meiofaunal taxa (i.e. copepods, nematodes and polychaetes). Moreover, DistLM
444 results suggest that, besides the effect of habitat size, macroalgal complexity, in accordance
445 with other studies (Gee and Warwick 1994; Danovaro and Fraschetti 2002; Arroyo et al. 2004;
446 Logan et al. 2008; Veiga et al. 2016) appears to have a significant role in determining the
447 abundance and community composition of meiofauna. In our study, the complexity of
448 macroalgae significantly influences the distribution of meiofauna, but only when we
449 considered the DP. In fact, we found a positive correlation between DP and abundance of total
450 meiofauna and of the principal taxa (i.e. copepods, nematodes and polychaetes). In contrast to

451 the results that other author found for macrofauna (Veiga et al. 2014; Torres et al. 2015), and
452 in accordance with Veiga et al. (2016) we evidenced that DP seems to be more relevant to
453 meiofaunal assemblages than DA. The DP indicates the degree of convolution of macroalgae
454 edge; high values indicate further division of space at smaller scales (MacAbendroth et al.
455 2005). Small animals, such as meiobenthic organisms, may live associated with parts of a
456 phytal structure that are not utilized by larger animals (i.e. macrofauna) (Veiga et al. 2016),
457 thus algae with more a complex structure, represented by higher DP values, would be expected
458 to support more small animals than structurally simple algae (Raffaelli et al. 2000; Schmid et
459 al. 2002). However DP significantly influenced only the abundance of crustaceans, copepods
460 in particular. This was in agreement with other research (Gibbons 1988; Hull 1997; Chemello
461 and Milazzo 2002) that revealed that crustaceans (i.e copepods, amphipods and ostracods)
462 were more abundant on finely branched algae than on those with wide thalli. Some copepods
463 evolved specific morphological features (such as suction mechanisms, clinging appendages
464 and mucus adhesion) that facilitate the adhesion on different algal surfaces (Hicks 1980; Bell
465 et al. 1987). Nevertheless, most of the meiofauna living on the macroalgae cannot be
466 considered true epiphytic organisms because they lack specialized structures. Macroalgae
467 provide three subhabitats for meiofauna: fronds, holdfasts and the deposited sediment and
468 detritus that accumulates at the bases of the stems (Arroyo et al. 2004).

469 The abundance of several taxa, primarily nematodes, is generally higher on the holdfast and is
470 influenced by the capacity of the macroalgae to trap sediment and detritus at the basal portion,
471 which, in turn, is related to algal biomass (Gibbons 1988; Danovaro and Fraschetti 2002; De
472 Oliveira et al. 2016).

473 Considering the coverage (%) of macroalgae in the three different zones of the investigated
474 vermetid reefs, we observed an increase of percentage contribution of macroalgae (i.e.
475 *Cystoseira* sp. and *J. rubens*) with higher habitat size and complexity (in particular of

476 perimeter) from the inner to the outer zone. This suggests the existence of a complexity
477 gradient that may further influence the horizontal distribution of meiofauna along the
478 vermetid reefs. Moreover, because the macroalgae can offer protection from turbulence and
479 desiccation (Gibbons 1988; Danovaro and Fraschetti 2002; Arroyo et al. 2004; Logan et al.
480 2008), the higher algal coverage on the outer zone could partly explain the higher abundance
481 of meiofauna found in the sediment of *cuvettes* located near the outer margin.

482 In the light of these results, we can conclude that vermetid reefs, in particular the “*cuvette*
483 zone”, represent a habitat suitable for the settlement of meiofaunal communities. Meiofaunal
484 organisms living in sediment inside *cuvettes* appeared to be influenced by physical and
485 hydrodynamic characteristic of the different sections of the reef, showing an increase in
486 abundance from the inner to the outer part of the reef. Moreover, the density and structure of
487 macroalgae present on the reef can play an additional role in hydrodynamic control and
488 structural effect on the covered substratum, shaping the structure of meiofaunal assemblages.

489 Meiofaunal organisms associated with different macroalgae, living on the investigated
490 vermetid reefs, appeared to be influenced by the algal architecture (in term of habitat size and
491 complexity). The higher algal cover and the presence of more complex macroalgae in the
492 outer zone of the reef may further influence the horizontal gradient of meiofauna density
493 distribution, making the outer zone more sheltered and complex and therefore more suitable
494 for the settlement of a greater number of meiofaunal organisms. These results confirm that
495 vermetid reefs, with their structural complexity, play an important role in structuring and
496 enhancing benthic fauna along coastlines and in facilitating the colonization of organisms in
497 physically stressful environments, such as intertidal habitats. The limited biogeographical
498 distribution of the vermetid reefs in the Mediterranean sea and the increasing amount of
499 potential anthropogenic threats would highlight the importance of vermetid reefs for
500 conservation purposes. Further studies on meiofauna and nematode diversity might provide

501 information on ecological importance of these bioconstructions useful for planning monitoring
502 and conservation strategies.

503 **Acknowledgements**

504 This study was carried out in the frame of the Project “Inventory of the Sicilian marine
505 biodiversity- Creation of a Regional Observatory of the Sicilian Biodiversity (ORBS) and
506 development of monitoring techniques useful for species management and habitat protection”
507 funded by the Dipartimento Regionale dell’Ambiente, Regione Sicilia (PO FESR 2007-2013-
508 Action Line 3.2.1.2).
509

510 **References**

- 511 Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance.
512 *Austral Ecol* 26: 32–46
- 513 Anderson MJ, Robinson J (2003) Generalised discriminant analysis based on distances. *Aust.*
514 *N.Z.J. Stat.* 45(3): 301–318
- 515 Antonioli F, Chemello C, Improta S, Riggio S (1999) *Dendropoma* lower intertidal reef
516 formations and their palaeoclimatological significance, NW Sicily. *Mar Geol* 161: 155–
517 170
- 518 Arroyo NL, Maldonado M, Pérez-Portela R, Benito J (2004) Distribution patterns of
519 meiofauna associated with a sublittoral *Laminaria* bed in the Cantabrian Sea (north-eastern
520 Atlantic). *Mar Biol* 144: 231–242
- 521 Attrill MJ, Strong JA, Rowden AA (2000) Are macroinvertebrate communities influenced by
522 seagrass structural complexity? *Ecography* 23: 114–121
- 523 Badalamenti F, Chemello R, Gristina M, Riggio S, Toccaceli M (1992) Caratterizzazione
524 delle Piattaforme a Molluschi Vermetidi nella costa tra Capo Gallo ed Isola delle Femmine
525 (PA): area proposta come riserva naturale marina; *Oebalia*, Suppl. 17: 547–549
- 526 Balistreri P, Chemello R, Mannino AM (2015) First assessment of the vermetid reefs along
527 the coasts of Favignana Island (Southern Tyrrhenian Sea). *Biodivers J* 6(1): 371–376
- 528 Bell SS, Walters K, Hall MO (1987) Habitat utilization by harpacticoid copepods: a
529 morphometric approach. *Mar Ecol Prog Ser* 35: 59–64
- 530 Bianchelli S, Pusceddu A., Canese S, Greco S, Danovaro R (2013) High meiofaunal and
531 nematodes diversity around mesophotic coral oases in the Mediterranean Sea. *PLoS One*
532 8(6), e66553
- 533 Bianchelli S, Pusceddu A, Buschi E, Danovaro R (2016) Trophic status and meiofauna
534 biodiversity in the Northern Adriatic Sea: insights for the assessment of good
535 environmental status. *Mar Environ Res* 113: 18–30
- 536 Bulleri F, Benedetti-Cecchi L, Acunto S, Cinelli F, Hawkins SJ (2002) The influence of
537 canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts
538 in the northwest Mediterranean. *J Exp Mar Biol Ecol* 267: 89–106
- 539 Cerrano C, Danovaro R, Gambi C, Pusceddu A, Riva A, Schiaparelli S (2010) Gold coral
540 (*Savalia savaglia*) and gorgonian forests enhance benthic biodiversity and ecosystem
541 functioning in the mesophotic zone. *Biodivers Conserv* 19(1): 153–167
- 542 Chemello R, Milazzo M (2002) Effect of algal architecture on associated fauna: some
543 evidence from phytal molluscs. *Mar Biol* 140(5): 981–990
- 544 Chemello R., Silenzi S (2011). Vermetid reefs in the Mediterranean Sea as archives of sea-
545 level and surface temperature changes. *Chem Ecol* 27: 121–127
- 546 Chemello R, Ciuna I, Pandolfo A, Riggio S (1998) Molluscan assemblages associated to the
547 intertidal vermetid formations: a morpho-functional approach. *Boll Malacol* 33: 105–114
- 548 Clarke KR (1993) Non parametric multivariate analyses of changes in community structure.
549 *Austral J Ecol* 18: 117–143
- 550 Clarke KR, Warwick RM (1994) Change in marine communities: An approach to statistical
551 analysis and interpretation. 2nd edn. Primer-e Ltd, Plymouth Marine Laboratory,
552 Plymouth, U.K.
- 553 Colombo F, Costa V, Dubois SF, Gianguzza P, Mazzola A, Vizzini S (2013) Trophic
554 structure of vermetid reef community: High trophic diversity at small. *J Sea Res* 77: 93–99

- 555 Consoli P, Romeo T, Giongrandi U, Andaloro F (2008) Differences among fish assemblages
556 associated with a nearshore vermetid *reef* and two other rocky habitats along the shores of
557 Cape Milazzo (northern Sicily, central Mediterranean Sea). *J Mar Biol Assoc U.K.* 88:
558 401–410
- 559 Coull BC, Wells JBJ (1982) Refuges from fish predation: experiments with phytal meiofauna
560 from the New Zealand rocky intertidal. *Ecology* 64: 1599–1609
- 561 Danovaro R., Fraschetti S (2002) Meiofaunal vertical zonation on hard bottoms: comparison
562 with soft-bottom meiofauna. *Mar Ecol Prog Ser* 230: 159–169
- 563 Danovaro R, Gambi C, Dell'Anno A, Corinaldesi C, Fraschetti S, Vanreusel A, Vincs M,
564 Gooday AJ (2008) Exponential decline of deep-sea ecosystem functioning linked to
565 benthic biodiversity loss. *Curr Biol* 18(1): 1–8
- 566 De Oliveira DA, Derycke S, Da Rocha MC, Barbosa DF, Decraemer W, Dos Santos GA
567 (2016) Spatiotemporal variation and sediment retention effects on nematode communities
568 associated with *Halimeda opuntia* (Linnaeus) *Lamouroux* (1816) and *Sargassum*
569 *polyceratium* Montagne (1837) seaweeds in a tropical phytal ecosystem. *Mar Biol* 163(5):
570 1–13
- 571 Donnarumma L, Terradas M, Appolloni L, Di Stefano F, Sánchez-Lizaso JL, Sandulli R,
572 Russo GF (2014) Associated benthic fauna to the vermetid *reefs* along the mediterranean
573 spanish coast. *Biol Mar Mediterr* 21 (1): 234–235
- 574 Duffy JE, Hay ME (1994) Herbivore resistance to seaweed chemical defence: the roles of
575 mobility and predation risk. *Ecology* 72: 1286–1298
- 576 Frame K, Hunt G Roy K (2007) Intertidal meiofaunal biodiversity with respect to different
577 algal habitats: a test using phytal ostracodes from Southern California. *Hydrobiologia* 586:
578 331–342
- 579 Franzitta G, Capruzzi E, La Marca EC, Milazzo M, Chemello R (2016) Recruitment patterns
580 in an intertidal species with low dispersal ability: the *reef*-building *Dendropoma cristatum*
581 (Biondi, 1859) (Mollusca: Gastropoda). *Ital J Zoo* 83 (3): 400–407
- 582 García-Charton JA, Williams I, Pérez-Ruzafa A, Milazzo M, Chemello R, Marcos C, Kitsos
583 MS, Koukouras A, Riggio (2000) Evaluating the ecological effects of Mediterranean
584 marine reserves: habitat, scale and the natural variability of ecosystems. *Environ Conserv*
585 27:179–199
- 586 Gee JJ, Warwick RM (1994) Metazoan community structure in relation to the fractal
587 dimension of marine macroalgae. *Mar Ecol Prog Ser* 103:141–150
- 588 Gestoso I, Olabarria C, Troncoso JS (2010) Variability of epifaunal assemblages associated
589 with native and invasive macroalgae. *Mar Freshwater Res* 61: 724–731
- 590 Gibbons MJ (1988) The impact of sediment accumulations, relative habitat complexity and
591 elevation on rocky shore meiofauna. *J Exp Mar Biol Ecol* 122: 225–241
- 592 Gibbons MJ (1991) Rocky shore meiofauna: a brief overview. *T Roy Soc S Afr* 47: 595–603
- 593 Giere O (2009) Meiobenthology. The microscopic motile fauna of aquatic sediments, 2nd
594 edn. Springer-Verlag, Berlin
- 595 Goren M, Galil BS (2001) Fish biodiversity in the vermetid *reef* of Shiqmona (Israel). *Mar*
596 *Ecol* 22: 369–378
- 597 Gutierrez JL, Jones CG, Strayer DL, Iribarne OO (2003) Mollusks as ecosystem engineers:
598 the role of shell production in aquatic habitats. *Oikos* 101(1): 79–90
- 599 Hayward PJ (1980) Invertebrate epiphytes of coastal marine algae. In: Price JH, Irvine DEG,
600 Farnham WF (eds) *The shore environment. Ecosystems Systematics Association*,
601 Academic, London, pp 761–787

- 602 Heip C, Vincx M, Vranken G (1985) The ecology of marine nematodes. Aberdeen University
603 Press
- 604 Hicks GRF (1980) Structure of phytal harpacticoid copepod assemblages and the influence of
605 habitat complexity and turbidity. *J Exp Mar Biol Ecol* 44: 157–192
- 606 Hicks GRF (1986) Distribution and behaviour of meiofaunal copepods inside and outside
607 seagrass beds. *Mar Ecol Prog Ser* 31: 159–170
- 608 Hooper GJ, Davenport J (2006) Epifaunal composition and fractal dimensions of intertidal
609 marine macroalgae in relation to emersion. *J Mar Biol Assoc U.K.* 86: 1297–1304
- 610 Hull SL (1997) Seasonal changes in diversity and abundance of ostracods on four species of
611 intertidal algae with differing structural complexity. *Mar Ecol Prog Ser* 161: 71–82
- 612 Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:
613 373–386
- 614 Kostylev VE, Erlandsson J, Ming MJ, Williams GA (2005) The relative importance of habitat
615 complexity and surface area in assessing biodiversity: Fractal application on rocky shores.
616 *Ecol Complex* 2: 272–286
- 617 Little C, Williams GA, Trowbridge CD (2009) The biology of rocky shores, 2nd ed. Oxford
618 University Press, New York
- 619 Logan, D, Townsend KA, Townsend K, Tibbetts IR (2008) Meiofauna sediment relations in
620 leeward slope turf algae of Heron Island reef. *Hydrobiologia* 610: 269–276
- 621 Mannino AM (1992) Studio fitosociologico della vegetazione mesolitorale a “Lithophyllum
622 lichenoides” PHILIPPI (Rhodophyceae, Corallinales). *Nat sicil*: 3–25
- 623 Mare MF (1942) A study of marine benthic community with special reference to the micro-
624 organism. *J Mar Biol Assoc U.K.* 25: 517–554
- 625 May RM (1972) Will a large complex system be stable? *Nature* 238: 413–414
- 626 McAbendroth L, Ramsay PM, Foggo A, Rundle SD, Bilton DT (2005) Does macrophyte
627 fractal complexity drive in vertebrate diversity, biomass and body size distributions? *Oikos*
628 111: 279–290
- 629 McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a
630 comment on distance-based redundancy analysis. *Ecology* 82: 290 – 297.
- 631 Milazzo M, Fine M, La Marca EC, Alessi C, Chemello C (2016). Drawing the line at
632 neglected marine ecosystems: ecology of vermetid reefs in a changing ocean. In *Marine*
633 *animal forests*, pp: 1– 23
- 634 Molinier R, Picard J (1953) Notes biologiques a propos d’un voyage d’étude sur les cotes de
635 Sicile. *Ann Inst Oceanogr (Paris)* 28: 163–188
- 636 Ólafsson E, Ingólfsson A, Steinarsdóttir MB (2001) Harpacticoid copepod communities of
637 floating seaweed: controlling factors and implications for dispersal. *Hydrobiologia* 453:
638 189–200
- 639 Pérez-García JA, Ruiz-Abierno A, Armenteros M (2015) Does morphology of host marine
640 macroalgae drive the ecological structure of epiphytic meiofauna. *J Mar Biol Oceanogr* 4:
641 2
- 642 Raffaelli D, Hall S, Emes C, Manly B (2000) Constraints on body size distributions: an
643 experimental approach using a small-scale system. *Oecologia*, 122: 389–398
- 644 Rasband WS (1997) Image J. U. S.Natl. Inst. Of Health, Bethesda (MD).
645 <http://rsb.info.nih.gov/ij/>.
- 646 Russo AR (1997) Epifauna living on sublittoral seaweeds around Cyprus. *Hydrobiologia* 344:
647 169–179

- 648 Safriel UN (1966) Recent vermetid formation on the Mediterranean shore of Israel. Proc.
649 Malac. Soc. Lond, 37:27–34
- 650 Safriel UN, Ben-Eliahu MN (1991) The influence of habitat structure and environmental
651 stability on the species diversity of polychaetes in vermetid *reefs* in: Bell S.S., McCoy D.E.
652 and Mushinsky R. (Eds). Habitat structure pp 349–372
- 653 Sarà G, Milanese M, Prusina I, Sarà A, Angel DL, Glamuzina B, Nitzan T, Freeman S,
654 Rinaldi A, Palmeri V, Montalto V, Lo Martire M, Gianguzza P, Arizza V, Lo Brutto S, De
655 Pirro M, Helmuth B, Murray J, De Cantis S, Williams GA (2014) The impact of climate
656 change on Mediterranean intertidal communities: losses in coastal ecosystem integrity and
657 services. Reg Environ Change 14(1): 5–17
- 658 Schmid PE, Tokeshi M, Schmid-Araya JM (2002) Scaling in stream communities. P Roy Soc
659 Lond B Bio 269: 2587–2594
- 660 Taniguchi H, Nakano S, Tokeshi M (2003) Influences of habitat complexity on the diversity
661 and abundance of epiphytic invertebrates on plants. Freshwater Biol 48: 718–728
- 662 Torres AC, Veiga P, Rubal M, Sousa-Pinto I (2015) The role of annual macroalgal
663 morphology in driving its epifaunal assemblages. J Exp Mar Biol Ecol 464: 96–106
- 664 Veiga P, Rubal M, Sousa-Pinto I (2014) Structural complexity of macroalgae influences
665 epifaunal assemblages associated with native and invasive species. Mar Environ Res 101:
666 115–123
- 667 Veiga P, Sousa-Pinto I, Rubal M (2016) Meiofaunal assemblages associated with native and
668 non-indigenous macroalgae. Cont Shelf Res 123: 1–8
- 669 Vizzini S, Colombo F, Costa V, Mazzola M (2012) Contribution of planktonic and benthic
670 food sources to the diet of the *reef*-forming vermetid gastropod *Dendropoma petraeum* in
671 the western Mediterranean. Estuar Coast Shelf Sci 96: 262–267
- 672 Wernberg T, Thomsen MS, Staehr PA, Pedersen MF (2004) Epibiota communities of the
673 introduced and indigenous macroalgal relatives *Sargassum muticum* and *Halidrys siliquosa*
674 in Limfjorden (Denmark). Helgoland Mar Res 58: 154–161
- 675
- 676

677 **Captions of Figures**

678 **Figure 1.** a) Sampling areas (Favignana Island and Capo Gallo) and b) sampling strategy
679 along the investigated vermetid reef. Here we indicate the positions of the *cuvettes* where we
680 collected the sediment samples: close to inner margin (Inner), in the middle of the “*cuvette*
681 zone” (Medium) and close to outer margin (Outer).

682 **Figure 2.** Total meiofauna abundance in the sediment inside the *cuvettes* at Capo Gallo and
683 Favignana located: close to the inner margin; in the middle of the “*cuvette zone*”; and close to
684 the outer margin (mean between the two sampled reefs in each area \pm SE).

685 **Figure 3.** Meiofauna community structure in the sediment inside the *cuvettes* at Capo Gallo
686 and Favignana, located: close to the inner margin; in the middle of the “*cuvette zone*”; and
687 close to the outer margin (mean between the two sampled reefs in each area \pm SE).

688 **Figure 4.** Total meiofauna abundance associated with the five investigated macroalgae taxa
689 (*Palisada perforata*, *Padina pavonica*, *Jania rubens*, *Dictyota* sp. and *Cystoseira* sp.)
690 colonizing the vermetid reefs at Capo Gallo and Favignana Island (mean between the two sites
691 in each area \pm SE).

692 **Figure 5.** Meiofauna community structure associated with the five investigated macroalgae
693 taxa (*Palisada perforata*, *Padina pavonica*, *Jania rubens*, *Dictyota* sp. and *Cystoseira* sp.)
694 colonizing the vermetid reefs at Capo Gallo and Favignana (mean between the two sampled
695 reefs in each area \pm SE).

696 **Figure 6.** Relationship between abundance of meiofauna (total meiofauna, copepods and
697 nematodes) and macroalgal habitat size (biomass) and complexity, expressed as fractal

698 dimension of area (DA) and perimeter (DP). We reported the value of R and P (***) = $P <$
699 0.001 , ** = $P < 0.01$, * = $P < 0.05$, n.s. = not significant).

700 **Figure 7.** Distance-based redundancy analysis (dbRDA) to investigate relationships between
701 meiofaunal community composition and macroalgal architecture: habitat size (biomass) and
702 complexity expressed as fractal dimension of area (DA) and perimeter (DP) of the five
703 macroalgae taxa: *Palisada perforata* (rhomboids), *Padina pavonica* (squares); *Jania rubens*
704 (circles), *Dyctiota* sp. (inverted triangles) and *Cystoseira* sp. (right triangles).