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1 **Species-Area Relationship (SAR) models as tools for estimating faunal**
2 **biodiversity associated with habitat builder species in sensitive areas: the case of**
3 **the Mediterranean stony coral (*Cladocora caespitosa*)**

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9 **Abstract**

10 Biodiversity associated with the Mediterranean stony coral *Cladocora caespitosa*, (Linnaeus, 1767)
11 was investigated at three levels: “microscale”, focused on macrobenthic invertebrates within
12 colonies; “mesoscale”, focused on epibenthic megafauna among colonies; “macroscale”, focused on
13 associated ichthyofauna. The aim was to quantify associated diversity in terms of species richness,
14 testing the efficiency of colony size (surface covered by a single colony) for the “microscale”, and
15 colony density or total coral coverage for “meso-“ and “macroscale” as predictors and the
16 consistency of models based on Species-Area Relationship (SAR) for those estimations. At level of
17 “microscale”, colony size was a good predictor, with richness of invertebrates increasing with the
18 increasing of surface covered by each colony of *C. caespitosa*, following Arrhenius model. At
19 levels of “mesoscale” and “macroscale”, richness of epibenthic megafauna and fish were not related
20 neither to colony density nor total coral coverage, but to sampled area, and frequency-based
21 estimates of richness were used. The importance of *C. caespitosa* varied according to the
22 investigation level, with most of taxa richness detected at the level of “microscale”.

23
24 **Keywords:** *Cladocora caespitosa*; habitat builder species; benthos; invertebrates; ichthyofauna;
25 Species-Area Relationship (SAR); Mediterranean Sea

1. INTRODUCTION

27
28 The Mediterranean stony coral *Cladocora caespitosa* (Linnaeus, 1767) is a well-known habitat
29 builder, physiologically and morphologically similar to the typical tropical reef-building corals, and
30 as such it is supposed to host a diversified faunal assemblage (Zibrowius 1980, Peirano et al. 1994).
31 The few papers available to date from Adriatic (Sciscioli and Nuzzaci 1970, Zavodnik 1976,
32 Schiller 1993, Pitacco et al. 2014, Pitacco et al. 2017), Ionian Sea (Lumare 1965) and Aegean Sea
33 (Arvanitidis and Koukouras 1994, Koukouras et al. 1998, Antoniadou and Chintiroglou 2010),
34 confirm that macrofaunal communities associated with *C. caespitosa* are particularly rich.
35 Nevertheless, information provided is extremely fragmented, since most of these works focused
36 only on invertebrates, and mostly on single taxonomic groups, such as polychaetes (Arvanitidis and
37 Koukouras 1994, Sciscioli and Nuzzaci 1970) and echinoderms (Zavodnik 1976), and the different
38 methodologies used make it difficult to compare results. Coral associated species could represent an
39 important food source for other invertebrates and benthic fishes, therefore areas with massive
40 presence of *C. caespitosa* are expected to attract them. Nevertheless, while fish assemblages
41 associated with other habitat builders, such as macroalgae and seagrasses have been intensively
42 investigated (e.g. Lipej et al. 2003, Pais et al. 2007, Orlando-Bonaca and Lipej 2007, Orlando-
43 Bonaca et al. 2008, Cheminée et al. 2016), there is a gap of knowledge on the role of *C. caespitosa*
44 for benthic fishes. *Cladocora caespitosa* is the only native colonial and obligate zooxanthellate
45 coral in the Mediterranean Sea (Zibrowius 1980) and it is present in the whole Mediterranean,
46 although is only locally abundant (Peirano et al. 1994). It has adapted to live in different
47 environments, from shallow photophilic algal communities to deeper circalittoral assemblages
48 (Zibrowius 1980, Schiller 1993, Kružić and Benković 2008, Kersting and Linares 2012, Chefaoui et
49 al. 2017, Kersting et al. 2017). Nevertheless, given its particular sensitivity to different types of
50 anthropogenic impacts and climate change (Rodolfo-Metalpa et al. 2005, Kersting et al. 2013,
51 2015) and the fact that its slow dynamics increases its vulnerability to catastrophic events (Kersting
52 et al. 2014), its populations are actually decreasing, and the species was included as “Endangered”

53 in the IUCN Red List (Casado de Amezua et al. 2015). The loss of this coral could be detrimental
54 also for invertebrates and fish living in symbiosis (especially if parasitic or obligate mutualistic)
55 with it and, at the same time, associated invertebrates may interfere positively or negatively with
56 coral recovery capacity after a stressful event, as it was reported for tropical corals (reviewed by
57 Baker et al. 2008). Nevertheless, given the scarce information available on its associated fauna, the
58 mutual influence between *C. caespitosa* and its associated benthic communities is still poorly
59 understood.

60 Models based on Species-area relationship (SAR) have been proposed in conservation biology to
61 project the expected loss of species richness from a region undergoing specified levels of habitat
62 degradation (*e.g.* Connor and McCoy 2001, Ulrich 2005) and to estimate local species richness for
63 hotspot identification (*e.g.* Veech 2000). SAR is among the best known and most studied paradigms
64 in ecology (Arrhenius 1921, Rosenzweig 1995). It describes the pattern in which the species
65 richness increases with the increasing sampling area, and is recognized as one of the few true laws
66 of ecology (Gotelli and Colwell, 2001). The species-area curve is central argument for the theory of
67 island biogeography (MacArthur and Wilson 1963), but the pattern holds not only for geographic
68 islands, that are pieces of land surrounded by water (MacArthur and Wilson 1963, Holt et al. 1999),
69 but also for 'island' system where similar habitat types are separated in space by relatively
70 unfavourable habitats islands (MacArthur 1972). SAR applications have been widely used for
71 terrestrial ecosystems, applied to plants (Arrhenius 1921, Gleason 1922) and birds (Preston 1960,
72 MacArthur and Wilson 1963), conversely there are considerably less similar studies for the marine
73 realm (McGuinness 1984; Chittaro 2002, Neigel 2003, Balasubramanian and Foster 2007, Reichert
74 et al. 2010), and most of them deal only with large scale patterns (Sabetta et al. 2007; Bevilacqua et
75 al. 2018).

76 The scope of the work was to improve the present knowledge on fauna associated with the
77 Mediterranean stony coral and test the efficiency of SAR models to estimate associated diversity, in
78 terms of species richness. The aim of the work was threefold: (i) to quantify and characterize

79 diversity associated with *C. caespitosa* in terms of species richness; (ii) to test the efficiency of
80 colony size (surface covered by a single colony, for the “microscale”), colony density and total
81 coral coverage (for “meso-“ and “macroscale”) as predictors of associated species richness; (iii) to
82 test the consistency of different SAR models for the estimation of species richness in areas with
83 high colony density. Investigation was performed at three different levels, using for each level
84 different sampling techniques and designs, and focusing on different scales (from square
85 centimetres to square metres) and taxonomic groups.

86

87 **2. MATERIAL AND METHODS**

88 **2.1. Study area**

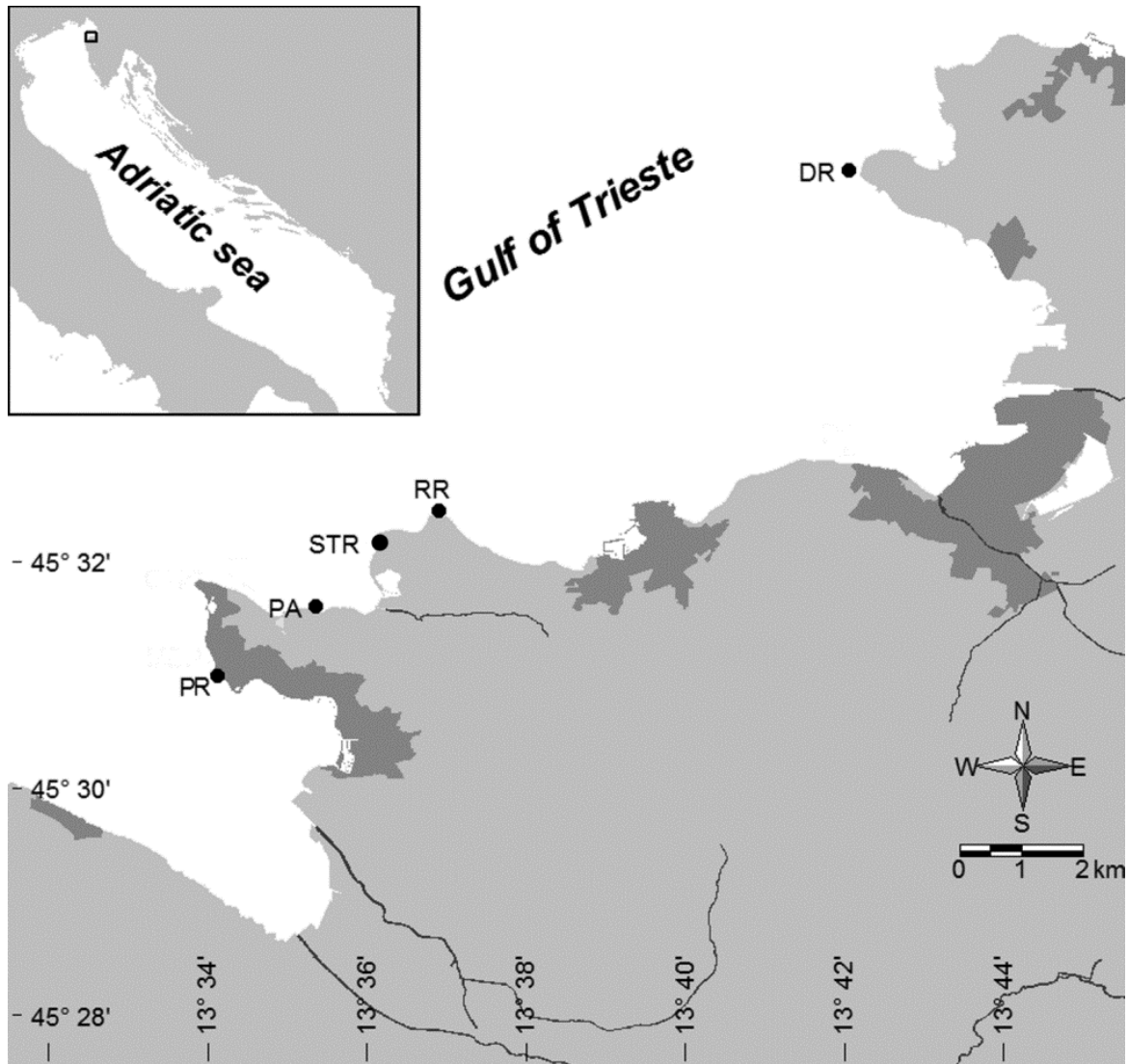
89 The Gulf of Trieste is a shallow semi-enclosed embayment located in the northernmost part of the
90 Adriatic Sea (Mediterranean Sea). It extends from Cape Savudrija (Croatia) to Grado (Italy) and
91 includes the entire Slovenian coast. The maximum depth (approximately 33 m) is found in waters
92 off Piran. The area is characterized by the lowest winter temperatures in the Mediterranean Sea,
93 which can fall below 10°C (Boicourt et al. 1999). Salinity is about 37 on average, but it is
94 influenced near the coast by fresh water inputs (Mozetič et al. 1998). The embayed situation of the
95 Gulf of Trieste, together with dominant winds blowing in an offshore direction (from the North-
96 East) and very shallow waters create a quite sheltered condition (Boicourt et al. 1999). The coastal
97 morphology of the study area varies from steep rocky cliffs to gradual sloping beaches consisting of
98 gravel and pebbles (Ogorelec et al. 1991). The rocky substratum of the Slovenian coast consists
99 mainly of Eocene flysch layers, with alternating solid sandstone and soft marl (Ogorelec et al.
100 1997). *C. caespitosa* is well distributed throughout the Slovenian Sea, and in some places it forms
101 beds (*sensu* Peirano et al., 1994) with very high density of living colonies per unit area (from 3 to
102 652 colonies/100m²; Lipej et al. 2016), although the average total coral coverage is not high (21%)
103 with a maximum of 56% (Zunino et al., 2018). Most of those areas are located in the infralittoral
104 zone, up to about 11 m depth, with the only exception of a biogenic formation located deeper, from

105 12.4 to 21 m depth. This solitary structure is surrounded by a muddy bottom, and completely
106 composed by a secondary detritic bottom mainly made of dead corallites of *C. caespitosa* (Lipej et
107 al. 2016). In past decades the Slovenian coastal sea suffered from many anthropogenic impacts such
108 as intensive fishing, sewage outfalls and mariculture (Francé and Mozetič 2006, Mozetič et al.
109 2008).

110 2.2. Field work

111 Sampling sites and procedures were chosen in order to limit as much as possible the impact on the
112 local benthic community. Five sampling sites, which were previously assessed as rich with
113 *Cladocora caespitosa* colonies (from 83 to 186 colonies/100m²; Lipej et al. 2016), were selected
114 along the Slovenian coast (Fig. 1): Debeli Rtič (DR), Pacug (PA), Piranček (PR), Cape Ronek (RR)
115 and Cape Strunjan (STR).

116
117 **Fig. 1** Map of the study area with indicated sampling sites: Debeli Rtič - DR, Pacug - PA, Piranček
118 - PR, Cape Ronek – RR and Cape Strunjan- STR.



119

120 Sampling surveys were performed from 2012 to 2015 with SCUBA diving in the infralittoral belt,
 121 between 4 m and 9 m of depth (Table 1). Sampled areas can be considered transitional zones
 122 between infralittoral and circalittoral belts, showing a coexistence of photophilic and sciaphilic
 123 algal assemblages (*personal observation*). In order to assess faunistic diversity associated with *C.*
 124 *caespitosa* a combination of standard techniques and non-destructive methods was used.

125

126

Table 1 Sampling sites with coordinates and depth range.

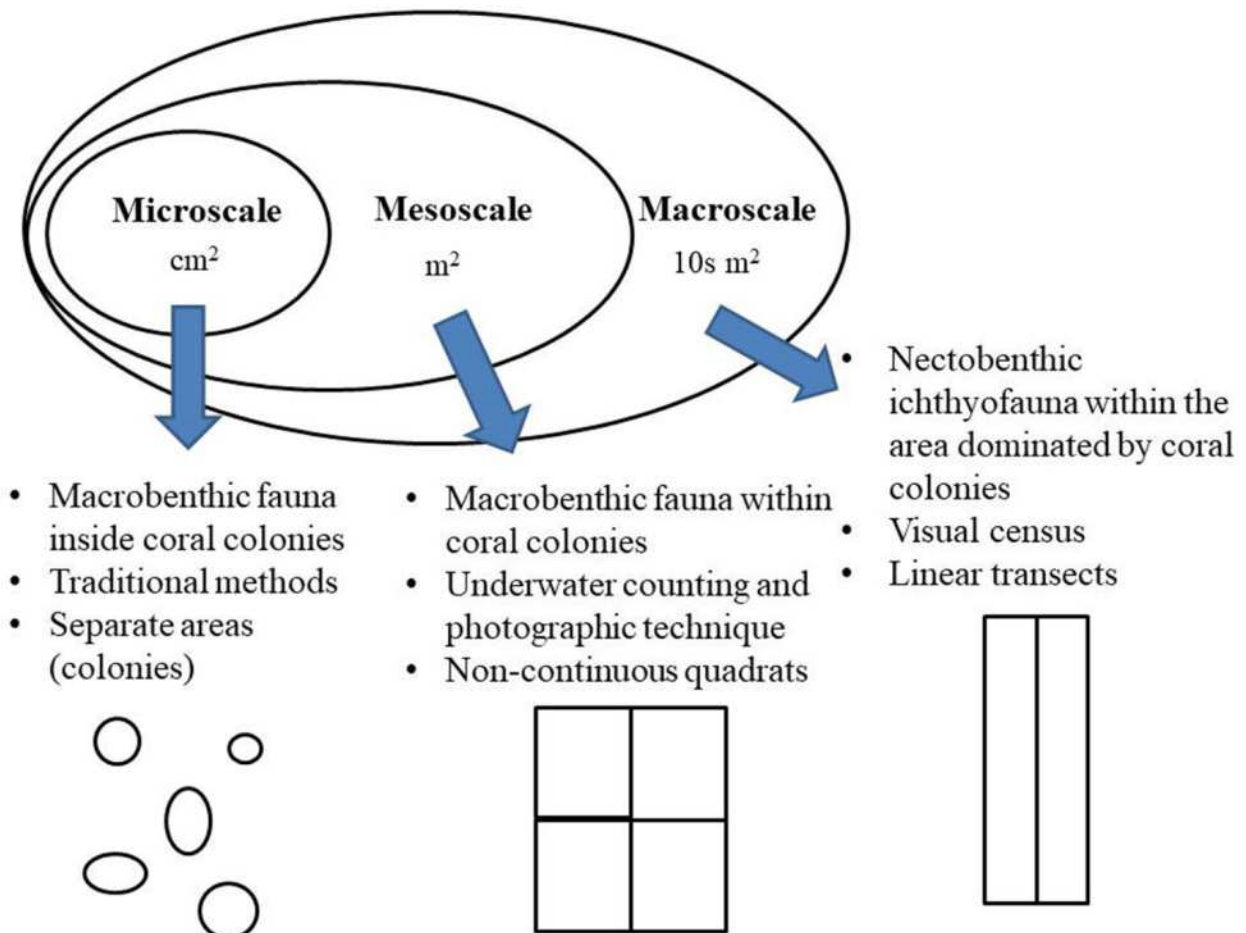
Code	Site	Latitude (N)	Longitude (E)	Depth range (m)
RR	Cape Ronek	45°32'25"	13°36'56"	6-10
PR	Piranček	45°31'38"	13°34'30"	5-10
STR	Cape Strunjan	45°32'5"	13°36'10"	3-6
PA	Pacug	45°31'34"	13°35'24"	5-8
DR	Debeli rtič	45°35'28"	13°42'88"	5-7

127

128 Research was carried out at three different levels, sampling physically independent areas with
 129 different sampling strategies and different focal targets (Fig. 2): (i) “microscale” level, biodiversity
 130 of invertebrates inside *C. caespitosa* colonies, scale of square centimetres; (ii) “mesoscale” level,
 131 biodiversity of epibenthic megafauna among colonies, scale of square meters; (iii) “macroscale”
 132 level, biodiversity of ichthyofauna within the area dominated by *C. caespitosa*, scale of tens of
 133 square meters, were sampled. For each level a different sampling design was followed.

134

135 **Fig. 2** Research design with the three levels of investigations. For each level are indicated: scale,
 136 target, methodology and sampling design.



137

138

139 At the microscale level macrobenthic organisms living inside coral colonies were targeted (Fig. 2).

140 Those animals are strictly associated with corals, so a destructive traditional method was necessary,

141 being the unique proper technique for determination of cryptic animals such as polychaetes.
142 Physically separate areas with different size, corresponding to colonies of *C. caespitosa* were
143 sampled in summer 2012 (Fig. 2). Five colonies of *C. caespitosa* from the most common size
144 classes were collected at each site, for a total of 25 colonies. Along the Slovenian coast colony sizes
145 were ranked in six different size classes based on the length of maximum axis (Schiller 1993,
146 Zunino et al. 2018): class I (maximum axis <5 cm), class II (5-10 cm), class III (10-15 cm), class IV
147 (15-20 cm), class V (20-25 cm), class VI (>25 cm). The biggest colony found by Zunino et al.
148 (2018) had a maximum axis of 68 cm, but the most frequent size class was class II (maximum axis
149 from 5 to 10 cm). Colonies of class VI were rare and observed only at two sites (Zunino et al.
150 2018). In order to reduce the impact of sampling procedure on *C. caespitosa* population only two
151 large-sized colonies were collected. In this way we could check if predictions based on small
152 colonies could be reliable also for the big ones (class IV). Only colonies fixed to small rocks and
153 detritus, which could be easily detached from the substrate without hammer and chisel, were
154 collected. Colonies were immediately put in plastic buckets, and then transported to the laboratory.
155 This method has proved to be efficient for investigating macroinvertebrates living in association
156 with tropical corals (Abele and Patton 1976). In addition, as living and dead coral colonies can host
157 different faunal assemblages (Cantera et al. 2003), a threshold of colonies with at least 50% of
158 living polyps was set during sampling, in order to reduce the potential bias. This parameter was
159 estimated before sampling by a SCUBA diver through visual analysis, by dividing the colony in
160 two parts by a virtual axis and selecting only colonies composed of at least 50% living polyps.

161 At the mesoscale level epibenthic megafauna inhabiting areas among *C. caespitosa* colonies was
162 targeted (Fig. 2). Sampling was performed during summer 2013 and 2014, analysing separate areas
163 with the same size (quadrats). Quadrat sampling method is a non-destructive diving visual census
164 methodology, used for benthic fish and invertebrate assemblages studies, particularly useful to
165 study sensitive or protected habitat (e.g. Nieder et al. 2000; Sswat et al. 2015; Yesson et al. 2016).
166 The term 'megafauna', was operatively defined as the benthic fraction with organisms large enough

167 to be identified in seafloor images (Gage and Tyler 1992), and in the present work it was used to
168 define benthic animals determined *in situ* or through photo analysis. A metal frame of 1×1 m
169 separated in 4 subquadrats was placed in areas where *C. caespitosa* was more abundant (minimum
170 of 2 colonies per quadrat). Each quadrat was photographed, species were determined to the lowest
171 possible taxonomic level *in situ* and organisms were counted and marked on a diver slate. For
172 colonial organisms colonies were counted. A total of 45 quadrats were analysed (18 in 2013 and 27
173 in 2014) with a minimum of 3 replicates per site. Quadrat size of 1×1 m was chosen as the most
174 appropriate, in terms of cost(time)/efficiency balance, after a preliminary test, comparing quadrats
175 of different sizes (0.5×0.5 m, 1×1 m and 2×2 m). Sampling time was dependent on the
176 heterogeneity of substrate inside the quadrats. The density (CC) of *C. caespitosa*, colony size, as the
177 surface covered by each colony (A), and the percentage of living polyps (LP) for each quadrat were
178 calculated later from photographs. In order to check if the sampling effort was appropriate to get a
179 general picture of biodiversity at the studied sites, additional 25 quadrats for each of four studied
180 sites (RR, PA, STR, and PR), were analysed with photographic techniques. Four photographs for
181 each quadrat were taken in 2014 and 2015, one for each subquadrat of 0.5×0.5m, for a total of 400
182 photographs per site. To reduced possible bias, visual count was performed always by the same
183 researcher.

184 At the macroscale level the associated nectobenthic ichthyofauna was targeted (Fig. 2). The
185 fieldwork was carried out by SCUBA diving from June to September of 2013, 2014 and 2015,
186 when the fish species were most active. Data were collected *in situ* using the visual transect
187 technique (Harmelin 1987), a common non-destructive underwater visual survey methods, preferred
188 when sampling in vulnerable habitat types or marine protected areas (e.g. La Mesa et al. 2017;
189 Emslie et al. 2018). Horizontal transects (MacPherson 1994, Orlando-Bonaca and Lipej 2005, Lipej
190 and Orlando-Bonaca 2006) from 30 to 50 m in length were laid out at different depths, depending
191 on the presence of colonies of *C. caespitosa*. Transect lengths were chosen in order to include
192 homogeneous habitat. Depth was more or less constant over the whole length of the transect. For

193 each range, a fixed transect was placed on the bottom with meter-marks. Fish were counted mostly
194 within 2 m, 1 m to the left and 1 m to the right of the line. Since diver disturbance could influence
195 the results (Emslie et al. 2018), when possible 2 consecutive passages on the same transect were
196 performed, to test the effect of such disturbance on species counts. During the surveys, a constant
197 swimming speed was maintained. A number from 2 to 6 transects were performed at each site each
198 year, for a total of 51 transects distributed over the five sampling sites. Species names and
199 abundances of fishes and number of colonies of *C. caespitosa* were marked on a diver slate during
200 diving. Visual count was performed always by the same researcher.

201

202 **2.3. Laboratory work and data processing**

203 For the microscale level, the percentage of living polyps (LP), previously assessed in the field, was
204 again confirmed at the laboratory by a different co-author, following the same methods described
205 above. Subsequently, maximum (length, D1) and minimum axis (width, D2) and height (H) (in cm)
206 of each colony were measured with a ruler. Finally, the area covered by each colony (A) (in cm²)
207 was calculated by the classic formula used for the calculation of the area of an ellipse: $A = (D1/2)$
208 $(D2/2) \pi$, and the volume (in cm³) was measured by water displacement. The net volume (V_{net}) was
209 calculated first, and then colonies were covered with plastic foil to measure the total volume (V_{tot}).
210 Interstitial volume (V_{int}) was calculated as follows: $V_{int} = V_{tot} - V_{net}$. All these analyses follows
211 methods already described and used by Schiller (1993), who performed his study in the very same
212 area, and Peirano et al. (2001). Then all coral colonies were broken down for sorting and
213 determination of associated macrobenthic animals. In order to remove sediment trapped between
214 corallites, samples were sieved through a 0.5 mm mesh, and the sieved material was then preserved
215 in 70% ethanol. Organisms that were alive at the moment of sampling were determined to the
216 lowest possible taxonomic level according to relevant literature and then they were counted.
217 Colonial species were also determined and their coverage on a surface of 20×20 cm was calculated,

218 but they were excluded from calculation of diversity indices. For determination a stereomicroscope
219 and a microscope were used for details (morphological characteristics).
220 At the mesoscale level all photographs taken underwater were analysed using PhotoQuad software
221 (Trygonis and Sini 2012). For the visual methods photographs were used to measure colony length
222 (D1), colony width (D2), and percentage of living polyps (LP) of each colony, and colony density
223 (CC) per each quadrat. The area covered by each colony (A) was calculated by the formula
224 described above for the microscale and used as colony size descriptor. For each quadrat the total
225 coral coverage (A_{cov}) was calculated as the sum of the areas covered by each colony (A). For the
226 photographic method photographs of each subquadrat (0.5x0.5 m) were analysed for benthic taxa
227 determination. Since the determination of certain species of invertebrates and macroalgae requires
228 sample collection and a detailed analysis in laboratory, some of them were left to the genus, family
229 level and the following operational definitions were employed.

230 **2.4. Data analysis**

231 For the microscale level data exploration techniques were used to check the presence of outliers,
232 influential points, and collinearity between variables. Log transformation was applied when needed.
233 Data exploration procedures followed Zuur et al. (2007) and were performed with R version 3.2.0
234 (R Core Team 2015). Relationships among colony parameters (D1, D2, H, A, V_{tot} and LP) were
235 tested with Spearman's coefficients – r_s (Spearman 1907), and chi square test applied to Kruskal-
236 Wallis ranks – KW (Kruskal and Wallis 1952) was used to check if those parameters differed
237 among sites. Cumulative curves for taxa richness with increasing sample volume (V_{tot}) were created
238 to check whether the sample size was representative for the sampled area. Curves were also created
239 for the dominant taxonomic groups separately. Trellis graphs were used to check whether the
240 relationship between colony size (A) and number of total taxa (S_{tot}) was independent from sampling
241 sites and depth. Graphs were created using Lattice package for R (Sarkar 2008).
242 The relationship between total number of taxa (S_{tot}) and colony size (covered area – A) was first
243 tested with Spearman's coefficients for non-parametric distributions (Spearman 1907). The same

244 analysis was used to test the relation between colony size (A) and taxa richness of the dominant
 245 phyla (polychaetes S_{poly} , molluscs S_{mol} and crustaceans S_{cr}) separately. Regression lines were
 246 calculated to describe the relationship between colony size (A) and richness of total taxa (S_{tot}),
 247 mollusc (S_{mol}), polychaete (S_{poly}) and crustacean richness (S_{cr}). Calculation were performed also
 248 using V_{tot} as colony size descriptor. Analyses on residuals were performed to verify the assumption
 249 of normality, homogeneity, independence and absence of pattern in the residuals for validation of
 250 regression models. The linear regression model on log-transformed data was compared with the
 251 non-linear regression models most frequently used to fit SAR data: Arrhenius, Gleason, Gitay and
 252 Lomolino (Dengler 2009). AIC (Akaike Information Criterion) (1) and Adjusted R-squared (2)
 253 were used to choose the best model describing the Species-Area Relationship. They are defined by:

$$254 \quad AIC = n(\log SS_{residual}) + 2(K+1) - n \log(n) \quad \dots (1)$$

$$255 \quad \text{Adjusted } R^2 = 1 - (SS_{residual}/(n-K))/(SS_{total}/(n-1)) \quad \dots (2)$$

256 Where n = sample size, $SS_{residual}$ =sum of squared deviations of observed values from fitted values,
 257 SS_{total} =sum of squared deviations of observed data from the mean, K = number of parameters. With
 258 a lower AIC, the model is considered better in explaining the data, conversely the higher the
 259 Adjusted R^2 the best the model. Calculations were performed using vegan package (Oksanen et al.
 260 2015) for R.

261
 262 For the mesoscale level data collected with the two methods (underwater counting and analysis of
 263 photographs) were analysed separately with the same statistical methods described below, and
 264 results were compared. Non-parametric Spearman's correlation – r_s (Spearman 1907) was used to
 265 test if colony density (CC) was related to sampling depth, percentage of living polyps (LP), and if
 266 observed species richness (S_{obs}) was related to colony density (CC), percentage of living polyps
 267 (LP), or total coral coverage (A_{cov}). Chi square tests applied to Kruskal-Wallis ranks – KW
 268 (Kruskal and Wallis 1952) was used to check if colony density (CC) and total coral coverage (A_{cov})
 269 differed significantly among sites.

270 To check whether sampling effort was appropriate for a good estimate of species richness of the
 271 studied area, species accumulation curves were performed for the total data set and for each site
 272 separately, in both cases with two different methods: (i) according to the original sequence of
 273 recording and (ii) by calculating the mean of species-area curve and its standard deviation from
 274 random order of quadrats, sampled without replacement. Calculations were performed using vegan
 275 package (Oksanen et al. 2015) for R.

276 In order to estimate the number of unseen species and add them to the observed species richness
 277 incidence-based estimates using the frequencies of species were used (Colwell and Coddington
 278 1994). The functions are the following: Chao bias-corrected (3), first order jackknife (4), bootstrap
 279 (5).

$$280 \quad S_P = S_0 + (a_1(a_1 - 1) / 2(a_2 + 1)) (N - 1) / N \quad \dots (3)$$

$$281 \quad S_P = S_0 + a_1((N - 1) / N) \quad \dots (4)$$

$$282 \quad S_P = S_0 + \sum_{i=1}^{S_0} (1 - p_i)^N \quad \dots (5)$$

283 where S_P is the extrapolated richness in a pool, S_0 is the observed number of species in the
 284 collection, a_1 and a_2 are the number of species occurring only in one or only in two sites in the
 285 collection, p_i is the frequency of species i , and N is the number of sites in the collection.

286 For the macroscale level the number of fish species observed in each transect was weighted
 287 according to the transect length. Density for 100 m² was calculated for fishes and colonies of *C.*
 288 *caespitosa*. Non-parametric Spearman's correlation (Spearman 1907) was used to test if colony
 289 density (CC) was related to sampling depth, fish richness, total fish densities and densities of the
 290 dominant species. Species accumulation curves, built with the same methods described above for
 291 the mesoscale, were calculated: (i) for the first, the second and for the two passages combined, to
 292 test the effect of successive passages on the same transect; (ii) for all transects together and for each
 293 site separately, to test the suitability of sampling effort to get a general picture of the fish
 294 community. Estimations of species pool were also performed with the same functions described

295 above for the mesoscale. Wilcoxon-Mann-Whitney (WMW) statistic was used to compare results of
296 both accumulation curves and species estimation (Mann and Whitney 1947).

297 A $p < 0.05$ was chosen as significance threshold. All calculations were performed using R version
298 2.4.0.

299

300 **3. RESULTS**

301 **3.1. “Microscale” level**

302 All measured attributes of colonies of *Cladocora caespitosa* (D1, D2, H, A, and V_{tot} ; $p < 0.05$),
303 except LP ($p > 0.05$), were strongly positively correlated (Supplementary material, Table S1),
304 confirming that the area covered by each colony (A) can be used as colony size descriptor. The
305 smallest studied colony ($A = 39.9 \text{ cm}^2$) was collected at site PA, while the biggest ($A = 937.1 \text{ cm}^2$)
306 was collected at site PR. All measured coral attributes (D1, D2, H, A, and V_{tot} , and LP) did not
307 varied significantly among the five sampling sites (KW, $p > 0.05$).

308 A total of 222 different taxa were found: 95 polychaetes, 64 molluscs, 43 crustaceans, 5 tunicates, 5
309 bryozoans, 3 sponges, 4 echinoderms, 1 cnidarian and 1 sipunculid. Among non-colonial organisms
310 11561 invertebrates were counted and 182 taxa were determined to the species level (Electronic
311 supplements, Table S2). Polychaetes were the most abundant (46%), followed by molluscs (26%)
312 and crustaceans (18%). The most frequent and abundant species (present in every colony) were the
313 bivalves *Rocellaria dubia*, and *Hiatella arctica*, the decapod *Athanas nitescens*, the polychaetes
314 *Lysidice ninetta* and *Eunice vittata* and sipunculids. The sampling effort (estimated as total sampled
315 volume - V_{tot}) for the microscale level was appropriate in order to get a representative picture of the
316 entire invertebrate community and of the dominant phyla (molluscs, polychaetes, and crustaceans)
317 considered separately (cumulative curves, supplementary material, Fig. S3).

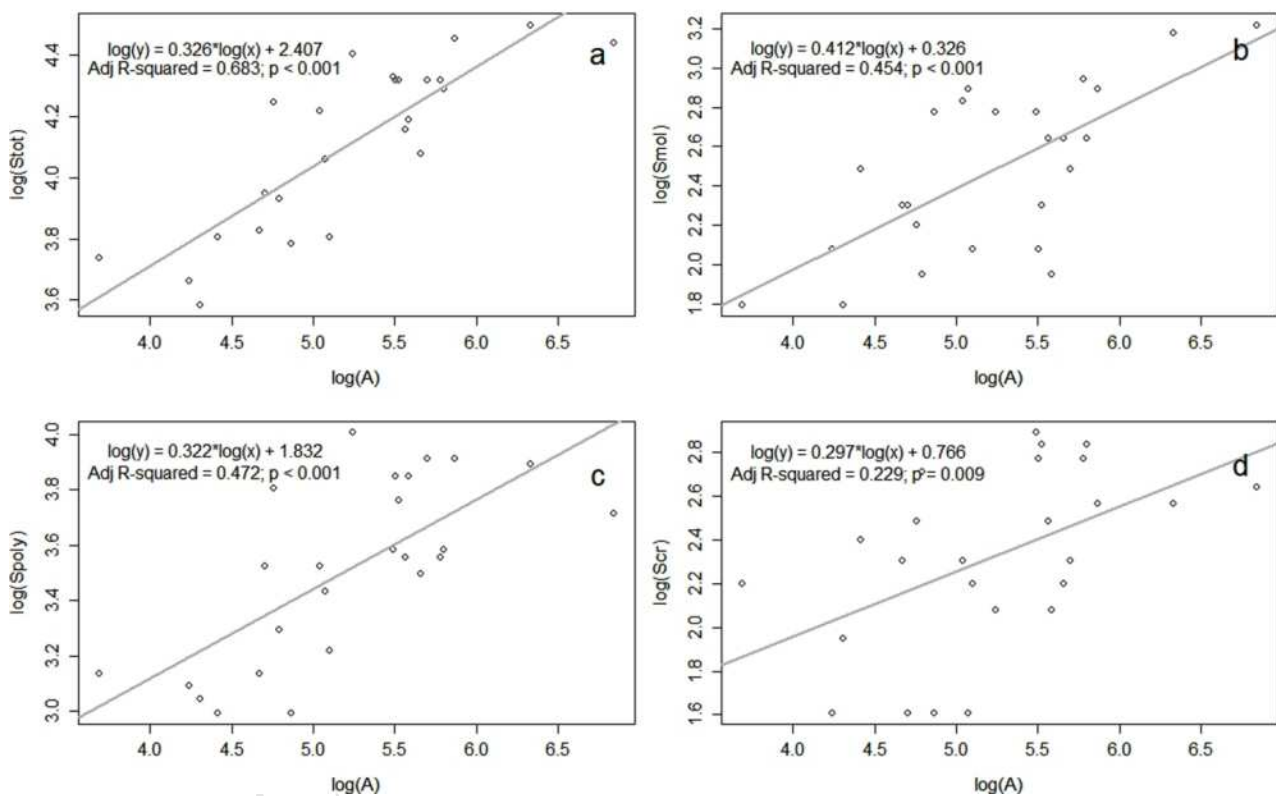
318 Total taxa richness S_{tot} increased with increasing A and the relationship was strong ($r_s = 0.813$; $p <$
319 0.001). This pattern was consistent in all sampled site (Trellis graph, supplementary material, Fig.
320 S4), and all sampling depths (Trellis graph, supplementary material, Fig. S5). The same relationship

321 held for richness of molluscs S_{mol} ($r_s = 0.622$; $p < 0.001$), polychaetes S_{poly} ($r_s = 0.711$; $p < 0.001$)
 322 and crustaceans S_{cr} ($r_s = 0.519$; $p < 0.01$) considered separately (Fig. 3).

323

324

325 **Fig. 3** Linear regressions between the area covered (A) by colonies of *C. caespitosa* in cm^2 and: (a)
 326 the total number of non-colonial invertebrates (S_{tot}), (b) total number of molluscs (S_{mol}), (c) total
 327 number of polychaetes (S_{poly}), (d) total number of crustaceans (S_{cr}). All axes are log-transformed.
 328 Dots = sampled colonies.



329

330

331 The best model describing how S_{tot} increased with A was a linear regression on log-transformed
 332 variables, following Arrhenius model. AIC values for the comparison among the most frequently
 333 used non-linear models (Arrhenius, Gleason, Gitay, and Lomolino) are shown in Table 2. Colony
 334 size (A) exerted a major influence on total invertebrate richness (S_{tot}) (regression in Fig. 3a explains
 335 about 68% of the relation between S and A). The efficiency of the model in predicting S_{tot} slightly

336 improved using total colony volume (V_{tot}) instead of area covered (A) as colony size descriptor and
 337 the same was observed considering only richness of polychaetes S_{poly} (AIC values, Table 2).

338

339 **Table 2** AIC values, and adjusted R-square ($Adj R^2$) for models comparison

Model	Variables	df	AIC	Adj R^2
Arrhenius	S_{tot} and A	3	187.5	
Gleason	S_{tot} and A	3	185.3	
Gitay	S_{tot} and A	3	186.0	
Lomolino	S_{tot} and A	3	186.2	
log-log linear regression	S_{tot} and A	3	-18.5	0.7
log-log linear regression	S_{tot} and V_{tot}	3	-19.9	0.7
log-log linear regression	S_{mol} and A	3	16.2	0.5
log-log linear regression	S_{mol} and V_{tot}	3	16.8	0.4
log-log linear regression	S_{poly} and A	3	2.3	0.5
log-log linear regression	S_{poly} and V_{tot}	3	0.3	0.5
log-log linear regression	S_{cr} and A	3	23.7	0.2
log-log linear regression	S_{cr} and V_{tot}	3	24.2	0.2

340

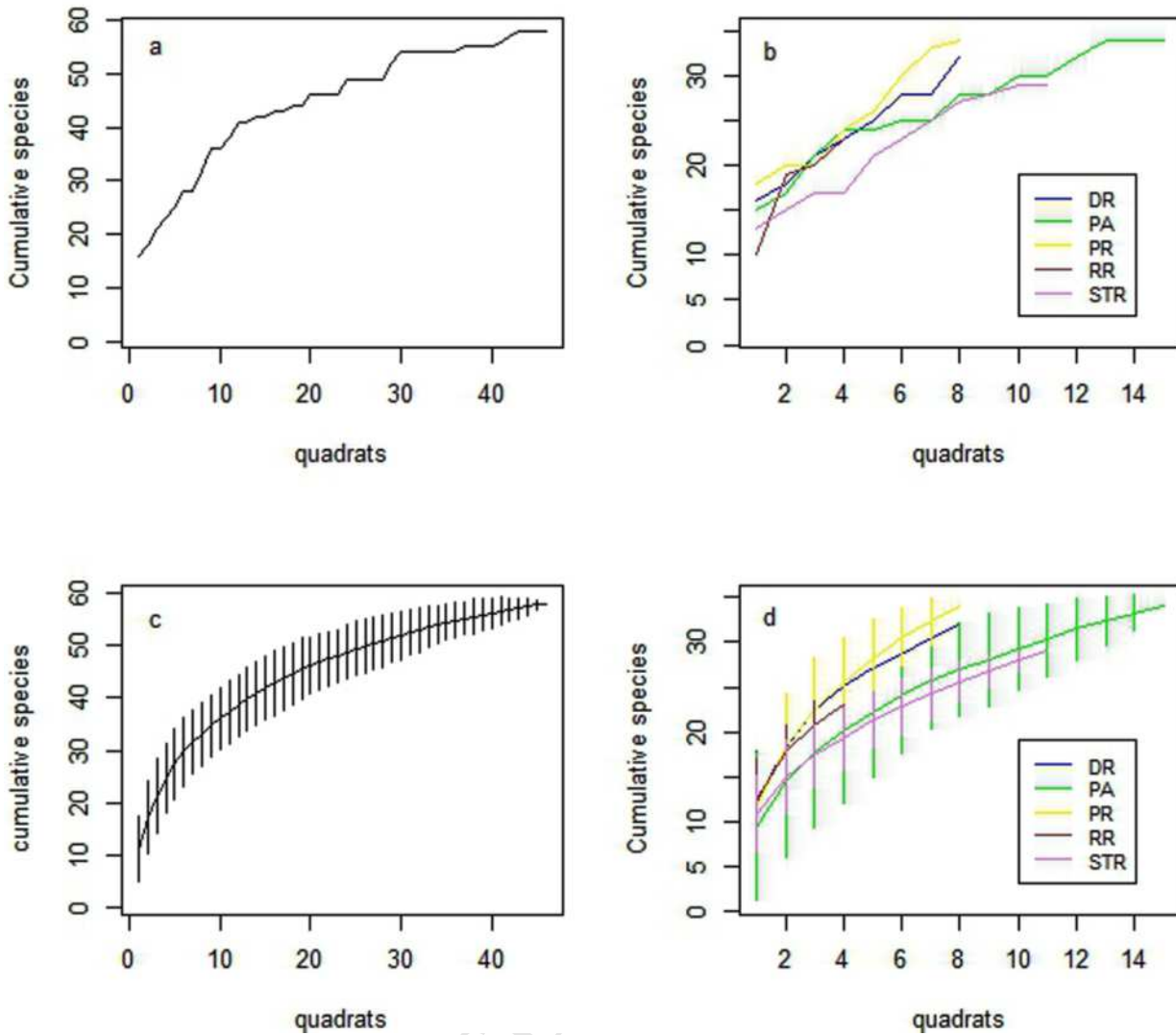
341 3.2. “Mesoscale” level

342 Colony size (A , $KW = 24.442$, $p < 0.001$), percentage of living polyps (LP , $KW = 16.285$, $p =$
 343 0.003), colony density (CC , $KW = 18.027$, $p = 0.001$), and total coral coverage (A_{cov} , $KW = 25.117$,
 344 $p < 0.001$), varied among the studied sites. The biggest colonies (A) were observed at site PR (941.1
 345 ± 370.8 SD cm^2), and the smallest at DR (216.5 ± 164.6 SD cm^2), the highest values of LP at site
 346 DR ($71 \pm 11\%$) and the lowest at site PA ($48 \pm 32\%$). The highest densities (CC) were observed at
 347 sites PA (7.1 ± 2.8 SD colony/ m^2) and PR (6.4 ± 3 SD colony/ m^2), the lowest at site STR (3.6 ± 1.3
 348 SD colony/ m^2); the highest total coral coverage (A_{cov}) was observed at site PR ($18.8 \pm 7.4\%$) and
 349 PA ($13.6 \pm 6.9\%$), the lowest at site DR ($4.3 \pm 3.2\%$) and STR ($5.3 \pm 3.3\%$). CC was positively
 350 correlated with sampling depth ($r_s = 0.586$, $p < 0.001$). Conversely, LP was not correlated with CC
 351 ($r_s = -0.217$, $p = 0.147$) nor with depth ($r_s = -0.278$, $p = 0.061$). No significant relationship was
 352 observed between the observed epibenthic megafaunal species richness (S_{obs}) and CC ($r_s = -0.087$,
 353 $p = 0.567$), LP ($r_s = 0.268$, $p = 0.07516$), nor total coral coverage (A_{cov} , $r_s = -0.068$, $p = 0.659$).

354 With underwater visual counting a total of 61 different taxa were found: 23 molluscs, 11 sponges, 4
355 echinoderms, 4 cnidarians, 3 polychaetes, 3 crustaceans, 3 tunicates, 2 bryozoans. A total of 6764
356 invertebrates and 1 fish were counted and 48 taxa were determined to the species level. Molluscs
357 were the most diversified (47 %) and abundant (79 %) taxa, followed by sponges (19 % of taxa and
358 16 % of abundance). With the photographic technique additional three species of invertebrates and
359 four of fish were observed, for a total of 55 different species. With the use of this technique,
360 molluscs and sponges were confirmed as the richest groups. Species accumulation curves for
361 epibenthic megafauna recorded with the underwater visual counting (Fig. 4) have horizontal
362 asymptotes when all collected samples were used, but not when a curve was drawn for each
363 sampling site. This suggested that more samples were needed to get a representative picture of each
364 site, and thus enabling a comparison.

365

366 **Fig. 4** Cumulative curves for benthic invertebrates at mesoscale level according to the original
367 sequence of recording (a, b) and from random order of quadrats, (c, d), for the entire dataset (a, c)
368 and for each site separately (b, d). Data were recorded in situ with underwater visual counting.
369 Vertical lines = SD.



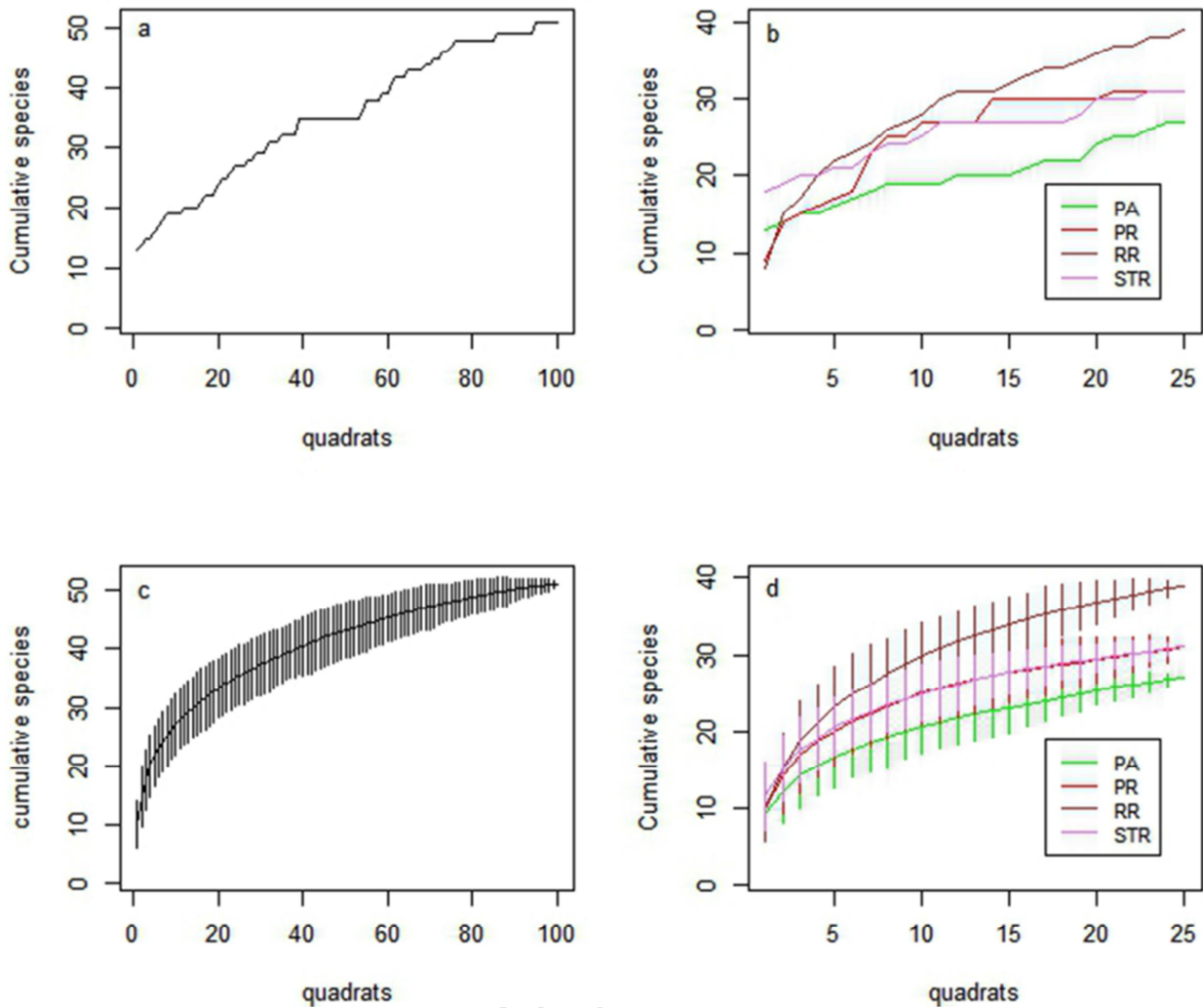
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374 **Fig. 5** Cumulative curves for benthic invertebrates at mesoscale level according to the original
 375 sequence of recording (a, b) and from random order of quadrats (c, d), for the entire dataset (a, c)
 376 and for each site separately (b, d). Data were obtained from photographs. Vertical lines = SD.



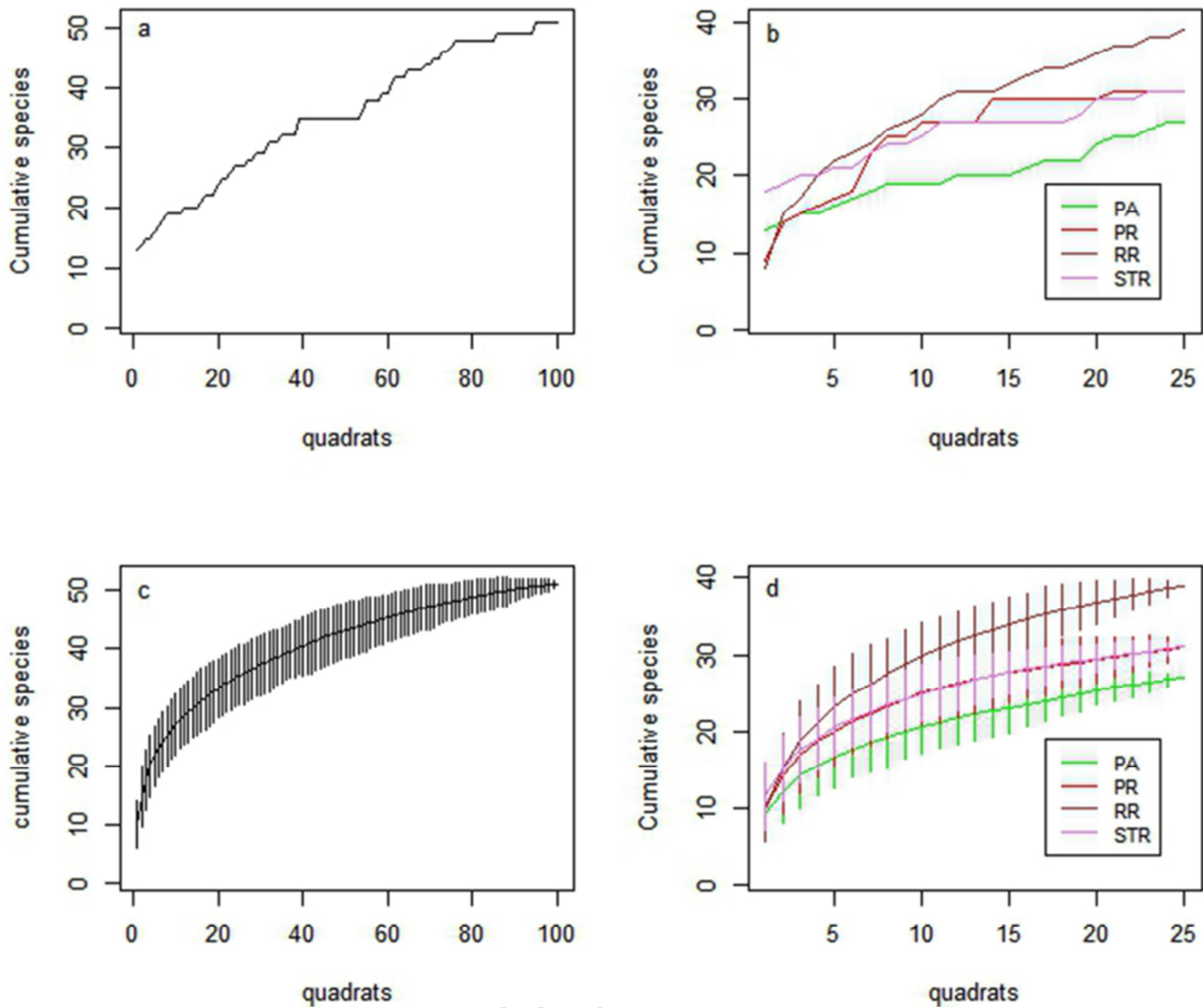
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378

379 Species accumulation curves for epibenthic megafauna recorded with the photographic technique
 380 (Fig. 5) instead were long enough to enable discrimination between sites: site RR showed the
 381 highest richness (> 40 taxa) compared with other sites (< 30 taxa).

382

383 **Fig. 5** Cumulative curves for benthic invertebrates at mesoscale level according to the original
 384 sequence of recording (a, b) and from random order of quadrats (c, d), for the entire dataset (a, c)
 385 and for each site separately (b, d). Data were obtained from photographs. Vertical lines = SD.



386

387

388 The two methods gave also different results in terms of estimation of species richness. Using data
 389 obtained with underwater counting with extrapolation techniques we obtained an expected total
 390 number of taxa ranging from 64 to 71, according to the different functions used (Table 3). From
 391 calculation based on photographic technique lower values were obtained, with total richness
 392 ranging from 56 to 62. The two different sampling techniques gave markedly different results also
 393 in terms of comparison of extrapolated taxa richness for each sampling site. Extrapolation from data
 394 obtained with underwater counting (Table 3) showed site RR as the poorest in terms of species
 395 richness, with $S_{obs}=23$, whereas using data obtained with photographic technique site RR resulted
 396 the richest with $S_{obs}=39$ (Table 3).

397

398 **Table 3** Estimates (\pm SE) of macrobenthic species richness for each site and for the whole area
 399 using different functions, with underwater counting (visual) and photographic technique (photo).
 400 DR =Debeli Rtič, PA = Pacug, PR = Piranček, RR = Cape Ronek, STR = Cape Strunjan, S_{obs} =
 401 observed number of taxa; chao = Chao bias-corrected function, jack1 = first order jackknife, boot =
 402 bootstrap, n = number of samples.

Site	method	S_{obs}	chao	jack1	boot	n
DR	visual	32	53 \pm 18	43 \pm 5	37 \pm 3	8
PA	visual	34	60 \pm 22	46 \pm 5	39 \pm 3	15
PA	photo	27	37 \pm 10	35 \pm 3	30 \pm 2	25
PR	visual	34	48 \pm 10	46 \pm 6	39 \pm 3	8
PR	photo	31	43 \pm 13	38 \pm 3	34 \pm 2	25
RR	visual	23	31 \pm 7	30 \pm 4	26 \pm 2	4
RR	photo	39	45 \pm 5	48 \pm 3	43 \pm 2	25
STR	visual	29	62 \pm 30	40 \pm 4	34 \pm 2	11
STR	photo	31	43 \pm 13	38 \pm 3	34 \pm 1	25
Total	visual	58	66 \pm 6	71 \pm 4	64 \pm 2	46
Total	photo	51	58 \pm 6	62 \pm 4	56 \pm 2	100

403
 404 The comparison between the two techniques showed that despite the bigger number of samples
 405 analysed, the total number of taxa identified with the photographic technique was lower than the
 406 one obtained with the underwater method (45 against 61 taxa) and this difference increase
 407 considering only lower taxonomical levels, such genus (31 against 50 genera) or species (26 against
 408 48 species). Considering all species recorded for mesoscale level, 46% of them were recorded with
 409 both methods, 48% with underwater counting and 6% only with photo analysis. Forty % of species
 410 recorded with underwater counting were recorded also at level of microscale.

411

412 3.3. “Macroscale” level

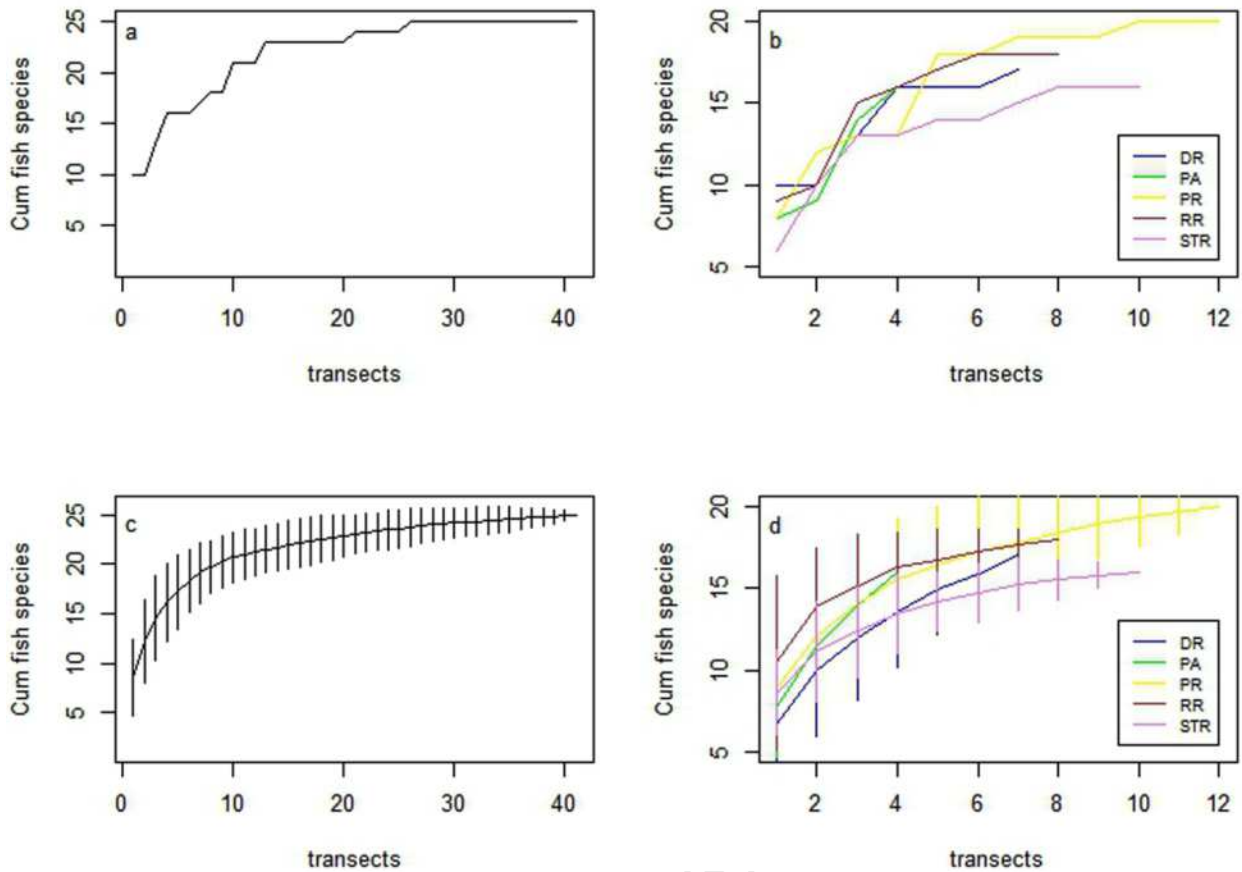
413 The density of colonies of *C. caespitosa* varied among sampling sites (KW = 32.1, $p < 0.001$).
 414 Considering all colonies from all sampling sites a relation between colony density and sampling
 415 depth ($r_s = 0.311$, $p = 0.020$) was observed. The highest density of coral colonies was observed at
 416 the deepest site PR (210 ± 51 colonies/100 m²), while the lowest was observed in more shallow

417 waters at sites DR (55 ± 35 colonies/100 m²), and STR (80 ± 25 colonies/100 m²). Fish richness
418 was not correlated with number of coral colonies ($r_s = 0.188$, $p = 0.170$), but there was a weak
419 increase of fish abundances with increasing density of colonies ($r_s = 0.359$, $p = 0.007$), mainly due
420 to abundances of *Gobius cruentatus* ($r_s = 0.552$, $p = 0.00001$), *Symphodus cinereus* ($r_s = 0.458$, $p =$
421 0.0004), and *Parablennius rouxi* ($r_s = 0.264$, $p = 0.05$).

422 A total of 1383 fish specimens were counted and 25 different species were identified
423 (Supplementary material, Table S2), among them only 8 were recorded at all sampling sites. The
424 most frequent species were *Serranus scriba*, *G. cruentatus*, *Chromis chromis*, *Diplodus vulgaris*,
425 *Serranus hepatus*, *S. cinereus*, *P. rouxi* and *Symphodus tinca*.

426 Results of fish counting did not differed significantly between the two successive passages on the
427 same transect, nor between each passage and the mean value of the two (WMW test, $p > 0.05$),
428 confirming that diver disturbance had no significant effect on species counts. Species accumulation
429 curves showed that the total number of transects performed was enough to get a representative
430 picture of fish richness of the study area (Fig. 6a, c). Comparing species accumulation curves for
431 each sampling site (Fig. 6b,d), we saw that the equilibrium was reached for a lower number of
432 species at site STR and RR, compared with site PR. At sites PA and DR the cumulative species
433 curve did not reach an asymptote, but the shape of cumulative curves indicate that species richness
434 at these sites should be higher than at STR. Expected fish richness differed significantly only
435 between sites RR and STR (WMW test, $p < 0.05$), with richness at STR lower than at RR.
436 Estimations using different extrapolation functions gave the same results (Table 4).

437
438 **Fig. 6** Species accumulation curves for fish species found at all sites (a, c) and at each site
439 separately (b, d), with transects in order of occurrence (a, b) and in random order (c, d). Each
440 transect is weighted according to its length. Vertical lines = SD.



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Table 4 Estimates (\pm SE) of fish richness for each site and for the whole area using different
449 functions. DR = Debeli Rtič, PA = Pacug, PR Piranček, RR = Cape Ronek, STR = Cape Strunjan,
450 S_{obs} = observed number of species; chao = Chao bias-corrected function, jack1 = first order
451 jackknife, boot = bootstrap, n = number of samples.

Site	S_{obs}	chao	jack1	boot	n
DR	17	24 \pm 7	23 \pm 3	20 \pm 2	7
PA	16	22 \pm 6	22 \pm 3	19 \pm 2	4
PR	20	24 \pm 5	24 \pm 2	22 \pm 2	12
RR	18	22 \pm 6	21 \pm 2	19 \pm 1	8
STR	16	17 \pm 1	18 \pm 1	17 \pm 1	10
Total	25	29 \pm 7	28 \pm 2	26 \pm 1	41

452

4. DISCUSSION

Climate change, in synergy with other anthropogenic pressures, is leading to a decline of populations of *C. caespitosa* across the Mediterranean (Casado de Amezua et al. 2015). Given its role of habitat builder its fate is strictly connected to the fate of its associated fauna, but knowledge on those relationships are still scant and fragmented (e.g. Koukouras et al. 1998, Pitacco et al. 2014). The present work provides the first investigation focused extensively on biodiversity associated with *C. caespitosa* at different levels. It's a pioneer work filling some gaps in basic knowledge and testing promising methods, that could be used to estimate the potential ecological effects of the loss of this coral also in other areas of the Mediterranean.

4.1. Macrobenthic invertebrates strictly associated with coral colony

Invertebrate community living inside coral colonies of *Cladocora caespitosa* was dominated by polychaetes, which is consistent with previous investigations on associated fauna in northern Adriatic (Pitacco et al. 2014) and other areas of the Mediterranean Sea (Lumare 1965, Koukouras et al. 1998). Their success was probably due to their higher level of differentiation with regards to feeding modes and motility compared with other taxonomic groups such as crustaceans, enabling them to colonize all different niches provided by coral colony. In tropical scleractinian corals some studies reported arthropods as the most frequent, abundant and rich group (Abele and Patton 1976, Garcia et al. 2008, Stella et al. 2011), whereas other studies found Polychaeta to be the richest group (Cantera et al. 2003). While a certain amount of information on arthropods associated with tropical corals is available, only few studies targeted polychaetes (140 papers for arthropods and only 10 for polychaetes, reviewed by Stella et al. 2011), and this could result in a general underestimation of the richness of associated tropical polychaetes.

In the present work some uncommon species were found, together with animals whose taxonomic position is still under debate. In particular, among mollusc species the presence of the alien mytilid *Brachidontes pharaonis* deserves particular attention, as it constitutes the first record of this taxon from Slovenia and the third confirmed from the Adriatic Sea (Lipej et al. 2017). Among

479 polychaetes the flabelligerid *Flabelligerina cinari* was recorded for the first time outside its *locus*
480 *typicus* in Turkish waters (Karhan et al. 2012). All reported species associated with *C. caespitosa*
481 (Koukouras et al. 1998, Pitacco et al. 2014, present work) have also been found in other habitats,
482 mainly hard substrate, so by now there are no evidences of obligatory relationships. The same
483 observation was made for species associated with another temperate coral *Oculina arbuscula* by
484 McCloskey (1970), whereas, obligatory relationships are quite common in tropics, involving mainly
485 decapod crustaceans (e.g. Castro 1978, Coles 1980).

486 The number of associated invertebrate taxa increases with *C. caespitosa* colony size (A),
487 confirming the Arrhenius (1921) model as the best SAR model. We can reasonably say that the
488 relationship between area (A) and species richness (S_{tot}) was independent from factors such as
489 sampling site and depth. Nevertheless, given the limited spatial scale and depth range of the present
490 work and the wide range of depth and habitats inhabited by *C. caespitosa*, additional investigation
491 in other areas of the Mediterranean are required to generalise. For dominant groups (polychaetes,
492 molluscs and crustaceans) considered separately there was also an increase of richness with
493 increasing colony size, so the SAR holds also for the single dominant phyla. Colony size, in terms
494 of surface covered by each colony (A), resulted therefore as a good predictor of species richness
495 (S_{tot}). A significant SAR according to Arrhenius (1921) model was found also for decapod
496 crustaceans associated with the tropical coral *Pocillopoda damicornis* by Abele and Patton (1976),
497 but their calculation of expected species number, based on number of individuals for different coral
498 size, lead to a significant overestimation. A positive relationship between colony size and associated
499 species richness was observed also by other authors for temperate and tropical corals (Koukouras et
500 al. 1998, Garcia et al. 2008). In most of those studies total colony volume (e.g. Abele & Patton
501 1976, Koukouras et al. 1998, Garcia et al. 2008, Belmaker 2009) and weight (e.g. Reed and
502 Mikkelsen 1987) were generally considered to offer the most appropriate parameters to estimate
503 coral size. Also in the present work, total colony volume (V_{tot}) resulted to be a better predictor and
504 slightly improved the model. This was due to the fact that the surface covered by colonies did not

505 represent the real surface available for macroinvertebrates to settle, which increased with the
506 complexity of the colony. This fact affects in particular molluscs, because they are mainly sessile
507 and endolithic, and to a lesser extent polychaetes, because even if they are mainly free living
508 (vagile), they are represented also by a consistent number of sessile and endolithic species. For
509 those groups a species-volume relation (SVR, *sensu* Belmaker 2009) could be more predictive for
510 species richness. Nevertheless, the strict correlation between total colony volume and the area
511 covered by colonies, suggested that both parameters could be used as colony size descriptor, and the
512 use of area covered by colonies resulted the best option, being a less destructive and less time
513 consuming measure.

514 Most of works based on SAR models were performed at larger scales (squared metres to squared
515 kilometers), also in marine environment (Smith and Witman 1999, Levin et al. 2009, Guilhaumon et
516 al. 2012), and very few papers investigated the relationship between area and species richness in
517 other marine habitats, such as boulders (McGuinness 1984), mussel beds (Witman 1985), and
518 artificial settling plates (Anderson 1999). Our results supported the applicability of SAR also at a
519 spatial scale of squared centimetres.

520 **4.2. Epibenthic megafaunal community associated with beds of *C. caespitosa***

521 The present work confirmed that the analysed beds of *C. caespitosa* are located in a transition zone
522 between infralittoral communities, with the presence of molluscs such as *Thylacodes arenarius* and
523 *Columbella rustica*, characteristic of the biocoenosis of Photophilic Algae (AP, Pérès and Picard
524 1964), and circalittoral communities, for the presence of coralline algae of genera *Lithophyllum* and
525 *Lithothamnion* (*personal observations*), characteristic of the biocoenosis of Coastal Detritic (DC,
526 Pérès and Picard 1964). Also macroalgal species observed were typical of both photophilic algal
527 assemblages (*Padina pavonica* and *Dictyota dichotoma*; Giaccone et al. 1994) and sciaphilic algal
528 assemblages (*Peyssonellia* spp., and *Halimeda tuna*; Giaccone et al. 1994, pre-coralligenous, *sensu*
529 Pérès and Picard 1964), but they showed low coverage and poorly developed thalli where coral beds
530 occur (*personal observations*). Such a composition differed from the biogenic formation of Cape

531 Ronek, located close to the studied sites (STR site) and hosting the highest density of living coral
532 colonies of the Slovenian area (up to 652 colonies/100m², mostly with maximum axis < 15 cm;
533 Lipej et al. 2016). On this formation the epibenthic community was also dominated by species
534 typical of the infralittoral belt (e.g. the sponge *Aplysina aerophoba* and coralline algae) but even
535 more by species typical of other habitats, such as the sponge *Geodia cydonium*, the sea cucumber
536 *Holoturia tubulosa*, the brittle star *Ophioderma longicauda*, and the sea urchins *Sphaerechinus*
537 *granularis* (Lipej et al. 2016) and *Psammechinus microtuberculatus* (Pitacco et al. 2014). To date
538 there is a lack of information on the composition of epibenthic communities of *C. caespitosa* beds
539 in other areas of the Mediterranean Sea, but since *C. caespitosa* is a species thriving along a wide
540 range of habitats and depth (Peirano et al. 1994, Kersting et al. 2017), the composition of
541 macrobenthic community associated with coral beds and banks is likely highly variable.

542 At level of mesoscale, observed epibenthic megafaunal species richness (S_{obs}) was not directly
543 related to colony density (CC), nor with total coral coverage (A_{cov}), therefore estimates of species
544 richness could not be based on colony presence or sizes. This could be due to the fact that, even if
545 average colony density was high, the total coral coverage was not, therefore *C. caespitosa* was not
546 the dominant species, as observed in other areas of the Mediterranean, where this species creates
547 banks (e.g. Mljet bank, Kružić and Benković 2008) or high concentrations of big colonies and
548 microreefs with high coral cover (Kersting & Linares 2012). Differences among sites were mainly
549 related to different abundance of the dominant species and presence of rare or occasional species.
550 Consequently, the variation of species richness was mainly related to the records of occasional and
551 uncommon species with increasing sampled area. The incidence-based estimates calculated are
552 popular ways of estimating the number of unseen rare species and are based on the frequencies of
553 rare species in a collection of sites. Adding this number to the observed number of species we
554 obtain a better estimation of species richness (Oksanen et al. 2015), and consequently a better
555 prediction of species loss in case of habitat degradation. Our results confirmed frequency-based

556 estimates on sampled areas as a suitable tool for species estimate for the mesoscale level, when
557 sampling effort is appropriate.

558 **4.3. Ichthyofauna in areas with beds of *C. caespitosa***

559 The Northern Adriatic ichthyofauna has lower species richness than other Adriatic areas (Orlando-
560 Bonaca and Lipej 2005). The number of species found within the present work showed that fish
561 assemblages associated with *C. caespitosa* beds are in accordance with average fish richness of
562 infralittoral habitats in the Gulf of Trieste (Orlando-Bonaca and Lipej 2005). As already observed at
563 the level of mesoscale, also at level of macroscale, there were no direct relations between fish
564 richness and colony density, and estimates of fish richness could not be based on colony sizes.
565 Previous results obtained from the very sampled area (Zunino et al. 2018) confirmed a generally
566 low total coral coverage, with a maximum of 49% at site PR and a minimum value of 6% at site
567 DR. High species number and density of fish are known to be related to high substratum complexity
568 (*i.e.* habitat heterogeneity), such as rocks and boulders opposed to sand or gravel (Macpherson
569 1994, Gratwicke and Speight 2005), providing more shelter for adults and recruits (Guidetti 2000,
570 Cheminée et al. 2016) as well as more nesting sites for spawning (Lipej et al. 2009). Similarly,
571 Balasubramanian and Foster (2007) identify an increase of habitat heterogeneity as an important
572 factor explaining the increase in species relative to space. Their study evidenced that species
573 richness of coral reef fishes in water of Santiago de Cuba is positively related to space (area and
574 volume) in all studied sites. Previously, Chittaro (2002) stated the importance of microhabitat
575 richness in increasing the coral fish species richness. Compared with other infralittoral habitat types
576 in the Gulf of Trieste, our results showed lower richness compared with highly structured habitat
577 types, such as *Cystoseira* algal belts (31 species) and higher richness compared with more
578 homogenous habitats, such as seagrass meadow (9 species) (Orlando-Bonaca and Lipej 2005). Fish
579 species recorded are all nektonic and epibenthic with the exception of *Chromis chromis*, which
580 is nektonic and diurnal planktivore (Bell and Harmelin-Vivien 1983). The most frequent and
581 abundant species (*Serranus scriba*, *Gobius cruentatus*, *Diplodus vulgaris*, *Serranus hepatus*,

582 *Symphodus cinereus*, *Parablennius rouxi* and *Symphodus tinca*) are considered resident species.
583 They are strictly related to the substrate, since their main source of food are benthic
584 macroinvertebrates. Only the density of *G. cruentatus*, *S. cinereus*, and *P. rouxi* showed a
585 correlation with the density of colonies of *C. caespitosa*. Colonies of *C. caespitosa*, with their
586 physical structure provide shelter for blennies and gobies, in fact both *P. rouxi*, and the less frequent
587 *Parablennius gattorugine* were observed to hide within colonies. *S. scribea*, *C. chromis* and *P. rouxi*,
588 are usually associated with rocky unvegetated areas or with short vegetation, and were already
589 recorded in the lower part of the infralittoral belt at the same depth range of the present work (4-10
590 m; Orlando-Bonaca and Lipej 2005). Such a habitat was not suitable for most species of labrids,
591 strictly associated with vegetated areas. *Symphodus cinereus*, was the only labrid that could be
592 considered resident and associated with *C. caespitosa*, while the wrasse *Symphodus roissali*, strictly
593 related to complex algal canopies in shallow depth, such as *Cystoseira* and *Halopithys* algal belts
594 (Orlando-Bonaca et al. 2008), was found only at one site (PR) between 5 and 6 m depth. The
595 occasional presence of species like *Pomatoschistus bathi* and *Gobius fallax*, was due to the ability
596 of *C. caespitosa* to settle also on debris, colonizing areas covered by sediment and gravel
597 (Zibrowius 1980), which is the habitat preferred by this two species (Lipej et al. 2005; Orlando-
598 Bonaca and Lipej 2005).

599 Also for the macroscale level, considering only the most frequent and abundant species,
600 assemblages were quite homogeneous among sampling sites, and depth, varying only for species
601 abundance. Consequently, variation of species richness with increasing sampled area was mainly
602 related to the records of occasional and uncommon species, confirming frequency-based estimates
603 on sampled area as a suitable tool for species estimate, and prediction of species loss in response to
604 habitat degradation.

605 **4.4. Comparison of diversity and methodology at the different levels**

606 The present work confirmed the important role of *C. caespitosa* as a habitat builder. In total about
607 300 taxa were recorded, counting for about 1/7 of the almost 2000 species known (Turk and Lipej

2002) for the study area (i.e. the Slovenian part of the Gulf of Trieste). At the same time our results showed how the importance of this coral depends on the strength of the associations between the coral itself and the focal associated taxonomic group. The relationship between the coral and the associated fauna was stronger at the level of microscale and weaker at the level of macroscale. The major component of biodiversity (almost 80%) recorded in the present work was detected at the microscale level (Table 5), which represented the most time-consuming and destructive part of the work (Table 6).

615

Table 5 Total number of taxa and individuals counted in the present work. For colonial organisms a colony was counted as one individual. * = colonial organisms excluded.

	Number of taxa	Abundance
Microscale	222	11561*
Mesoscale photo	46	/
Mesoscale visual	61	6765
Total mesoscale	71	/
Macroscale	25	1383
Total	290	19709

618

The finding of rare and very poorly known species among the invertebrates associated with *C. caespitosa* at this level showed how the present knowledge is still limited and how the loss of this precious habitat builder could negatively affect certain species before they are fully known or even yet discovered. Also results obtained at the mesoscale level showed that beds of *C. caespitosa* in the studied area host rich and diversified communities of invertebrates. Nevertheless, the number of taxa recorded with the visual technique represented only the 21 % of total taxa found with the present work, and the number of taxa recorded with the photographic technique only 16 %, and not direct relationship was found between species richness and coral colony. This underestimation of total invertebrate diversity at this level was mostly due to the methodology. With fast and non-destructive methods only larger epibenthic animals detectable with SCUBA-diving and from

629 pictures (megafauna), were considered, overlooking the smallest cryptic ones, hidden among rocks
 630 and algae, such as polychaetes.

631

632 **Table 6** Comparison of methods applied at different scales. ¹ = hours spent underwater; ² =
 633 dimension of sampling units; ³ = total surface analysed; ⁴ = % of taxa determined till the level of
 634 species. x = few hours, xx = few days, xxx = many days, xxxxx = many months.

	Microscale	Mesoscale photo	Mesoscale visual	Macroscale
Sampling unit	Colony (cm ²)	Quadrat (m ²)	Quadrat (m ²)	Transect (m)
Time for sampling ¹	x	xx	xxx	xx
Time for sample/data processing	xxxxx	xxx	x	x
Number of sampled units	25	100	45	51
Sampling grain ²	0.01 to 0.09 m ²	0.25/1 m ²	0.25/1 m ²	60/100 m ²
Sampling extent ³	0.588 m ²	100 m ²	45 m ²	4804 m ²
Accuracy of determination ⁴	80%	59%	79%	100%
Repeatability	no	yes	no	no

635

636 At the level of macroscale, richness of fish associated with *C. caespitosa* beds represent 1/10 of the
 637 259 fish species recorded in the Gulf of Trieste, 1/7 of the 184 species recorded in Slovenian waters
 638 (Marčeta 1999) and 1/17 of the 440 species recorded for Adriatic Sea (Lipej and Dulčić 2010).
 639 Nevertheless, those species represent only 8 % of total taxa richness recorded in the present work,
 640 and a direct relationship with colonies of *C. caespitosa* was observed only for few species, those for
 641 which coral physical structures provide shelter.

642 At level of microscale there was a direct relationship between species richness and colony size, so
 643 estimates based on the SAR could be suitable methods to estimate species richness strictly
 644 associated with corals in a non-destructive way. The largest colony found along the Slovenian coast
 645 so far (Zunino et al. 2018) had 68 cm of length (estimated volume = 19369 cm³). The prediction
 646 based on calculated regressions, using the covered surface (A) as size descriptor, suggests that such
 647 a colony may host a total of 130 taxa (95% confidence intervals: 105-162), among them 39 taxa of
 648 molluscs (95% confidence intervals: 29-53) and 61 (95% confidence intervals: 43-85) taxa of

649 polychaetes. The poor fit of species/area regression for crustaceans, leave a certain bias on eventual
650 estimates of crustacean richness. Although such extrapolations should be treated with caution,
651 especially since colonies larger than 50 cm are rather rare in the studied area (Schiller 1993, Kružić
652 et al. 2014, Zunino et al. 2018) our results supported the suitability of SAR to predict species
653 extirpation resulting from the loss of coral colonies, bed or banks. Communities living inside
654 colonies of *C. caespitosa* did not varied among sites. Given the limited differences among sites in
655 the study area, estimates based on SAR are consistent for all sites analysed and can be reasonably
656 extended to other similar sites along the Slovenian coast. The habitat and depth range in which this
657 coral lives is likely to influence the composition of its associated macrofauna, and this could be an
658 interesting focus for future investigations. In the Aegean Sea Koukouras et al. (1998) found
659 differences between macroinvertebrates associated with *C. caespitosa* inhabiting at different depths
660 (3-5 vs 15-19 m), surrounded by different assemblages (photophilic algal assemblage vs biogenic
661 bank surrounded by gravel and sand). In the same areas, notwithstanding compositional
662 differences, a positive relationship between *C. caespitosa* colony volume and number of associated
663 polychaetes was observed (Arvanitidis and Koukouras 1994), supporting the possible extension of
664 the application of SAR models to other Mediterranean areas. Additional studies are needed in order
665 to refine those estimates and to extend them to *C. caespitosa* colonies in other habitats and areas of
666 the Mediterranean Sea.

667

668 At level of meso- and macroscale the stable components of fish and invertebrate assemblages
669 associated with beds of *C. caespitosa* have specific characteristics compared with surrounding
670 infra- and circalittoral assemblages, despite slight differences among sites. Given the structure of
671 epibenthic megafauna and fish community, frequency-based estimates were suitable to estimate
672 species richness based on sampling area at both meso- and macroscale level. Differently from the
673 microscale level, at level of meso- and macroscale colonies species richness was not correlated with
674 size nor density of *C. caespitosa*. Comparison with other habitat types suggested that species

675 richness at those levels likely responded to habitat heterogeneity, related not only to the presence of
676 colonies of *C. caespitosa*, but also to the different typology of substrate and the presence of other
677 benthic species, such as sponges and seaweeds. Therefore, colony density and coverage were not
678 suitable predictors of species richness at meso- and macroscale levels. Habitat degradation and loss
679 is considered as one among the most important drivers responsible for species extinctions (Schipper
680 et al. 2008). Consequently, the frequency-based estimates calculated on sampled area could be
681 suitable for the prediction of reducing diversity related to loss of areas with high colony density, but
682 did not allow to disentangle the effect of the loss of coral itself from other factors increasing habitat
683 heterogeneity at the study site.

684

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700

701 **Conflict of interest statement**

702 On behalf of all authors, the corresponding author states that there is no actual or potential conflict
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704

ACCEPTED MANUSCRIPT

705

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Highlights

- *Cladocora caespitosa* is an important habitat builder
- Quantification of its importance varied according to investigation scale, method and target
- Colony size: good predictor of associated taxa richness with Arrhenius model
- Sampled area: good predictor for fish and epibenthic megafauna richness
- Epibenthic megafauna and fish richness is no related with colony density or coverage