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Coralligenous assemblages along their geographical distribution: Testing of concepts and implications for management

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Abstract

1. The coralligenous habitat was studied at the large Mediterranean scale, by applying a standardized, non-destructive photo-sampling protocol, developed in the framework of the CIGESMED project.

2. The results provided evidence to support the following statements: (a) the assem-blage pattern is not homogeneously distributed across the four Mediterranean ecoregions studied (*biotic gradients hypothesis*); and (b) the assemblage pattern does not change significantly when the information is aggregated to higher taxonomic levels (*taxonomic sufficiency hypothesis*).

3. Surrogate taxonomic categories higher than species, such as genus and family, can be used to reveal the multivariate pattern of the coralligenous assemblages.

4. Although preliminary at the pan-Mediterranean scale, these outcomes set the scene for future comparisons as more data sets become available but also for comparisons between taxonomic and functional patterns.

KEYWORDS

algae, benthos, biodiversity, biogeography, circalittoral, coastal, habitat management, invertebrates, reef

1 | INTRODUCTION

Coralligenous habitat is a calcareous formation, primarily composed by long-lived encrusting red algae and, secondarily, by sessile invertebrates growing on submerged reefs under dim light conditions; it is considered as an endemic, protected Mediterranean habitat (Ballesteros, 2006). Although prevailing between 20 and 120 m depth, sometimes large, continuous formations of this habitat occurs in shallow waters under high turbidity (Casellato & Stefanon, 2008). Along with similar formations (bio-concretions), it has contributed to the formation of benthic biogenic structures over geological time, resulting in geomorphological changes of the benthic environment (Bracchi, Basso, Marchese, Corselli, & Savini, 2017). The coralligenous habitat provides a number of microhabitats, in the form of numerous crevices and cavities generated by the overlapping growth of algal thalli and by the bioeroding action of some sponges and bivalves (Ballesteros, 2006). This unique habitat, together with seagrass meadows and marine caves, is acknowledged as a hot-spot of marine biodiversity in the Mediterranean (Boudouresque et al., 2016; Gerovasileiou & Voultsiadou, 2012; Martin & Gattuso, 2009). Under the Habitats Directive (92/43/EU), coralligenous assemblages may be collectively addressed under the generic habitat type Reefs (1170), which, however, lacks priority conservation status. Recognizing its unique ecological importance, as well as the main threats that it has faced during recent decades, coralligenous habitat has been put forward to be assigned as a distinct habitat category and with a priority conservation status by UNEP (1998). More specifically, the mass mortality events frequently experienced in the Mediterranean Sea (Cerrano et al., 2000; Coma et al., 2009) related to global climate change have encouraged decision makers to take some necessary precautions for the protection of this unique habitat. Coralligenous habitat has also been declared as a protected habitat under the Mediterranean Fisheries Regulation (1967/2006), particularly because of its sensitivity to mechanical impact from fisheries, as well as its importance in hosting various life cycle stages of numerous commercial fish and invertebrates. However, so far, the Mediterranean countries have not taken any action on the protection and monitoring of this particular habitat, most probably because: (a) there is only detailed mapping in a few places in the entire basin; and (b) a comprehensive study at the basin scale has not been in place. Apart from its ecological and economic importance, coralligenous habitat hosts many species that have been granted a protected status by numerous international treaties. For example, almost all endangered and threatened species of Porifera, Cnidaria, and Echinodermata listed in Annex II of the Barcelona Convention live in or depend upon coralligenous habitats (UNEP/RAC/SPA, 2018). Moreover, it has been proposed that the structural and functional features of coralligenous habitat (e.g. species composition, functional groups, coverage of builders and bioeroders) should be considered as indicators in assessing the environmental quality of coastal waters and the seafloor integrity according to the Marine Strategy Framework Directive (2008/56/EC) (Cecchi, Gennaro, Piazzi, Ricevuto, & Serena, 2014; Deter, Descamp, Ballesta, Boissery, & Holon, 2012; Gatti et al., 2012; Sartoretto et al., 2017). However, as is often the case in other benthic habitats, coralligenous habitat is under threat from various stressors such as sedimentation (Airoldi, 2003), mechanical damage (e.g. diving and fishing activities, Balata, Piazzi, Cecchi, & Cinelli, 2005; Ferrigno, Appolloni, Russo, & Sandulli, 2018; Garrabou, Sala, Arcas, & Zabala, 1998; Linares et al., 2010), pollution (Hong, 1983), invasions by alien species (Piazzi, Balata, & Cinelli, 2007), and global warming (Cerrano et al., 2000; Coma et al., 2009; Linares et al., 2010). Coralligenous habitat predominantly occurs in the northern part of the Mediterranean, while only a few scattered records exist from the southern coastline and the Levantine Basin, partly because of the hydrographical conditions and partly the uneven sampling efforts in the regions (Martin et al., 2014). Coralligenous habitat appears to be common in the Adriatic, Aegean, and Tyrrhenian Seas, and the Algero-Provencal Basin (Giakoumi et al., 2013). However, detailed mapping is very limited and covers only 30% of the total coastline (Martin et al., 2014). Moreover, few data exist on the ecology and diversity of coralligenous habitat beyond the north-western Mediterranean Basin. This lack of adequate data represents a big challenge for the effective management and conservation of this sensitive and vulnerable habitat (Giakoumi et al., 2013).

Another big challenge for its effective management is the choice of appropriate methods to assess and monitor the environmental status and health of the coralligenous habitat (Piazzi et al., 2019). This is a rather complex issue because: (a) data have to be collected by non-destructive methods, such as imaging and remote sensing, as destructive sampling is not a viable option for this sensitive habitat that hosts many slow-growing and late-successional species, several of which are listed as endangered or protected (Bianchi et al., 2004; RAC/SPA-UNEP/MAP, 2014); and (b) a number of rapid assessment techniques (RATs) need to be tested by as many datasets from all over the Mediterranean Sea as possible in order to decide which of the

above-mentioned methods may provide reliable evidence to serve current research activities and management purposes. The development and application of the RATs has been discussed over recent decades because: (a) the governmental commitments to a number of European and International treaties and conventions (e.g. Marine Strategy Framework Directive, Barcelona Convention); (b) the decreasing funding resources available for environmental status assessment and monitoring; and (c) in most cases environmental managers and decision-makers need this type of biodiversity information very quickly (Féral et al., 2003).

Accordingly, the utility of optimum techniques for rapid biodiversity and environmental status assessment and monitoring has been advocated in a plethora of scientific works regarding the benthic domain (e.g. Arvanitidis et al., 2009; Clarke & Warwick, 2001; Ferraro & Cole, 1995; Olsgard, Somerfield, & Carr, 1998; Somerfield & Clarke, 1995; Vanderklift, Ward, & Jacoby, 1996; Warwick, 1988; Warwick & Clarke, 1998; Warwick & Light, 2001; Warwick, Platt, Clarke, Agard, & Gobin, 1990). Two major scientific concepts have been instrumental to the development of the baseline studies for comparisons and of the development of RATs:

(a) *Biotic gradients* across the Mediterranean and the Black Seas have been identified since the classic review on Mediterranean benthos by Pérès (1967). Such gradients have been observed in both shallow and deep waters (Bellan-Santini, 1985; Fredj & Laubier, 1985) and can be the product of either the biogeography of the biota and associated with certain environmental variables (e.g. salinity and food availability, Arvanitidis et al., 2002; Surugiu et al., 2010) or of anthropogenic disturbance (Sala et al., 2012). They can be detected either in the number of taxa or in the composition of the assemblages they form.
(b) *Taxonomic sufficiency* concept: it has been frequently assumed that the taxonomic level required to meet the objectives of an environmental monitoring study with the least possible cost and time investment is higher than species (Ferraro & Cole, 1995; Kingston & Riddle, 1989; Warwick, 1988). This is because the identification of taxa down to the species level may not always be necessary to determine spatial or temporal patterns, especially when these patterns are clear, such as those established along pollution gradients (Ferraro & Cole, 1995; Pearson & Rosenberg, 1978; Olsgard et al., 1998; Warwick, 1988).

To date, no detailed study on the coralligenous assemblages has been performed at the ecoregion (large-Mediterranean) scale. Coordinated research effort in three countries (Turkey, Greece, and France), in the framework of the CIGESMED project (EU FP7 ERA-NET; www.cigesmed.eu), made it possible for the coralligenous habitat of four out of eight Mediterranean ecoregions (Algero-Provencal Basin, and Ionian, Aegean, and Levantine Seas; *sensu* Giakoumi et al., 2013; Notarbartolo di Sciara & Agardy, 2010; Spalding et al., 2007) to be jointly studied for the first time by applying a standardized sampling protocol.

This paper aims to assess the variability of the coralligenous assemblage structure across the Mediterranean Sea ecoregions. In particular, two major hypotheses are tested: (a) that the coralligenous assemblage pattern is not homogeneous at locations across the Mediterranean ecoregions considered (*biotic gradients*); and (b), that the assemblage pattern does not change significantly when the information is aggregated to higher taxonomic levels (*taxonomic sufficiency*). Finally, the results of this study are discussed in the context of the effective management of this habitat.

2 | MATERIAL AND METHODS

2.1 | Study area

Coralligenous communities were studied at nine locations distributed in the three basins (western, central, and eastern) and in four out of eight Mediterranean ecoregions (Algero-Provencal Basin, and Ionian, Aegean, and Levantine Seas) in 2014 and 2015. Continuous and generally vertically-inclined habitats were chosen at the locations: two stations in the Aegean (Turkey), Levantine (Turkey), and Ionian Seas (Greece), respectively, and three stations in the Algero-Provencal Basin (France; Figure 1). The main characteristics of the different stations are presented in Table 1. The sampling depth was 25–30 m at all stations, except for Zakynthos Island (Ionian Sea), where continuous coralligenous occurred only in deeper waters (38 m).

2.2 | Sample collection

A single campaign was organized at each station for the quantitative sampling of the coralligenous habitat using a standardized non-destructive photo-sampling protocol (David et al., 2014, 2015), which is available at the CIGESMED website (http://www.cigesmed.eu/Characterization-by-photo-quadrats).

Custom-made quadrats, of 50 × 50 cm in dimension, were used at each station for the collection of image samples, based on the experience gained from the fieldwork and analyses made for coralligenous habitats in the western and eastern Mediterranean Seas. Each image sample (sampling unit) was composed of nine quadrats placed in a 3 × 3 square structure, covering a total area of 2.25 m^2. Three replicate image samples (9 quadrats each), placed ca. 10 m away from each other, were taken at each station. The sampling depth was the depth at which the middle quadrat was placed. In the field, samples of some species (e.g. coralline algae, sponges, bryozoans), which are difficult to identify from pictures, were taken in order to identify them under the microscope in the laboratory.

2.3 | Sample analyses

The image samples were subsequently analysed using the photoQuad software (Trygonis & Sini, 2012; freely available at: http://www.mar.aegean.gr/sonarlab/photoquad/index.php). For the assessment of species composition and percentage coverage, 100 points were

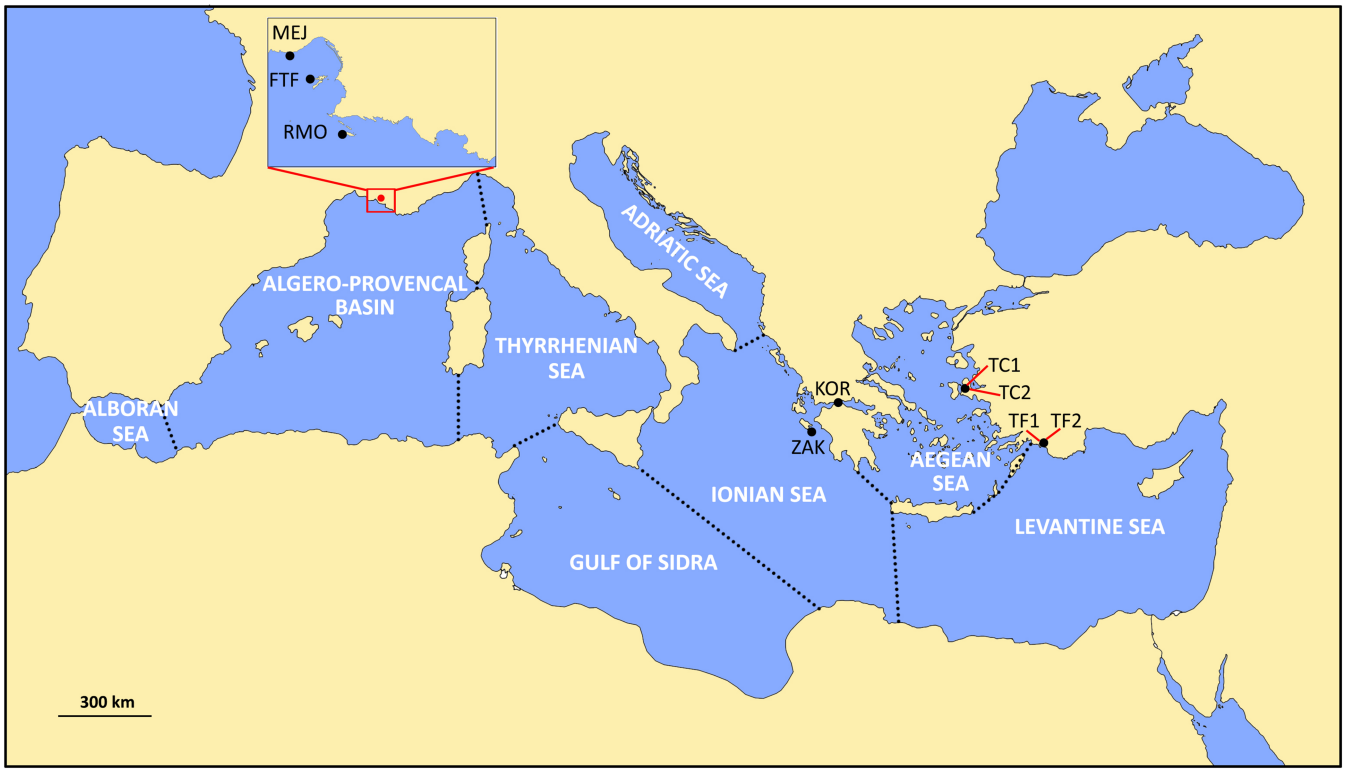


FIGURE 1 The location of sampling stations across the Mediterranean Sea

TABLE 1 Coordinates and typology of coralligenous habitats per station

Stations	Codes	Coordinates		Depth (m)	Orientation	Inclination	Rugosity
AEGEAN SEA							
Ildır Bay (Yarık Taş)	TC1	38°27′23″N	26°21′39″E	25	N	Vertical	Medium–large
Ildır Bay (Çifte Adalar)	TC2	38°23′45″N	26°26′55″E	25	NW	Vertical	Medium–large
LEVANTINE SEA							
Fethiye Bay (Afkule)	TF1	36°34′34″N	29°01′47″E	25	NW	Vertical	Medium–large
Fethiye Bay (Sarıyarlar)	TF2	36°36′46″N	29°02′06″E	25	NW	Vertical	Medium–small
IONIAN SEA							
Korinthiakos Bay (Lambiri)	KOR	38°19′17″N	21°58′23″E	25	N	Vertical	Medium–large
Zakynthos (Mavros Kavos)	ZAK	37°38′52″N	20°50′46″E	38	NW	Inclined/subvertical	Medium–large
ALGERO-PROVENCAL BASIN							
Gulf of Lions (Tiboulen du Frioul)	FTF	43°16′49″N	5°17′10″E	28	N	Vertical	Medium–large
Gulf of Lions (Moyade)	RMO	43°10′36″N	5°22′14″E	28	S	Vertical	Medium–large
Gulf of Lions (Méjean)	MEJ	43°19′42″N	5°13′29″E	28	S	Vertical	Medium–large

uniformly applied over each image. By focusing explicitly on the sessile taxa, a species by quadrat matrix using percentage coverage values was first created. This initial matrix was subsequently averaged by sampling station. The information included in the matrix was aggregated into five higher than species taxonomic levels: genera (79 taxa), families (60), orders (30), classes (12), and phyla (9). Then, coverage values of all taxa were square-root transformed prior to the analysis. Finally, the Bray–Curtis index (Bray & Curtis, 1957) was applied to construct the triangular resemblance matrices.

2.4 | Statistical analyses

The first hypothesis (*biotic gradients*) was tested by means of both uni- and multivariate techniques: number of taxa (S), and Shannon–Weaver diversity (H′) and Pielou's evenness (J′) indices were calculated to explore the community species richness, diversity and equitability, respectively. Then the Permutational Analysis of Variance (PERMANOVA) using 'locations' (four levels: locations in the Algero-Provencal Basin, and Ionian, Aegean, and Levantine Seas) as a fixed

TABLE 2 List of species found and their mean percent coverages per station

Ecoregions	Aegean Sea		Levantine Sea		Ionian Sea		Algero-Provencal Basin		
Stations	**TC1**	**TC2**	**TF1**	**TF2**	**K0R**	**ZAK**	**FTF**	**RMO**	**MEJ**
CHLOROPHYTA									
Caulerpa cylindracea Sonder, 1845	0.9	0.1	-	-	-	-	-	-	-
Codium bursa (Olivi) C. Agardh, 1817	-	0.3	-	-	-	-	0.1	-	-
Codium effusum (Rafinesque) Delle Chiaje, 1829	-	-	-	-	-	0.2	-	-	0.3
Flabellia petiolata (Turra) Nizamuddin, 1987	1.9	0.9	-	-	-	-	0.9	1.5	20.9
Halimeda tuna (J.Ellis & Solander) J.V. Lamouroux, 1816	0.1	0.3	-	-	-	-	-	-	0.2
Palmophyllum crassum (Naccari) Rabenhorst, 1868	0.8	0.6	0.6	1.2	0.1	3.3	-	0.2	-
Pedobesia simplex (Meneghini ex Kützing) M.J. Wynne & F. Leliaert, 2001	0.2	0.4	-	7.2	-	-	-	-	-
Pseudochlorodesmis furcellata (Zanardini) Børgesen, 1925	1.3	0.3	-	-	-	-	-	-	-
Valonia utricularis (Roth) C. Agardh, 1823	-	0.1	-	-	-	-	-	-	-
Chlorophyta (sp.)	-	-	-	-	-	-	0.2	0.3	-
RHODOPHYTA									
Amphiroa rigida J.V. Lamouroux, 1816	-	0.2	5.3	0.1	-	-	-	-	-
Amphiroa rubra (Philippi) Woelkerling 1983	-	-	0.4	0.9	-	-	-	-	-
Lithophyllum sticteaforme (J.E. Areschoug) Hauck, 1877	19.6	0.1	-	-	-	-	-	-	-
Lithophyllum spp.	-	-	-	-	0.4	2.2	0.2	2.8	13
Lithothamnion crispatum Hauck, 1878	-	-	7.9	2	-	-	-	-	-
Meredithia microphylla (J. Agardh) J. Agardh, 1892	0.1	-	-	-	-	-	-	-	-
Mesophyllum alternans (Foslie) Cabioch & M.L. Mendoza, 1998	-	32.7	13	6.9	-	-	-	-	-
Mesophyllum expansum (Philippi) Cabioch & M.L. Mendoza, 2003	0.7	-	21.3	18.7	-	-	-	-	-
Mesophyllum philippi (Foslie) W.H. Adey, 1970	-	-	-	0.1	-	-	-	-	-
Mesophyllum spp.	-	-	-	-	0.1	1.9	-	0.1	-
Neogoniolithon hauckii (Rothpletz) R.A.Townsend & Huisman 2018	-	-	-	-	1.8	0.7	-	-	-
Peyssonnelia dubyi P.L. Crouan & H.M. Crouan, 1844	9	7.4	0.9	2.3	-	-	-	-	-
Peyssonnelia heteromorpha (Zanardini) Athanasiadis 2016	0.1	0.2	21	5.6	-	-	-	-	-
Peyssonnelia rosa-marina Boudouresque & Denizot, 1973	-	-	-	-	-	1.1	-	-	-
Peyssonnelia rubra (Greville) J. Agardh, 1851	0.1	1.5	0.4	1.6	-	6.9	-	-	-
Peyssonnelia squamaria (Gmelin) Decaisne, 1842	21.2	14.8	8.8	14.4	-	10.1	-	-	-
Peyssonnelia spp.	-	-	-	-	19.8	16.1	3.2	12.2	27
Sphaerococcus sp.	0.2	-	-	-	-	-	-	-	-
Rhodophyta (spp.)	-	-	-	-	2.4	14.2	1.5	0.5	0.1
OCHROPHYTA									
Dictyota dichotoma (Hudson) J.V. Lamouroux, 1809	-	0.3	-	-	-	-	-	-	-
Lobophora variegata (J.V. Lamouroux) Womersley ex E.C. Oliveira, 1977	0.3	0.6	-	-	-	-	-	-	-
Ochrophyta (sp.)	-	-	-	-	-	-	0.4	-	0.1
TURF ALGAE	-	1.1	2.4	0	6.3	2.6	0.1	0.6	7.3
PORIFERA									
Acanthella acuta Schmidt, 1862	-	-	-	-	0.2	-	0.1	-	-
Agelas oroides (Schmidt, 1864)	7.5	1.7	0.3	2	6.2	5.3	0.2	0.3	0.1
Aplysina aerophoba (Nardo, 1833)	-	0.2	0.1	0.1	-	-	-	-	-
Aplysina cavernicola (Vacelet, 1959)	-	0.1	-	-	-	-	0.2	-	-

TABLE 2 (Continued)

Ecoregions	Aegean Sea		Levantine Sea		Ionian Sea		Algero-Provencal Basin		
Stations	**TC1**	**TC2**	**TF1**	**TF2**	**K0R**	**ZAK**	**FTF**	**RMO**	**MEJ**
Aplysilla rosea (Barrois, 1876)	-	-	-	-	0.1	-	-	-	-
Aplysilla sulfurea (Schulze, 1878)	-	-	-	-	-	-	-	0.1	-
Axinella cannabina (Esper, 1794)	-	-	-	-	2.1	-	-	-	-
Axinella damicornis (Esper, 1794)	0.3	0.1	-	-	0.1	-	1.2	0.7	0.2
Axinella polypoides Schmidt, 1862	-	0.3	-	0.1	-	-	0.2	0.1	-
Axinella verrucosa (Esper, 1794)	-	-	-	-	-	-	0.3	0.1	0.1
Axinella spp.	-	-	0.1	-	-	0.3	-	-	-
Cacospongia mollior Schmidt, 1862	-	-	-	-	-	0.1	-	-	-
Corticium candelabrum Schmidt, 1862	-	-	-	-	0.1	-	-	-	-
Chondrilla nucula Schmidt, 1862	-	0.1	-	-	-	-	-	-	-
Chondrosia reniformis Nardo, 1847	-	2.7	-	0.2	4.3	0.9	-	-	0.1
Cliona celata Grant, 1826	0.6	0.1	-	0.1	0.1	-	-	-	-
Cliona schmidtii (Ridley, 1881)	0.1	0.1	-	0.1	0.3	-	-	-	-
Cliona viridis (Schmidt, 1862)	-	-	-	0.1	0.2	0.3	-	-	-
Crambe crambe (Schmidt, 1862)	0.1	-	-	-	-	-	-	-	-
Dictyonella incisa (Schmidt, 1880)	-	-	-	-	0.7	-	-	-	-
Dictyonella sp.	-	-	-	-	-	-	-	0.2	0.2
Dysidea fragilis (Montagu, 1814)	-	-	-	-	0.3	0.3	-	0.2	-
Haliclona (reniera) aquaeductus (Schmidt, 1862)	-	-	-	-	-	-	0.1	-	-
Haliclona (halichoclona) fulva (Topsent, 1893)	0.1	0.2	-	-	0.5	0.1	0.8	-	-
Haliclona (soestella) mucosa (Griessinger, 1971)	-	-	-	-	0.3	0.1	0.5	0.4	0.1
Haliclona sp.	-	-	-	-	-	0.1	-	-	-
Hemimycale columella (Bowerbank, 1874)	-	-	-	-	-	0.1	-	-	-
Hexadella pruvoti Topsent, 1896	-	-	-	-	0.2	-	-	-	-
Hexadella racovitzai Topsent, 1896	-	-	-	-	0.2	-	-	-	-
Ircinia variabilis (Schmidt, 1862)	-	-	-	-	2	-	-	-	-
Ircinia sp.	-	0.1	-	-	-	-	-	-	-
Oscarella balibaloi Pérez, Ivanisevic, Dubois, Pedel, Thomas, Tokina & Ereskovsky, 2011	-	-	-	-	3.4	-	-	-	-
Oscarella imperialis Muricy, Boury-Esnault, Bézac & Vacelet, 1996	-	-	-	-	-	0.1	-	-	-
Oscarella lobularis (Schmidt, 1862)	-	-	-	-	-	-	7.1	-	-
Oscarella tuberculata (Schmidt, 1868)	-	-	-	-	0.1	-	0.3	-	-
Oscarella sp.	-	-	-	-	-	-	1.2	0.4	-
Penares sp.	-	-	-	-	-	0.2	-	-	-
Petrosia (petrosia) ficiformis (Poiret, 1789)	-	-	-	0.3	0.2	-	0.7	-	-
Phorbas sp.	0.6	-	-	-	-	-	-	-	-
Phorbas fictitius (Bowerbank, 1866)	-	0.1	-	-	-	-	-	-	-
Phorbas tenacior (Topsent, 1925)	1	1	-	0.1	3.2	-	0.2	0.1	0.2
Pleraplysilla spinifera (Schulze, 1879)	0.1	-	-	-	1.5	0.5	-	-	-
Prosuberites longispinus Topsent, 1893	-	-	-	-	0.6	-	-	-	-
Sarcotragus sp.	0.1	-	-	-	-	-	-	-	-
Sarcotragus foetidus Schmidt, 1862	-	-	-	-	-	0.4	-	-	-
Sarcotragus spinosulus Schmidt, 1862	1	0.1	-	-	-	-	-	-	-
Spirastrella cunctatrix Schmidt, 1868	10.8	2	0.6	3.7	8.8	6.4	-	-	-

TABLE 2 (Continued)

Ecoregions	Aegean Sea		Levantine Sea		Ionian Sea		Algero-Provencal Basin		
Stations	**TC1**	**TC2**	**TF1**	**TF2**	**K0R**	**ZAK**	**FTF**	**RMO**	**MEJ**
Spongia (spongia) officinalis Linnaeus, 1,759	-	-	-	-	0.2	-	-	-	-
Porifera (spp.)	0.1	-	-	-	-	0.3	10.8	8.5	0.7
CNIDARIA									
Alcyonium coralloides (Pallas, 1766)	-	-	-	-	-	-	-	0.1	0.7
Caryophyllia inornata (Duncan, 1878)	-	-	-	-	1.9	-	-	-	-
Corallium rubrum (Linnaeus, 1758)	-	-	-	-	-	-	0.1	0.3	0.7
Cladocora caespitosa (Linnaeus, 1767)	-	-	-	-	-	-	0.1	-	-
Eudendrium sp.	-	-	-	-	-	-	-	-	0.1
Eunicella cavolini (Koch, 1887)	-	-	-	-	-	-	0.2	0.1	10.1
Hoplangia durotrix Gosse, 1860	-	-	-	-	3	-	1.1	1.3	-
Leptopsammia pruvoti Lacaze-Duthiers, 1897	0.5	0.2	-	-	0.4	2.1	2.5	2.6	0.1
Leptogorgia sarmentosa (Esper, 1789)	-	-	-	-	-	-	0.1	-	-
Madracis pharensis (Heller, 1868)	0.1	-	-	0.1	2.5	0.1	-	-	-
Paramuricea clavata (Risso, 1826)	-	-	-	-	-	-	16.7	28.2	0.2
Parazoanthus axinellae (Schmidt, 1862)	-	-	-	-	-	-	10.8	0.1	0.2
Polycyathus muellerae (Abel, 1959)	-	-	-	-	1.7	-	-	-	-
Phyllangia americana mouchezii (Lacaze-Duthiers, 1897)	-	-	-	-	-	-	0.1	-	-
Hydrozoa (sp.)	-	-	-	-	-	0.1	-	-	-
Scleractinia (sp.)	-	-	-	-	-	-	0.3	0.1	-
Octocorallia (sp.)	-	-	-	-	-	-	0.1	-	-
PLATYHELMINTHES									
Yungia aurantiaca (Delle Chiaje, 1822)	-	-	-	-	-	-	-	-	0.1
POLYCHAETA									
Hermodice carunculata (Pallas, 1766)	-	0.1	-	-	-	-	-	-	-
Protula tubularia (Montagu, 1803)	-	0.1	0.1	-	-	-	-	-	-
Salmacina sp./*Filograna* sp.	-	-	-	-	0.1	-	0.1	0.1	0.1
Serpulidae (sp.)	-	-	-	-	0.89	0.04	-	-	-
MOLLUSCA									
Lithophaga lithophaga (Linnaeus, 1758)	0.1	-	-	0.1	0.1	-	-	-	-
Ostrea sp.	-	-	-	-	0.1	-	-	-	-
Peltodoris atromaculata Bergh, 1880	-	-	-	0.1	-	-	-	-	-
Rocellaria dubia (Pennant, 1777)	-	-	-	-	0.2	-	-	-	-
BRYOZOA									
Adeonella/*Smittina* spp.	-	-	-	-	1.4	0.3	-	-	-
Adeonella calveti (Canu & Bassler, 1930)	-	-	-	-	-	-	0.1	0.2	-
Beania magellanica (Busk, 1852)	-	-	-	-	-	0.1	-	-	-
Caberea boryi (Audouin, 1826)	-	-	0.1	-	-	-	-	-	-
Cellaria sp.	-	-	-	-	0.1	-	-	-	-
Celleporina caminata (Waters, 1879)	0.1	0.2	-	-	-	-	-	-	-
Dentiporella sardonica (Waters, 1879)	-	-	-	-	-	-	0.1	0.1	0.1
Myriapora truncata (Pallas, 1766)	-	-	-	-	-	0.5	0.4	1	1
Pentapora fascialis (Pallas, 1766)	-	-	-	-	-	-	-	0.1	-
Reteporella sp.	-	-	-	-	-	-	0.1	0.2	-
Reteporella grimaldii (Jullien, 1903)	-	-	-	-	-	-	-	0.1	-
Rhynchozoon neapolitanum Gautier, 1962	-	-	-	-	2.9	0.1	-	-	-

TABLE 2 (Continued)

Ecoregions	Aegean Sea		Levantine Sea		Ionian Sea		Algero-Provencal Basin		
Stations	**TC1**	**TC2**	**TF1**	**TF2**	**K0R**	**ZAK**	**FTF**	**RMO**	**MEJ**
Schizomavella (*Schizomavella*) *mamillata* (Hincks, 1880)	-	-	-	-	2.8	0.4	-	-	-
Schizomavella sp.	-	-	-	-	-	-	0.1	0.2	0.5
Schizoretepora serratimargo (Hincks, 1886)	-	-	-	-	0.1	-	-	-	-
Scrupocellaria sp.	-	-	-	0.6	-	-	-	-	-
Smittina cervicornis (Pallas, 1766)	-	-	-	-	-	-	0.7	0.4	0.2
Turbicellepora avicularis (Hincks, 1860)	-	-	-	-	-	-	-	0.3	-
Turbicellepora coronopus (Wood, 1844)	-	-	-	-	0.1	-	-	-	-
Bryozoa (spp.)	0.1	0.2	-	0.5	0.2	0.2	0.4	0.2	-
ECHINODERMATA									
Antedon mediterranea (Lamarck, 1816)	-	-	1	0.2	-	-	-	-	-
Echinaster sepositus (Retzius, 1783)	-	-	-	-	-	-	-	0.1	0.1
Hacelia attenuata Gray, 1840	0.1	-	-	-	-	-	-	-	-
Paracentrotus lividus (Lamarck, 1816)	-	0.1	-	-	-	-	-	-	-
Sphaerechinus granularis (Lamarck, 1816)	0.1	0.2	-	-	-	-	-	-	-
TUNICATA									
Didemnum commune (Della Valle, 1877)	-	-	-	-	-	0.4	-	-	-
Didemnum maculosum (Milne Edwards, 1841)	-	-	-	-	-	0.1	-	-	-
Didemnum sp.	-	-	-	-	0.8	-	-	-	-
Halocynthia papillosa (Linnaeus, 1767)	-	0.1	-	-	0.3	0.1	0.1	0.1	0.1
Polyclinum aurantium (Milne-Edwards, 1841)	-	-	-	-	-	-	0.1	0.1	0.1
Pycnoclavella sp.	-	-	-	-	-	-	0.1	-	-

factor (categorical variable) was applied to check for differences in the univariate community measures. The assemblage multivariate pattern was explored and visualized using the principal coordinate analysis (PCoA) (Torgerson, 1958), applied on the Bray–Curtis resemblance matrices at the species level and at the two levels of replication: image sample and location. PERMANOVA was carried out to test for potential differences in the coralligenous assemblage structure among locations. Finally, the Similarity Percentages Analysis (SIMPER) (Clarke, 1993) was applied to the species matrices in order to identify those species which significantly contributed to the (dis)similarity of groups of samples in the coralligenous assemblages.

The second hypothesis (*taxonomic sufficiency*) was tested by means of the second-stage multidimensional scaling (MDS) (Somerfield & Clarke, 1995). This technique can visualize changes in coralligenous assemblage patterns deriving from different taxonomic levels at the two different spatial levels (i.e. image sample and station). The resemblance matrices of species coverage values, at each of the six taxonomic levels considered here, were first constructed. These matrices were then correlated using a rank correlation between their corresponding elements (samples). The significance of these inter-matrix correlations was tested by using the RELATE technique (Clarke & Gorley, 2006). Subsequently, a second-stage resemblance matrix was constructed, which can be used to display interrelationships between patterns derived from different taxonomic levels.

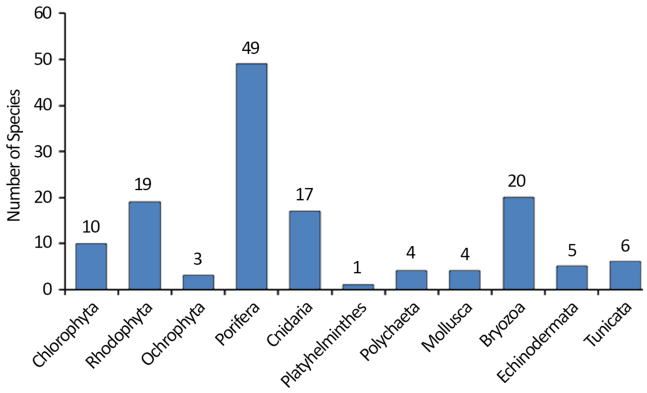


FIGURE 2 Total number of species recorded per taxonomic group at all stations

Finally, the non-metric MDS algorithm was applied on this second-stage resemblance matrix to visualize to what extent patterns deriving from the different taxonomic levels are close to each other or not. Finally, in order to test for the significance of the differences in the groups of either images or stations, at all levels of the aggregated information, that is from species to phyla, an analysis of similarities (ANOSIM) was applied (Clarke, 1993). All analyses were performed using the PRIMER v7 package (Clarke & Gorley, 2006; Clarke, Gorley, & Warwick, 2014).

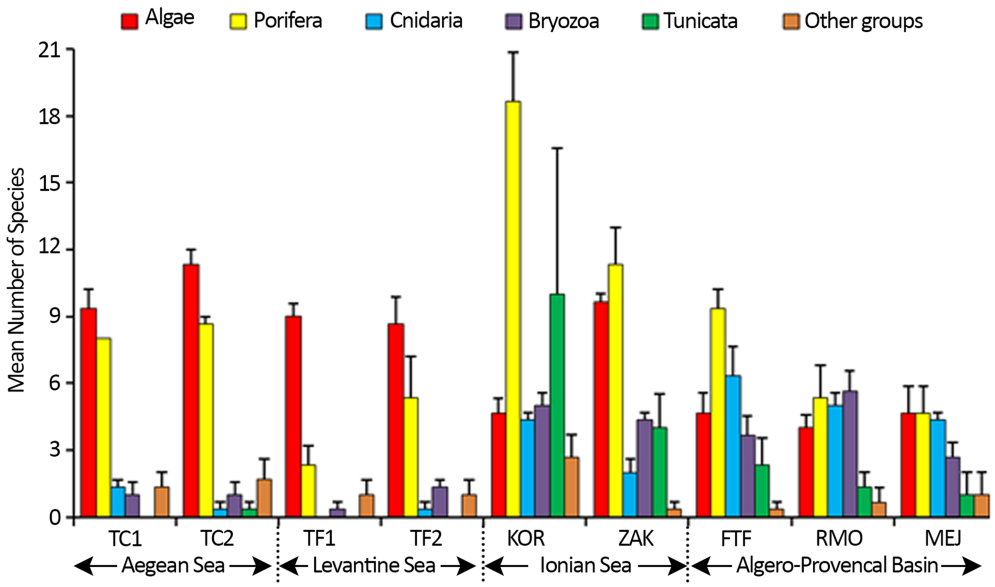


FIGURE 3 Average number of species recorded per station. Bar denotes standard error

TABLE 3 Overall and pairwise PERMANOVA tests applied on the number of species of the main taxonomic groups. Locations in ecoregions: 1. Aegean Sea, 2. Levantine Sea, 3. Ionian Sea, 4. Algero-Provencal Basin

Source of variation	Algae				Porifera			Cnidaria			Bryozoa			Tunicata		
	df	MS	Pseudo-*F*	*P*	MS	Pseudo-*F*	*P*	MS	Pseudo-*F*	*P*	MS	Pseudo-*F*	*P*	MS	Pseudo-*F*	*P*
Locations	3	47.6	13.5	*	140	13.9	*	39.3	26.6	*	25.5	16.2	*	65	4.3	*
Residual	23	3.5			10			1.5			1.6			15		
Pairwise comparisons of locations																
		t	*P*		*t*	*P*		*t*	*P*		*t*	*P*		*t*	*P*	
1 vs 2		1.67	ns		3.88	**		1.90	ns		0.35	ns		1	ns	
1 vs 3		2.35	ns		3.23	*		3.45	**		7.41	*		2.07	*	
1 vs 4		7.41	*		0.15	ns		6.34	*		3.75	**		2.07	ns	
2 vs 3		1.27	ns		4.76	*		4.81	*		8.45	*		2.12	*	
2 vs 4		5.77	*		1.76	ns		7.65	*		4.03	*		2.36	ns	
3 vs 4		2.47	**		4.24	*		2.55	**		0.84	ns		2	*	

Abbreviations: ns, non-significant.
$^{*}P < 0.01$, $^{**}P < 0.05$.

3 | RESULTS

3.1 | Testing of the biotic-gradients hypothesis

The analysis of the photo-quadrat samples revealed the presence of 138 species (95 sessile and 43 sedentary species) belonging to 11 taxonomic groups (Chlorophyta, Rhodophyta, Ochrophyta, Porifera, Cnidaria, Bryozoa, Polychaeta, Platyhelminthes, Mollusca, Echinodermata, and Tunicata) across all studied stations (Table 2; Figure 2). Porifera (49 species) and Bryozoa (20 species) were the dominant groups in terms of the number of species. Algae (including Chlorophyta, Rhodophyta, and Ochrophyta) were represented by 30 species. The presence of other groups was limited to a few species. Only one alien species (*Caulerpa cylindracea*) was found at station TC1, covering 3% of the total area.

Porifera appeared to be a diverse group in all locations, reaching a maximum (33 species) at the location in the Ionian Sea. Rhodophytes attained highest species richness values at the locations in the Aegean and Levantine Seas (13 species), while the highest number of cnidarian species (13) was found at the location in the Algero-Provencal ecoregion (Figure 3). Only 11 species were shared by all the Mediterranean locations studied. Some stations (KOR and MEJ) had high coverage of turf algae, which were composed of small green and brown filamentous species, as observed in the photo-quadrats.

The number of species in each sampling unit (image sample) ranged from 10 (station TF2) to 42 (station KOR). The number of species of the most abundant, in terms of coverage, taxonomic groups of coralligenous assemblages varied significantly among the Mediterranean locations studied (PERMANOVA, $P < 0.01$; Table 3).

TABLE 4 Overall and pairwise PERMANOVA tests applied on the percentage coverage of the main taxonomic groups in locations. Locations in ecoregions: 1. Aegean Sea, 2. Levantine Sea, 3. Ionian Sea, 4. Algero-Provencal Basin

		Chlorophyta			Rhodophyta			Porifera			Cnidaria			Bryozoa			Tunicata		
Source of variation	**df**	**MS**	**Pseudo-F**	***P***	**MS**	**Pseudo-F**	***P***	**MS**	**Pseudo-F**	***P***	**MS**	**Pseudo-F**	***P***	**MS**	**Pseudo-F**	***P***	**MS**	**Pseudo-F**	***P***
Locations	3	52.6	2.27	ns	2,854	11.5	*	491	5.45	*	1,139	21.8	*	21.1	6.02	*	0.80	4.32	*
Residual	23	44.9			248			90			52			3.5			0.18		
Pairwise comparisons of locations																			
		t	*P*		*t*	*P*		*t*	*P*		*t*	*P*		*t*	*P*		*t*	*P*	
1 vs 2		0.22	ns		1.67	ns		3.54	*		1.39	ns		0.74	ns		1	ns	
1 vs 3		1.98	ns		2.08	ns		1.78	ns		1.99	*		2.97	*		2.07	*	
1 vs 4		0.92	ns		4.08	*		0.60	ns		5.49	*		2.77	*		2.07	ns	
2 vs 3		1.39	ns		2.94	**		4.42	*		2.14	*		2.63	**		2.12	*	
2 vs 4		0.79	ns		4.83	*		1.74	ns		5.59	*		1.99	ns		2.36	ns	
3 vs 4		1.44	ns		1.97	ns		2.18	**		3.88	*		1.88	ns		2	**	

Abbreviations: ns, non-significant.
*$P < 0.01$, **$P < 0.05$.

The pair-wise tests revealed that the number of species of algae did not change significantly among the neighbouring locations (Aegean, Levantine, and Ionian Seas). The average number of algae was always higher at the locations in the eastern Mediterranean (Aegean and Levantine Seas), the number of sponge species was always higher in the Ionian Sea, and the numbers of cnidarian and bryozoan species were higher in the western Mediterranean (Figure 3).

The coverage of the taxonomic groups in coralligenous habitats differed significantly among locations in the ecoregions (PERMANOVA, $P < 0.01$; Table 4). The pairwise tests showed that the percentage coverage of rhodophytes differed significantly in distant locations. The cnidarian coverage differed significantly among locations, with the exception of the Aegean and Levantine Seas. The average coverage of rhodophytes was higher than 50% at five stations (TC1, TC2, TF1, TF2, and ZAK) and reached up to 80% at station TF1 (Figure 4). The highest coverage of Porifera was at station KOR (36%), while for Cnidaria, stations FTF (32%) and RMO (33%) had the highest coverage. Turf algae were observed at all stations (except for TC1) and their highest maximum and mean coverage values were encountered at MEJ (max: 16%, mean: 6.3%) and KOR (max: 12%, mean: 7.3%; Figure 4).

Differences in species richness (S), diversity (H′) and evenness (J') indices among locations were all significant (PERMANOVA, $P < 0.01$; Table 5). Interestingly, the community parameters estimated in two distant locations (Aegean Sea and Algero-Provencal Basin) were not statistically different (pairwise tests). The maximum mean number of species (S = 38), diversity index value (H′ = 4) and evenness index value (J' = 0,76) were calculated at station KOR. The Ionian stations (KOR and ZAK) presented the highest mean values of S, H′ and J′, while the Algero-Provencal stations the lowest values of H′ and J′ (Figure 5).

The coralligenous assemblage composition of the locations in the four ecoregions studied were significantly different (PERMANOVA, Pseudo-F: 13.2, $P < 0.01$). The pair-wise tests indicated that all locations significantly differ from each other ($t > 2.87$, $P < 0.01$). The application of the PCoA showed that there are four distinct groups of samples, corresponding to the locations sampled (Figure 6). The first two axes of the PCoA graph explained 57% of total variance. The average similarity of stations within each of the Mediterranean ecoregions was higher than 40%, reaching 63% in the Levantine Sea, 57% in the Aegean Sea, 56% in the Ionian Sea, and 42% in the Algero-Provencal Basin (Table 6), which is indicative of a possible gradient across the ecoregions considered in this study. The SIMPER analysis indicated that some sponge and rhodophyte species contributed much to the dissimilarity of assemblages among the ecoregions (Table 6). The species that have the longer vectors along the first PCoA axis (multiple correlation $-0.3 > R > 0.3$) were *Peyssonnelia squamaria* ($R = 0.4$), *Mesophyllum alternans* ($R = 0.36$), *Peyssonnelia* spp. ($R = -0.36$), and *M. expansum* ($R = 0.31$); those that have the longer vectors along the second PCoA axis were *Spirastrella cunctatrix* ($R = 0.39$), *Agelas oroides* ($R = 0.32$), and *P. clavata* ($R = -0.30$).

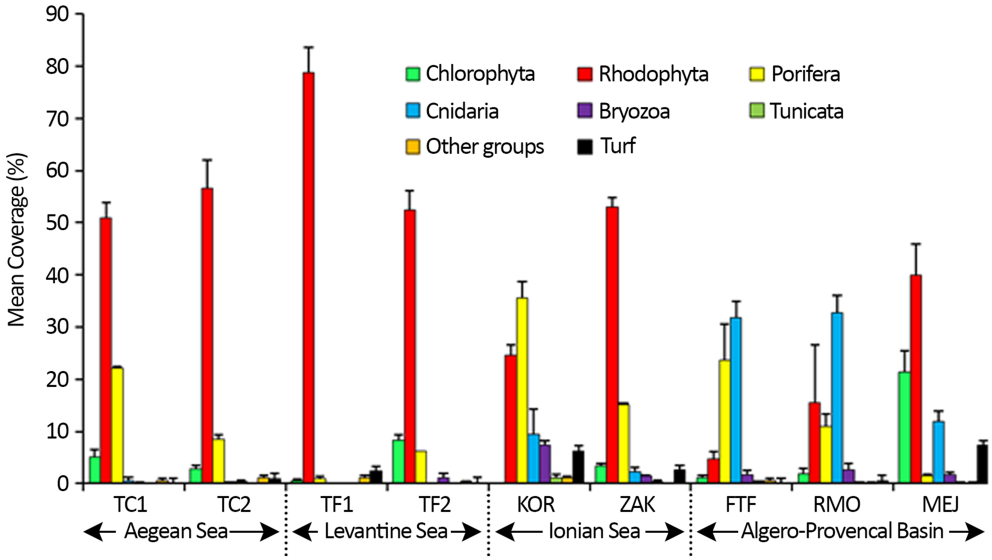


FIGURE 4 Average percentage coverage of taxonomic groups and algal turf recorded per station. Bar denotes standard error

TABLE 5 Overall and pairwise PERMANOVA tests applied on the community parameters. Locations in ecoregions: 1. Aegean Sea, 2. Levantine Sea, 3. Ionian Sea, 4. Algero-Provencal Basin

		Number of species			Diversity index			Evenness index		
Source of variation	**df**	**MS**	**Pseudo-*F***	***P***	**MS**	**Pseudo-*F***	***P***	**MS**	**Pseudo-*F***	***P***
Locations	3	379	18.9	*	1.91	21.6	*	0.05	14.3	*
Residual	23	20			0.09			0.003		
Pairwise comparisons of locations										
		t	*P*		*t*	*P*		*t*	*P*	
1 vs 2		3.99	**		0.32	ns		3.24	**	
1 vs 3		4.88	**		6.39	**		4.79	**	
1 vs 4		0.05	ns		1.12	ns		1.11	ns	
2 vs 3		6.7	**		5.61	**		0.58	ns	
2 vs 4		2.9	**		1.33	ns		4.37	**	
3 vs 4		4.3	**		6.78	**		5.67	**	

Abbreviations: ns, non-significant.
*$P < 0.01$, **$P < 0.05$.

3.2 | Testing of the taxonomic sufficiency hypothesis

When the information was aggregated to higher taxonomic levels, the ecoregion trend remained similar although smoother from the level of orders and upwards. However, the ANOSIM tests were always significant at all levels from species to phyla at the ecoregion scale, based on image samples (Data S1). On the plots of the second-stage MDS (Figure 7), patterns derived from the species level appeared to be closer to those derived from genera and families than to those from the remaining taxonomic levels. This similarity trend remained the same at both scales: image and station. The RELATE technique applied to every pair of the resemblance matrices deriving from the six taxonomic levels considered showed that they all are positively and significantly correlated to each other (Data S2). Resemblance matrices of species and phyla were always the least correlated (0.78 at the image and 0.66 at the station scale), while those of genera and families were the highest correlated to each other (0.97 at image and 0.98 at the station scale). These results mean that as the information is aggregated from species to phyla the multivariate pattern between them differs maximally by 37%, while those patterns between species and genera and species and families differ maximally by 27%.

4 | DISCUSSION

The present study shows that coralligenous assemblages are different in the various Mediterranean ecoregions, investigated in this study. This result is in agreement with previous studies, confirming the high ecological and biodiversity importance attributed to coralligenous habitats (Ballesteros, 2006; Hong, 1982; Laubier, 1966), as well as the high value of the ecosystem services they provide to mankind (e.g. food, carbon sequestration, water filtration, coastline stabilization) (Thierry De Ville D'Avray, 2018). However, coralligenous habitats

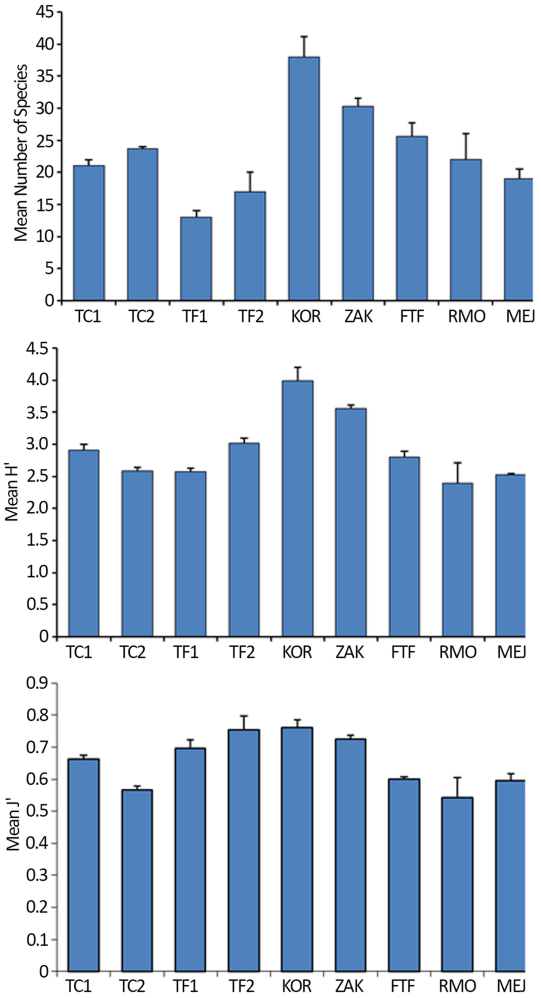


FIGURE 5 Average values of the number of species (S), the diversity index (H′), and the evenness index (J′). Bar denotes standard error

are more diversified than estimated as, due to the methodology applied (i.e. photo-quadrat method), a number of species living in crevices of biogenic constructions were not determined. The number of taxa belonging to each taxonomic group varied among basins; sponges were the most diversified at all studied locations, followed by bryozoans, rhodophytes, and cnidarians. However, different taxa dominated the different locations (ecoregions) of the Mediterranean Sea. Shallow coralligenous assemblages (at 25–50 m) in the eastern Mediterranean are known to be composed of a richer sponge fauna, while large alcyonarians and gorgonians are rare or absent ('facies oriental', Pérès & Picard, 1958; but see Piazzi et al., 2019; Sini, Kipson, Linares, Koutsoubas, & Garrabou, 2015). The present study confirmed this finding that sponges dominated the eastern Mediterranean coralligenous habitats, with *Spirastrella cunctatrix* and *Agelas oroides* the most characteristic species.

The absence of erect bryozoans (e.g. *Myriapora truncata*, *Pentapora fascialis*, and *Reteporella grimaldii*), which are abundant in the western Mediterranean coralligenous habitats (Casoli et al., 2017), also characterized the Turkish stations of the eastern Aegean and the northern Levantine Sea, as is the case in other areas of the north Aegean Sea (Sini, Garrabou, & Koutsoubas, 2014) and the north Adriatic Sea (Casellato & Stefanon, 2008). It is known that the presence of suspension feeders in coralligenous habitats largely depends on current strength and availability of food (Ballesteros, 2006; Longo et al., 2018). Gorgonians are generally reported to be abundant in areas rich in suspended organic matter, while sponges, bryozoans and scleractinian corals prefer more oligotrophic waters (Gili & Ballesteros, 1991).

Sini et al. (2014) reported that Porifera were the most diverse taxonomic group in the coralligenous habitat of the Aegean Sea, representing an overall coverage of 28%, with *Agelas oroides*, *Chondrosia reniformis*, *Crambe crambe*, and *Spirastrella cunctatrix* making the greatest contribution. The widespread sponge species *Agelas oroides* and *Spirastrella cunctatrix* in the eastern Mediterranean species were also common in coralligenous habitats of the Tyrrhenian Sea (Ferdeghini, Acunto, Cocito, & Cinelli, 2000). In the north Aegean Sea, Antoniadou, Voultsiadou, and Chintiroglou (2006) showed that the frequently distributed and abundant species in the coralligenous habitats were *A. oroides* (max. 30 ind.m^{-2}) and *Diplastrella bistellata* (max. 22 ind.m^{-2}). Sini et al. (2014) reported that Porifera were the most diverse taxonomic group in the coralligenous habitat of the Aegean Sea, representing an overall coverage of 28%, with *Agelas oroides*, *Chondrosia reniformis*, *Crambe crambe* and *Spirastrella cunctatrix* making the greatest contribution. However, it has been emphasized that endolithic sponges represent higher species richness and biomass when compared to those in the epibenthic layer of the coralligenous habitat (Calcinai et al., 2015). Therefore, the species number encountered in the present study seems to represent only a fraction of the sponge inventory of this habitat.

The importance of cnidarians in the coralligenous assemblages differed across the localities studied; their average coverage in the Algero-Provencal Basin was almost six times higher than those in the Aegean and Levantine Seas, and two times higher than that in the Ionian Sea. The gorgonians were totally lacking from the eastern Mediterranean stations, whereas two large-sized species *Paramuricea clavata* and *Eunicella cavolini* occupied >18% of total area of coralligenous habitats in the Algero-Provencal Basin. It is known that gorgonian assemblages are rarely reported in areas shallower than 40 m depth in the eastern Mediterranean (Çinar, Gönülal, & Öztürk, 2018; Salomidi, Smith, Katsanevakis, Panayotidis, & Papathanassiou, 2009). However, facies with *E. cavolini* and *P. clavata* occur widely in the north Aegean Sea (Gerovasileiou, Sini, Poursanidis, & Koutsoubas, 2009; Sini et al., 2015). Gorgonian-dominated habitats provide a three-dimensional complexity to the epibenthic layer that forms a number of microhabitats, increasing the local diversity (Cerrano et al., 2010; True, 1970). Gorgonians can also reduce the growth of erect algae and favour the settlement of encrusting algae and sessile invertebrates (Ballesteros, 2006; Laubier, 1966). The disappearance of gorgonians from coralligenous assemblages might cause a shift from assemblages formed by encrusting coralline algae to filamentous algae assemblages, decreasing complexity and resilience of coralligenous habitats (Ponti et al., 2014).

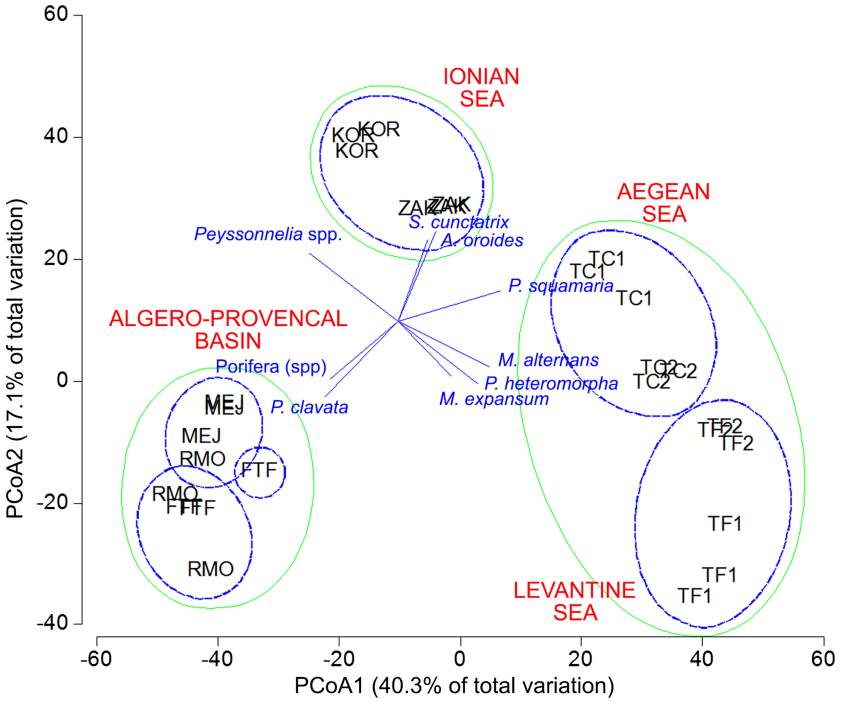


FIGURE 6 Principal coordinate analysis (PCoA) showing the similarity among replicated samples of stations, based on coverage data of all species. Green lines indicate a similarity level of 20%, blue lines indicate a similarity level of 40%. Vectors represent the species that relatively highly correlated with PCoA1 and PCoA2 (multiple correlation, $r > 0.3$)

TABLE 6 Results from SIMPER Analysis showing the species contributing the most (>7%) to the formation of groups indicated in Figure 10

	Aegean Sea	Levantine Sea	Ionian Sea	Algero-Provencal Basin
Average similarity (%)	**57**	**63**	**56**	**42**
Flabellia petiolata	-	-	-	10
Mesophyllum alternans	7	16	-	-
Mesophyllum expansum	-	24	-	-
Peyssonnelia dubyi	19	-	-	-
Peyssonnelia heteromorpha	-	13	-	-
Peyssonnelia squamaria	25	15	-	-
Peyssonnelia spp.	-	-	18	21
Rhodophyta (spp.)	-	-	9	-
Agelas oroides	10	-	11	-
Porifera (spp.)	-	-	-	16
Spirastrella cunctatrix	11	-	13	-
Paramuricea clavata	-	-	-	13

Coralligenous assemblages were reported to have been invaded by alien species, such as *Caulerpa* spp. and *Womersleyella setacea* (Piazzi et al., 2007). *Caulerpa cylindracea* has been found to cover almost 60% of coralligenous habitats along the coast of Livorno (Piazzi & Balata, 2009). In our case, *Caulerpa cylindracea* was only found at one station (TC1 in the Aegean Sea), with a low coverage (3%). Although absent in the present study, the red turf alga *Womersleyella setacea* can form a dense carpet over encrusting coralines, thus inhibiting their photosynthetic activities and growth (Cebrian & Rodríguez-Prieto, 2012).

Four distinct epibenthic coralligenous assemblages were identified in the present study, based on coverage of the main builders and constituents (coralline algae, sponges, and cnidarians). The eastern Mediterranean assemblages lacked gorgonians, whereas the average coverage of *Paramuricea clavata* reached 28% in the western Mediterranean. The eastern Mediterranean assemblages were largely composed of encrusting coralline algae and sponges, in agreement with the findings published by Sini (2015) and Sini et al. (2014). The eastern Mediterranean assemblages (Aegean and Levantine Seas) were somewhat similar to that (i.e. an assemblage characterized by massive sponges, non-calcareous encrusting algae [*Peyssonnelia* spp.] and ascidians) reported from the Adriatic Sea by Falace et al. (2015), although ANOSIM tests clearly demonstrate their biotic multivariate patterns are different. The results of this first large-scale Mediterranean approach demonstrated that coralligenous assemblages present a clear biotic gradient across the ecoregions considered, which can be detected when using species composition information patterns: the multivariate biotic patterns

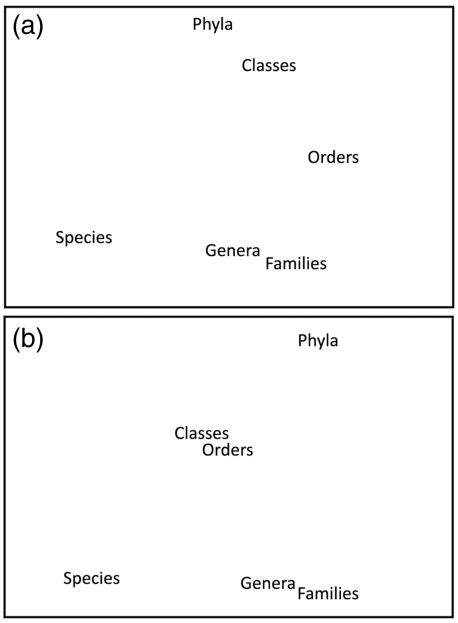


FIGURE 7 Second-stage multidimensional scaling plots, comparing inter-matrix relations between patterns from multiple taxonomic levels and at various geographical scales. (A) Image sample (stress = 0); (B) stations in ecoregions (stress = 0)

of the locations within each of the ecoregions are more similar to each other than to those from the other ecoregions. This is in good agreement with the first hypothesis regarding the biotic gradient concept (Arvanitidis et al., 2002; Bellan-Santini, 1985; Fredj & Laubier, 1985; Pérès, 1967; Surugiu et al., 2010).

The biotic multivariate pattern remains stable as the information is aggregated from species to higher taxonomic levels. Groups of samples that correspond to the different Mediterranean ecoregions are significantly different from each other at all taxonomic levels from the species to phylum. These findings confirm the second hypothesis on the taxonomic sufficiency concept, that is the assemblage pattern does not change significantly when the information is aggregated to higher taxonomic levels. Also, the comparison of the patterns deriving from the different taxonomic levels, as depicted in the second-stage non-metric MDS plots, shows the pattern coming from the species level to be most closely similar to those from genera and families. These results are in agreement with those from the previous studies focusing on the taxonomic sufficiency concept but in soft-bottom habitats (Ferraro & Cole, 1995; Kingston & Riddle, 1989; Warwick, 1988). For an adequate assessment of the spatial structure of the coralligenous assemblage it is sufficient to identify the taxa at the family level since their patterns are >70% similar to those of genera and species. This similarity of the multivariate patterns decreases slightly to >60% at the phylum level, but that is still acceptable as a surrogate taxonomic level to focus on in an assessment study, especially in areas for which baseline studies exist.

Based on these results, a biogeographic gradient along the Mediterranean ecoregions (Giakoumi et al., 2013; Notarbartolo di Sciara & Agardy, 2010; Spalding et al., 2007) is revealed. Thus, our findings suggest a major longitudinal gradient of coralligenous assemblages, which is characterized by low percentages of common dominant species across the ecoregions. This large-scale spatial diversification of assemblage structure may be the result of geographical, historical (evolutionary), and/or environmental forcing (Gaston, Chown, & Evans, 2008).

The above results further support our argument from the taxonomic sufficiency hypothesis, in that a cost–benefit-balanced monitoring of the coralligenous habitat can be accomplished at least at local and ecoregional spatial scales by using much less biological information, scientific expertise and resources. As patterns of the coralligenous communities used for monitoring remain much the same when the information is aggregated from the species to family level, it follows that trained technicians, para-taxonomists, students, or, in some cases, even trained citizen scientists may undertake the classification of the individuals on the photo-quadrats into families. This process can be achieved in a more industrial, faster, and cheaper way rather than the classification of the individuals into species by professional taxonomists. Hence, cost-effective conservation initiatives may be designed and implemented while citizen science networks may also contribute towards this end through data gathering and reporting to scientists and managers (Gatti et al., 2016; Gerovasileiou et al., 2016).

5 | CONCLUSIONS

The present study provides sound evidence on the utility of a standardized non-destructive photo-sampling protocol, developed in the framework of the CIGESMED project, in order to adequately study the coralligenous assemblages of the Mediterranean and test basic scientific concepts: biotic gradients and taxonomic sufficiency.

Sound data and information on the assemblage patterns have been created in the course of this project, which will serve as a body of evidence against which the results of future monitoring and conservation actions can be compared.

Surrogate taxonomic categories, higher than species such as genus and family, can be used to assess the multivariate pattern of the coralligenous assemblages. Even at the level of the phylum, little of the pattern structure is lost, which saves considerable time, effort, and investment during the assessment and monitoring of any conservation action on the coralligenous assemblages.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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