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Coralligenous formations dominated by *Eunicella cavolini* (Koch, 1887) in the NE Mediterranean: biodiversity and structure

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Abstract

Coralligenous formations are biogenic structures typical of the underwater Mediterranean seascape. Their intricate, multi-layered species assemblages are composed of perennial, long-lived organisms, particularly vulnerable to natural or human-induced disturbances. Despite their high ecological role and conservation value, few studies have addressed these assemblages outside the NW Mediterranean. This is the first quantitative assessment of coralligenous in the N Aegean Sea (NE Mediterranean), specifically focusing on the upper bathymetric limit of assemblages that are dominated by the yellow gorgonian *Eunicella cavolini*. The number and percent cover of macrobenthic species were studied at depths of 18 to 35 m, using a photoquadrat method. A total of 99 benthic taxa were identified, out of which 89 perennial ones were used to investigate spatial patterns in assemblage structure, composition, and biodiversity. A mean number of 47 perennial taxa were recorded per site, with encrusting coralline algae and sponges being the dominant groups in percent cover and species number, respectively. Across the studied localities, structural complexity and community composition were overall similar, but assemblages presented distinctive differences at the site level, thus highlighting the role of local abiotic and anthropogenic factors in the shaping of the coralligenous. Compared to the rest of the Mediterranean, assemblages hosted a similar number of taxa. However, the number and percent cover of erect bryozoans were generally low, while, apart from *E. cavolini*, other erect anthozoan species were absent. This work provides important reference data for comparisons and monitoring at a local or Mediterranean scale.

Keywords: Benthic communities; Coralligenous; Gorgonians; *Eunicella cavolini*; Biodiversity; Conservation; Mediterranean; Aegean Sea; Photoquadrat sampling.

Introduction

Coralligenous formations developing on hard substrates under dim light conditions are complex biogenic structures typical of the benthic Mediterranean seascape (Ballesteros, 2006). They encompass a wide range of species assemblages, which contribute to the build-up of these bioherms through the multi-layered accumulation of encrusting coralline algae and the calcareous remains of animal species (Sarà, 1969; Sartoretto *et al*., 1996). Coralligenous assemblages provide key marine habitats that play a pivotal role in the maintenance of marine biodiversity; they host more than 10% of the known Mediterranean marine species, including a large number of endemic, vulnerable and protected organisms (Boudouresque, 2004; Ballesteros, 2006; Coll *et al*., 2010). Moreover, they serve as reservoirs of natural resources, offering important fisheries grounds, aesthetic seascapes for diving tourism, and a wide range of raw materials (e.g. Ballesteros, 2006; Lloret, 2010; Salomidi *et al*., 2012). Among the most typical taxonomic groups that characterise coralligenous assemblages are encrusting coralline rhodophytes (especially of the families Corallinaceae and Peyssonneliaceae), sponges, cnidarians, and bryozoans. A key aspect of coralligenous, however, is that most of the habitat-forming species present slow growth, and thereby low resilience to imminent threats and disturbances (Sartoretto *et al*., 1996; Garrabou & Ballesteros, 2000; Garrabou & Zabala, 2001; Linares *et al*., 2007; Teixidó *et al*., 2011a). Mechanical damage (mainly caused by destructive fishing practices), sedimentation, increased nutrient loads, mass mortality events related to positive thermal anomalies of the water column, and invasive species are amongst the main disturbances that severely affect coralligenous assemblages, both at the species and at the community level (Bavestrello *et al*., 1997; Piazzi *et al*., 2007;

Garrabou *et al*., 2009; Cebrian *et al*., 2012; Piazzi *et al*., 2012; Maldonado *et al*., 2013; Teixidó *et al*., 2013).

The "*Action Plan for the conservation of the coralligenous and other calcareous bio-concretions in the Mediterranean Sea*" formulated by UNEP-MAP-RAC/SPA (2008) was the first direct acknowledgement of the importance of coralligenous assemblages as a priority habitat in the Mediterranean. This action plan solidified the significance of coralligenous within the scientific community, identified main threats, and underpinned the need to obtain further information regarding the distribution, community composition, dynamics, and conservation status at a Mediterranean level. During the same period, the Marine Strategy Framework Directive – MSFD 2008/56/EC (EU, 2008) introduced the notion of "seafloor integrity" as one of the eleven indicators to evaluate the Good Environmental Status of the marine environment. This ecosystem-based approach substantiated the need to assess and systematically monitor biogenic structures, such as coralligenous assemblages (Rice *et al*., 2012; Borja *et al*., 2013), and instigated research initiatives that established standardised methodological protocols for the study of biodiversity trends (e.g. Kipson *et al*., 2011; Casas-Güell *et al*., 2015, 2016) and health status of coralligenous (e.g. Deter *et al*., 2012; David *et al*., 2014; Ruitton *et al*., 2014; Gatti *et al*., 2015; Montefalcone *et al*., 2017; Piazzi *et al*., 2017; Sartoretto *et al*., 2017; Piazzi *et al*., 2018a). Still, most of the published work focuses on the NW Mediterranean region, while information from other parts of the basin, such as the eastern Ionian and Aegean Seas, is mostly limited to opportunistic surveys and qualitative assessments (e.g. Gerovasileiou *et al*., 2009; Salomidi *et al*., 2009; Issaris *et al*., 2012).

The presence of coralligenous formations in the Aegean Sea was first documented in the late 1950s by Pérès & Picard (1958) and Laborel (1960). In these early expeditions, scientists reported on the occurrence of coralligenous formations in this ecoregion (*sensu* Spalding *et al*., 2007), either as outcrops of the littoral rock developing in the lower infralittoral and circalittoral zones, or as biogenic banks surrounded by detritic substrates (also known as *coralligène de plateau*) found at depths of up to 120 m. Recent mapping efforts have validated the presence of numerous coralligenous formations in most parts of the Aegean Sea (Georgiadis *et al*., 2009; Giakoumi *et al*., 2013; Sini *et al*., 2017). However, the community structure, biodiversity and ecology of these formations remain largely underexplored, while their conservation status is effectively unknown. As highlighted by Sini *et al*. (2017), coralligenous habitats, amongst other ecological features, are locally neglected by existing management schemes such as MPAs, NATURA 2000 sites or Mediterranean fisheries regulations (e.g. Council Regulation 1967/2006 EC; EU, 2006). This underlines the need for dedicated scientific studies that will systematically assess and monitor coralligenous assemblages (e.g. Teixidó *et al*., 2011a; Casas-Güell *et al*., 2015), in order to facilitate the development of meaningful marine spatial plans and conservation actions (Sini *et al*., 2017). Such an approach is vital for the Aegean Sea, an area exposed to severe alterations caused by overexploitation of fisheries resources, sea surface temperature rise, and the introduction of invasive species (Raitsos *et al*., 2010; Coll *et al*., 2011; Katsanevakis *et al*., 2014; Tsikliras *et al*., 2015; Zenetos *et al*., 2018).

This study reports on the assemblage structure and biodiversity of coralligenous formations dominated by the yellow gorgonian *Eunicella cavolini* in three distinct geographic localities of the N Aegean Sea. Focusing on the upper bathymetric limit of this habitat type, we use a spatially structured sampling design and a photoquadrat method to quantitatively assess community and biodiversity patterns across different spatial scales. The information provided through this work offers valuable data that can be used as a reference for future comparisons.

Materials and Methods

Sampling design

Six coralligenous assemblages were investigated within three distinct geographic localities of the N Aegean Sea, which are situated several hundreds of km apart: two sites in the locality of Pelio (Ag. Vasso and Lefteris), two in Chalkidiki (Nemessis and Spilia) and two in the island of Lesvos (Palios and Kalloni) (Fig. 1, Table 1). Within a locality, the distance between sites was greater than 2 km. All assemblages were dominated by the yellow gorgonian *E. cavolini*, which forms a typical ecological facies of the coralligenous across the Mediterranean (UNEP-MAP-RAC/SPA, 2009; Sini *et al*., 2015). At each site, samples were obtained within the upper bathymetric limit of this facies, at depths ranging between 18 and 35 m. Field surveys were carried out from late May to early September. Most sites were sampled in 2011 except for Kalloni site that was sampled in 2013.

Sampling was conducted through a photographic

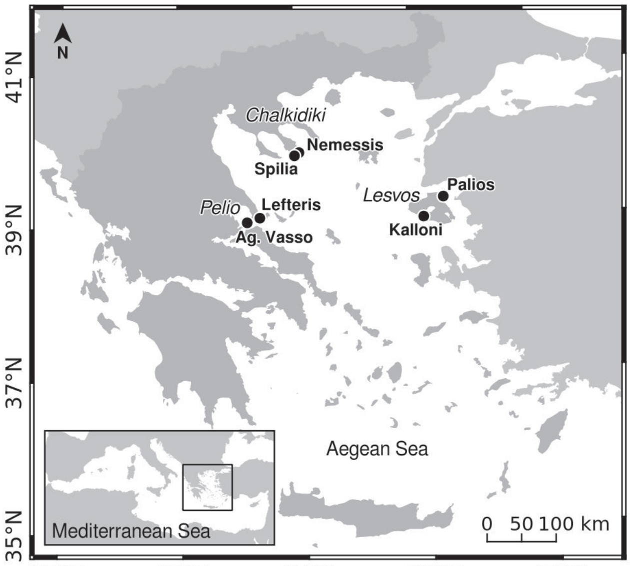

Fig. 1: Map of the Aegean Sea, depicting sites (in black circles and bold) and localities (italics).

Table 1. Characteristics of the N Aegean Sea sites tabulated by locality. Density values of *Eunicella cavolini* were obtained from Sini *et al*. (2015). The + symbol in depth range indicates that coralligenous assemblages expanded to greater depths; ± denotes standard deviation.

Locality	Site	Depth range (m)	Sampled depth (m)	Latitude	Longitude	Habitat	Inclination	*E. cavolini* density (mean ± SD m^{-2})
Pelio	Ag. Vasso	30–50+	30–35	39°05'08"N	23°07'48"E	Rocky outcrops	Sub-vertical	7.8 ± 5.9
	Lefteris	20–30	25–30	39°08'31"N	23°20'39"E	Reef wall	Vertical	10.4 ± 8.2
Chalkidiki	Nemessis	30–50+	30–35	39°56'46"N	23°59'10"E	Reef Wall	Sub-vertical	11.4 ± 8.3
	Spilia	32–50+	32–35	39°56'38"N	23°57'31"E	Reef wall	Sub-vertical	13.3 ± 5.0
Lesvos	Palios	30–44	30–35	39°19'42"N	26°26'10"E	Reef wall	Sub-vertical	6.0 ± 5.3
	Kalloni	10–27	18–25	39°04'56"N	26°05'25"E	Rocky outcrops	Sub-vertical	23.5 ± 19.2

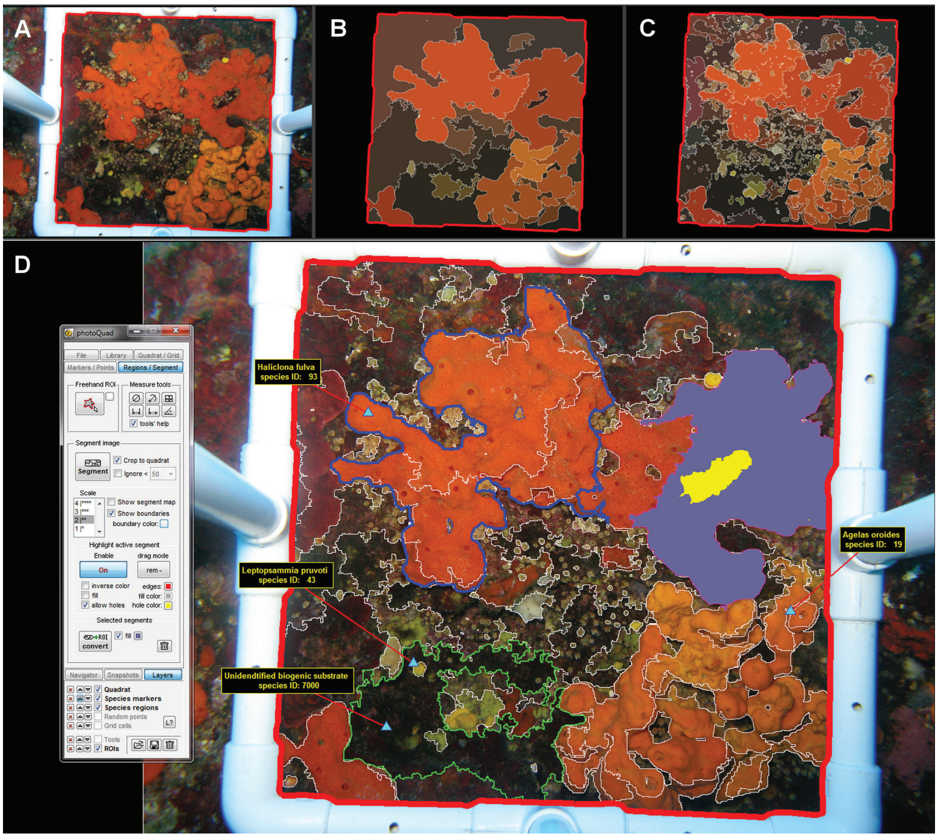

Fig. 2: Screenshots of the photoQuad software depicting a) the raw image sample in which the quadrat area is defined by the red line; b-c) different segmentation levels of the raw image sample; d) interactive processing of the segmented image. Blue and green lines denote assigned species and substrate categories. Purple and yellow patches represent selected image segments which have not yet been assigned to a category.

method, which involves the acquisition of benthic images using a 25×25 cm quadrat frame (Kipson *et al*., 2011). Each sample consisted of eight images, covering a total surface area of 5000 cm^2. The first image of each sample was taken from a haphazardly chosen position within the coralligenous assemblage, whereas the remaining seven images were obtained in a contiguous manner (Fig. S1). A total of three samples were collected per site, summing up to a total surface area of 15000 cm^2 per site, following the minimum sampling area requirements proposed by Kipson *et al*. (2011). Photographs were obtained using a Canon G9 powershot camera (12.1 MP resolution), which was mounted on a custom-made quadrat frame to maintain a fixed distance and position of the device from the sampled surface (Fig. S1a). Photoquadrat sampling provides a fast and non-destructive way to sample vulnerable or difficult to approach benthic habitats, such as the Mediterranean coralligenous, and yields a permanent record that enables direct visual comparisons and monitoring (Bianchi *et al*., 2004; Deter *et al*., 2012). To overcome the limitations involved in the identification of organisms through image samples alone (Bianchi *et al*., 2004), photoquadrat sampling was combined with *in situ* observations and collection of voucher specimens used for further processing and identification in the laboratory (Fig. S1b). The presence of potential stressors or threats

Table 2. List of morpho-functional groups adapted from Garrabou *et al*. (1998) and Casas-Güell *et al*. (2015).

Morpho-functional group	Description
Seasonal algal turf	Annual erect or semi-erect fleshy algal species, with one or multiple zones of attachment to the substratum; includes algal cushions or thin sheets with mixtures of algal species.
Seasonal animal turf	Small seasonal animal species, mainly bryozoans and hydrozoans, usually forming animal cushions or thin sheets with mixtures of species.
Seasonal mixture complex turf	Small seasonal algae and animal species (mainly bryozoans and hydrozoans), sediment, detritus and fragments; normally forming cushions or thin sheets with mixtures of species.
Perennial algal turf	Perennial dense thick filamentous turf algae with the ability to maintain permanent carpets (e.g. *Pseudochlorodesmis furcellata*, the invasive species *Womersleyella setacea*).
Perennial algal encrusting	Species growing mainly as two-dimensional sheets; more or less completely attached to the substratum.
Perennial algal erect	Species attached to the substratum, usually with a unique zone of basal attachment to the substratum (visible even during winter).
Perennial animal boring	Excavating or boring organisms living within the rock (e.g. *Cliona viridis*).
Perennial animal cup	Solitary corals attached to the substratum all along their basal area.
Perennial animal encrusting	Species of sponges, cnidarians, bryozoans and tunicates growing as two-dimensional sheets; more or less completely attached to the substratum.
Perennial animal epibiont	Species growing over other invertebrates or calcareous algae (mainly polychaetes e.g. *Salmacina dysteri*, *Filograna implexa*).
Perennial animal massive	Mound species of sponges and cnidarians with vertical and lateral growth; normally attached to the substratum all along their basal area.
Perennial animal tree	Erect species of cnidarians and bryozoans, more or less branched; usually with a single point of attachment to the substratum.

(such as fishing gear and mucilaginous algal aggregates) was qualitatively noted during each dive to acquire some extra information regarding the present status of the assemblages.

Processing of photographic samples

Photographic quadrat samples were analysed using the image segmentation tool provided by the photoQuad software (Trygonis & Sini, 2012). Image segmentation refers to the automatic partitioning of the source photograph into distinct segments (patches) that share similar colour properties (see also Teixidó *et al*., 2011b). Individual segments were then interactively selected by the user in order to be assigned to specific taxa or any other custom category (Fig. 2). Finally, the relative proportion of individual species and substrate categories to the total quadrat area (percent cover) was automatically calculated by the software.

Sessile organisms were identified to the lowest possible taxonomic level. Visually similar taxa that could not be identified through photographs were aggregated into a) multi-species groups (as in the case of *Crambe crambe/Spirastrella cunctactrix* and *Filograna implexa/Salmacina dysteri*), b) groups of higher taxonomic levels (e.g. genus *Bugula* spp., family Serpulidae indet. - indeterminable), or c) clusters of distinctive morphological features (such as mucilaginous algae and black/grey encrusting sponges). All sessile organisms, including the aforementioned taxonomic groups and morphological clusters (hereafter collectively referred to as species) were then classified within 9 morpho-functional groups based on their taxonomy, generation time and growth form, according to Garrabou *et al*. (1998) and Casas-Güell *et al*. (2015) (Table 2). A full list of the species identified through image samples, and their corresponding morpho-functional groups, is provided in Table S1. The taxonomic names used were cross-checked via the World Register of Marine Species (WoRMS Editorial Board, 2018).

Data treatment and statistical analysis

Number of species and percent cover per morpho-functional group were initially calculated for each sample. For the investigation of community parameters (i.e. biodiversity, structural complexity and species composition), only perennial species were considered to reduce the potential effects of seasonality. Overall, a spatially structured design was followed using geographic localities (3 levels, located hundreds of km apart) as a random factor, and sites (2 levels, located more than 2 km apart) as a random factor nested within localities. Number of perennial species (presence/absence transformation) and percent cover data (square-root transformation) were used to investigate structural complexity and species composition through multivariate analyses based on Bray-Curtis resemblance matrices (Anderson, 2001). Permutational analysis of variance (PERMANOVA; 9999 permutations) was used to check for statistical differences at distinct spatial scales. Additional pairwise comparisons were performed for groups of data when the main tests indicated significant differences. Non-metric multidimentional scaling (MDS) ordinations were employed for the graphical depiction of spatial patterns. Similarity percentage analyses (SIMPER) were used to investigate the level of similarity/dissimilarity between localities and sites, and to identify the taxa with the greatest contribution to the observed patterns.

For the study of biodiversity, only perennial organisms identified to a low taxonomic level were used, i.e. 81 taxa identified to species or genus level. Biodiversity was assessed by quantifying alpha (α-) diversity (mean number of perennial taxa per site), gamma (γ-) diversity (total number of perennial taxa per locality), and beta (β-) diversity (the percentage of unshared perennial taxa using multivariate distance between group centroids determined by the PERMDISP procedure). PERMDISP is a statistical technique used for comparing the degree of sample dispersion of different groups, based on a distance matrix. When PERMDISP is applied to a Jaccard distance presence/absence matrix, it can be regarded as equivalent to a test for similarity in β-diversity among groups (Anderson *et al.*, 2006). For the comparison of α-diversity between sites and localities, a PERMANOVA (9999 permutations) analysis was conducted based on untransformed data and a Euclidean distance matrix (Anderson, 2001). The relative contribution of individual species to the total biotic cover per site was visualized through the construction of a pseudo-colour map. All analyses were carried out using PRIMER v6 software with PERMANOVA+ add-on package (Clark & Gorley, 2006; Anderson *et al.*, 2008).

Results

Structural components

The combined investigation of photoquadrats, field observations and voucher specimens led to the identification of 99 macrobenthic taxa belonging to 10 higher taxonomic groups, namely Porifera (40 taxa), Rhodophyta (12), Cnidaria (11), Bryozoa (11), Chlorophyta (7), Tunicata (6), Annelida (5), Mollusca (4), Ochrophyta (2) and Foraminifera (1) (see Table S1 for a full list). All sites pooled, Porifera had the highest number of species (mean ± standard deviation = 20.5 ± 4, $n = 18$ samples), followed by Rhodophyta (9.2 ± 3), Cnidaria (5.8 ± 2), Bryozoa (5.5 ± 3), and Chlorophyta (4 ± 2.2).

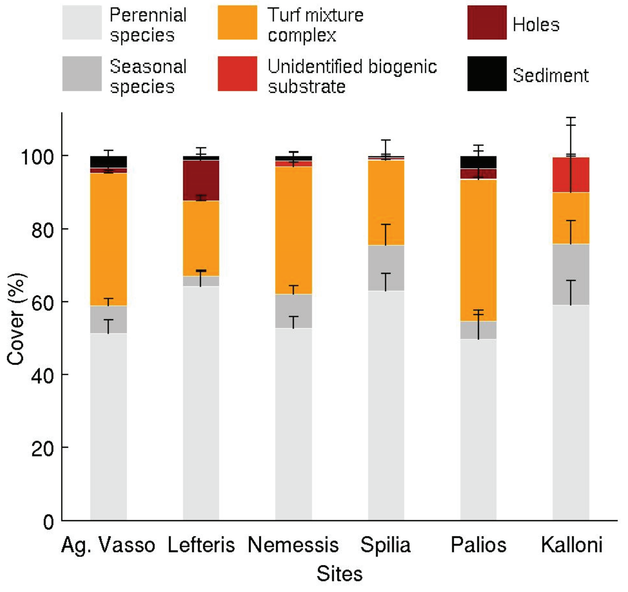

Fig. 3: Mean percent cover (%) of the main substrate categories recorded per site. Total area sampled per site is 1.5 m^2, corresponding to $n = 3$ samples (8 images each). Error bars denote standard deviation.

The percent cover of the different substrate or biotic categories recorded is presented in Fig. 3. Biotic elements (including perennial species, seasonal species and turf mixture complex) had the greatest percent cover of the sampled surface area (93.7 ± 4%, $n = 18$ samples), ranging from 88% at Lefteris site (Pelio locality) to 99% at Spilia site (Chalkidiki locality). The lower mean biotic cover at Lefteris site was related to the pronounced cover of holes (11.1 ± 3.4%, $n = 3$ samples), indicating increased substrate rugosity. Sediment cover was less than 5% per site, while unidentified biogenic substrate was mainly recorded at the Kalloni site (9.7 ± 8.6%, $n = 3$ samples).

Out of the 99 taxa recorded, 10 were seasonal (percent cover: 8.9 ± 5%, $n = 18$ samples) and 89 were perennial (percent cover: 56.7 ± 6%, $n = 18$ samples). The perennial morpho-functional group with the highest number of species across all sites (Fig. 4a-f) was the Animal encrusting (11.4 ± 2.8, $n = 18$ samples) followed by Algae encrusting (6.4 ± 2.4), Animal massive (4.4 ± 2.6), Animal tree (4.4 ± 1.4), and Animal cup (2.7 ± 1.6). The remaining groups, namely, Algae erect, Algae turf, Animal borer and Animal epibiont, were mainly represented by only one or two species. In terms of percent cover (Fig. 4g-l**)**, Algae encrusting (25.6 ± 16.3%, $n = 18$ samples) was the most abundant perennial morpho-functional group across all sites. Animal massive (12.6 ± 9.7%) and Animal encrusting (11 ± 11.6%) also had a relatively large contribution to percent cover, especially at the Pelio and Lesvos localities. The Animal tree group (3.7 ± 2%) was mainly represented by *E. cavolini*, while Algae erect (2.4 ± 4.2%) was more abundant at the two sites of Chalkidiki locality. The remaining groups had a very low contribution to the overall biotic cover, less than 1% each. The relative contribution of benthic perennial species to the total biotic cover per site, tabulated by morpho-functional group is presented in Figure 5.

Assemblage structure, based on perennial morpho-functional group data, displayed no significant differences at the locality level (number of species: $F_{(2,17)} = 4.0$, $p > 0.05$; percent cover: $F_{(2.17)} = 2.8$, $p > 0.05$). However, it was significantly different at the site level, both in terms of species number ($F_{(2,17)} = 2.7$, $p < 0.05$) and percent cover ($F_{(2,17)} = 3.9$, $p < 0.05$; Table S2). Pairwise comparisons indicated significant differences in species number between the Ag. Vasso and Lefteris sites (Pelio locality) (Table S2). The Lefteris site had a higher number of species belonging to the groups Animal encrusting (Lefteris 15.3 ± 1.1, $n = 3$ samples; Ag. Vasso: 12 ± 1, $n = 3$ samples), Animal tree (Lefteris: 5.3 ± 2; Ag. Vasso: 3.7 ± 1.1) and Animal cup (Lefteris: 5.7 ± 0.6; Ag. Vasso: 3.3

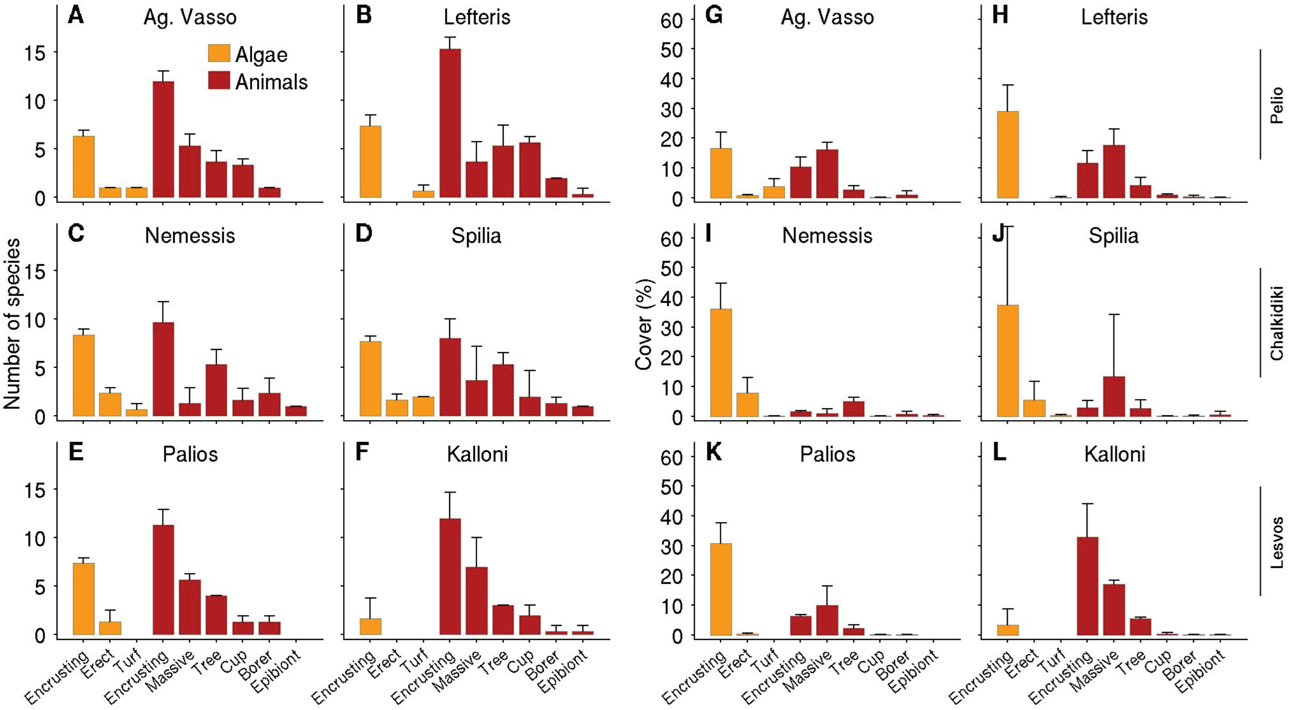

Fig. 4: (a-f) Mean number and (g-l) mean percent cover (%) of perennial morpho-functional algal and sessile animal groups recorded per site, tabulated by geographic locality (Pelio, Chalkidiki, Lesvos). Total area sampled per site is 1.5 m^2, corresponding to $n = 3$ samples (8 images each). Error bars denote standard deviation.

± 0.6), whereas Ag. Vasso had a higher number of Animal massive (Lefteris: 3.7 ± 2; Ag. Vasso: 5.3 ± 1). In terms of percent cover, significant differences were observed between the Ag. Vasso and Lefteris sites (Pelio locality), and also between the Palios and Kalloni sites (Lesvos locality). Specifically, within the Pelio locality, Lefteris site was characterized by a greater percent cover of Algae encrusting (29.1 ± 9%) compared to Ag. Vasso (16.6 ± 5.3%). At the Lesvos locality, Palios site was dominated by Algae encrusting (Palios: 30.8 ± 6.8%; Kalloni: 3.3 ± 5.4%), whereas Kalloni site was dominated by Animal encrusting (Palios: 6.3 ± 0.5%; Kalloni: 32.9 ± 11.2%).

Community composition

Community composition, based on number and percent cover of perennial species, displayed no significant differences at the locality level (number of species: $F_{(2,17)} = 1.7$, $p > 0.05$; percent cover: $F_{(2.17)} = 1.5$, $p > 0.05$), but was significantly different at the level of sites nested within locality (number of species: $F_{(3.17)} = 5.0$, $p < 0.05$; percent cover: $F_{(3.17)} = 4.8$, $p < 0.05$; Table S3). Pairwise comparisons indicated significant differences between the Ag. Vasso and Lefteris sites (Pelio locality), and the Palios and Kalloni sites (Lesvos locality), both in terms of number of species and percent cover (Table S3). The resulting spatial patterns are presented in Fig. 6.

According to the SIMPER analyses, the overall percentage similarity among all localities of the N Aegean was 44% (Table 3). Pelio displayed the highest within-locality similarity (62%), followed by Chalkidiki (58%) and Lesvos (39%). The highest between-locality dissimilarity (Table S4) was observed between Chalkidiki and Lesvos (66%) followed by Pelio and Lesvos (60%), and finally Pelio and Chalkidiki (54%). The species per morpho-functional group with the greatest contribution to the observed similarity or dissimilarity at the level of localities are presented in Table 3 and Table S4, respectively. Specifically, seven species accounted for approximately 50% of the overall similarity observed among all N Aegean localities, namely, Encrusting calcareous algae, *Peyssonnelia squamaria*, *Peyssonnelia* spp., *Mesophyllum* spp., *Crambe crambe/Spirastrella cunctatrix*, *Agelas oroides*, and *E. cavolini*. Species belonging to the Algae encrusting and Animal encrusting groups, along with the massive sponge *A. oroides*, had the greatest contribution to the observed similarity in Pelio (72.9%). Algae encrusting species together with *F. petiolata* made up the greatest percentage of similarity in Chalkidiki (69.3%), whereas several species belonging to the Algae encrusting, Animal encrusting and Animal massive groups contributed to the similarity of Lesvos (73.5%).

At the level of sites, average dissimilarity between Ag. Vasso and Lefteris (Pelio locality, Table S5) was 44%, mainly due to the greater percent cover of Chlorophyta (*Cladophora pellucida* and *Flabellia petiolata*) and of the massive sponge *A. oroides* at Ag. Vasso, while Lefteris site had a higher percent cover of several Algae encrusting species and the massive sponge *Chondrosia reniformis*. Between the Palios and Kalloni sites (Lesvos locality, Table S6), the average dissimilarity was 75%. Palios had a higher percent cover of the Algae encrusting group (*Neogoniolithon mamillosum*, *Lithophyllum*

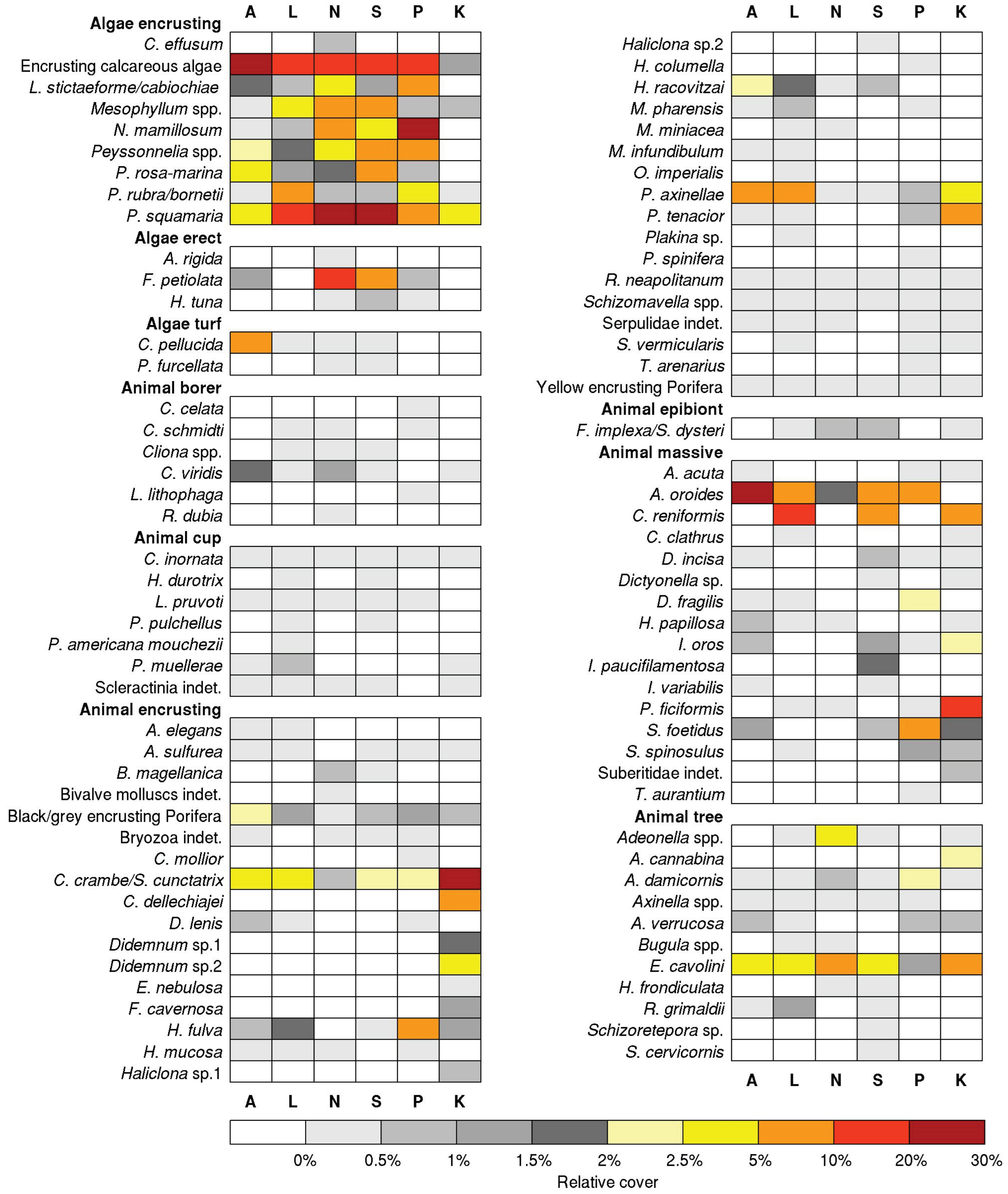

Fig. 5: Relative contribution (%) of benthic perennial species to the total biotic cover per site, tabulated by morpho-functional group. Columns represent sites, denoted by upper-case letters; A: Ag. Vasso, L: Lefteris, N: Nemessis, S: Spilia, P: Palios, K: Kalloni. Relative cover sums to 100% per site.

stictaeforme/cabiochiae, *Peyssonnelia* spp., and Encrusting calcareous algae), while *A. oroides* was the most abundant animal species. At Kalloni site, the group with the highest mean percent cover was Animal encrusting (*C. crambe/S. cunctatrix*, *Cystodytes dellechiajei*, *Phorbas tenacior*), along with Animal massive, mainly due to *Petrosia ficiformis* and *C. reniformis*.

Biodiversity patterns

The mean number of species per site (α-diversity; Table 4) ranged between 23 ± 4.8 at Kalloni and 33 ± 4.2 at Lefteris, and presented no significant differences both at the level of localities ($F_{(2.17)} = 3.48$, $p > 0.05$) and at the level of sites ($F_{(3.17)} = 1.08$, $p > 0.05$; Table S7). The per-

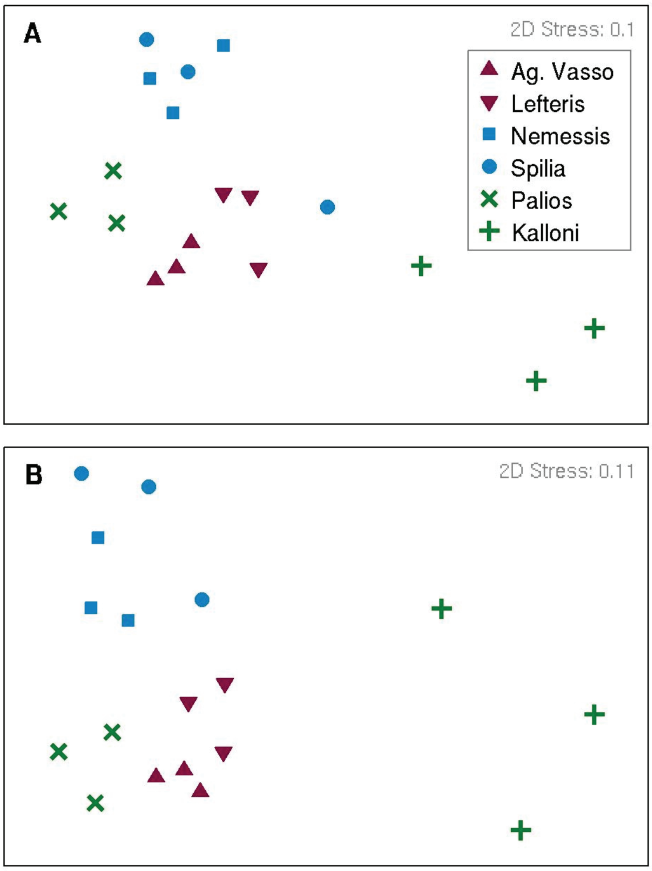

Fig. 6: Multidimensional scaling analysis (MDS) of coralligenous assemblages based on a) percent cover (square root transformation) and b) number of perennial species (presence/absence transformation). Points indicate the $n = 3$ samples (8 images each) acquired per site; colours and symbols denote geographic locality.

centage of unshared species (β-diversity; Table 4, Table S7) was similar across sites, but was significantly different between localities; Lesvos values (42.3 ± 1.8%) were higher compared to Pelio (28.7 ± 1.4%) and Chalkidiki (31.8 ± 1.4%). In terms of γ-diversity, the total number of taxa observed was similar across localities; Lesvos had the highest number of species (58), followed by Pelio (54), and Chalkidiki (52) (Table 4).

Discussion

The results show that coralligenous assemblages of the N Aegean Sea dominated by *E. cavolini* in waters shallower than 40 m encompass an extensive number of conspicuous sessile organisms, including several protected and commercially important species (see also Table S8 for a full inventory). Most of the species recorded herein have also been noted in coralligenous communities that develop over a similar depth range in the NW Mediterranean (e.g. Cocito *et al.*, 2002; Kipson *et al.*, 2011; UNEP-MAP-RAC/SPA, 2011; Deter *et al.*, 2012; Gatti *et al.*, 2012; Teixidó *et al.*, 2013; Piazzi *et al.*, 2014), the Adriatic (Ponti *et al.*, 2011; Kipson, 2013), the Ionian Sea (Longo *et al.*, 2018), and in other hard substrate sciaphilous assemblages of the N Aegean Sea (Antoniadou *et al.*, 2006).

Algae encrusting was the most abundant morpho-functional group at the majority of sites. The calcareous species *N. mamilosum*, *L. stictaeforme/cabiochiae*, *Mesophyllum* spp. and *P. rosa-marina* were among the main contributors of this group, but their relative contribution to the total percent cover varied among sites. These four taxa have been identified as the main algal bio-constructors of coralligenous formations in most regions of the Mediterranean (Feldmann, 1937; Hong, 1983; Piazzi *et al.*, 2010; Teixidó *et al.*, 2013), and differences in their relative contribution to coralligenous built-ups have been related to depth, light, temperature, and hydrodynamic conditions (Giaccone, 1968; Sartoretto *et al.*, 1996; Garrabou & Ballesteros, 2000; Ballesteros, 2006).

In terms of animal species, most sites were characterised by an extensive cover of sponges, which present different forms and functional roles in the structuring of the coralligenous frameworks. These included a) encrusting species (e.g. *C. crambe/S. cunctatrix*, *Dysidea fragilis*, *Haliclona fulva*) that expand over large surface areas and play a structural role by binding different substrate components (Fagerstrom, 1991; Cocito, 2004); b) massive (e.g. *A. oroides*, *C. reniformis*, *Sarcotragus foetidus*) and erect sponges (e.g. species of the genus *Axinella*) which, alongside the gorgonian *E. cavolini*, contribute to the three-dimensional complexity of assemblages and provide additional microhabitats for numerous macro- or micro-dwelling species (Koukouras *et al.*, 1985; Cúrdia *et al.*, 2015; Gerovasileiou *et al.*, 2016); and c) species of the genus *Cliona* which, together with sea urchins and the molluscs *Rocellaria dubia* and *Lithophaga lithophaga*, represent the main bio-eroders of coralligenous throughout the Mediterranean (Cerrano *et al.*, 2001; Ballesteros, 2006). The percent cover of other animal species was low and only locally pronounced at few sites. Specifically, even though bryozoans represent an important component of coralligenous assemblages in other parts of the Mediterranean (e.g. Ferdeghini *et al.*, 2000, 2001; Kipson *et al.*, 2011; Piazzi *et al.*, 2014), the number of conspicuous, erect bryozoan species was relatively low at the investigated sites, and their total cover was less than 1%. Furthermore, although a considerable number of scleractinian species were recorded, there was an overall lack of large anthozoans, such as alcyonarians or gorgonians (apart from *E. cavolini*). This observation is in agreement with previous reports regarding other regions of the Aegean Sea and the rest of the Mediterranean, which suggest that due to the higher water temperatures and more oligotrophic conditions, large anthozoans are usually limited to deeper waters (Pérès & Picard, 1958; Laborel, 1960; Zabala & Ballesteros, 1989; Salomidi *et al.*, 2009).

The total number of taxa (including both perennial and seasonal) recorded in the Aegean is comparable to the total numbers reported from coralligenous assemblages dominated by the red gorgonian *Paramuricea clavata* in the Central and Northern Adriatic (Kipson, 2013) and the NW Mediterranean (Kipson *et al.*, 2011; Casas-Güell

Table 3. Summary of similarity percentage analysis (SIMPER) listing species per morpho-functional group (MFG) that cumulatively contribute 80% to the observed similarity (Bray Curtis) of coralligenous assemblages in the N Aegean (overall) and within localities (Pelio, Chalkidiki, Lesvos). Analysis was performed on square-root transformed data of perennial species percent cover.

Similarity							
Overall (43.8%)	%	Pelio (62.2%)	%	Chalkidiki (58.1%)	%	Lesvos (39.4%)	%
Algae encrusting							
Encrusting calc. algae	13.9	Encrusting calc. algae	13.2	*P. squamaria*	16.7	Encrusting calc. algae	8.0
P. squamaria	10.6	*P. squamaria*	7.7	Encrusting calc. algae	13.2	*N. mamillosum*	4.7
Peyssonnelia spp.	4.8	*Peyssonnelia* spp.	3.3	*Mesophyllum* spp.	7.9	*P. squamaria*	4.5
Mesophyllum spp.	4.4	*P. rubra/bornetii*	2.6	*Peyssonnelia* spp.	5.8	*L. stictaeforme/ cabiochiae*	2.8
L. stictaeforme/cabiochiae	3.8	*Mesophyllum* spp.	2.5	*L. stictaeforme/ cabiochiae*	5.0	*Peyssonnelia* spp.	2.7
N. mamillosum	3.1	*P. rosa-marina*	2.2	*N. mamillosum*	4.7		
P. rubra/bornetii	2.5	*L. stictaeforme/ cabiochiae*	2.0	*P. rosa-marina*	3.3		
P. rosa-marina	2.1			*P. rubra/bornetii*	2.3		
Algae erect							
F. petiolata	2.8	–		*F. petiolata*	10.4	–	
Algae turf							
–		*C. pellucida*	2.7	–		–	
Animal encrusting							
C. crambe/S. cunctatrix	6.6	*P. axinellae*	9.6	*C. crambe/S. cunctatrix*	2.6	*C. crambe/S. cunctatrix*	12.3
P. axinellae	4.1	*C. crambe/S. cunctatrix*	5.5	–		*H. fulva*	6.0
Black/grey encrusting Porifera	4.0	*H. racovitzai*	4.5	–		Black/grey encrusting Porifera	4.4
C. reniformis	2.6	Black/grey encrusting Porifera	3.8	–		*P. tenacior*	4.1
–		*C. reniformis*	2.4	–		*P. axinellae*	3.0
–		–		–		*Schizomavella* spp.	2.8
–		–		–		*C. dellechiajei*	2.7
–		–		–		–	
Animal massive							
A. oroides	6.3	*A. oroides*	13.6	–		*P. ficiformis*	5.6
–		–		–		*A. oroides*	3.5
–		–		–		*C. reniformis*	3.4
–		–		–		*S. foetidus*	3.0
Animal tree		–					
E. cavolini	8.4	*E. cavolini*	6.6	*E. cavolini*	7.1	*E. cavolini*	6.8
–		–		*Adeonella* spp.	2.9	–	

Table 4. Measures of α- (mean number of perennial taxa per site), β- (percentage of unshared perennial taxa), and γ- (total number of perennial taxa per locality) diversity. ± denotes standard error.

Locality/Site	α-diversity	β-diversity	γ-diversity
Pelio	–	28.7 ± 1.4	54
Ag. Vasso	28.7 ± 1.5	21.7 ± 1.9	–
Lefteris	33.3 ± 4.2	21.5 ± 1.6	–
Chalkidiki	–	31.8 ± 1.4	52
Nemessis	26.0 ± 4.4	21.4 ± 1.9	–
Spilia	26.7 ± 6.1	27.3 ± 2.7	–
Lesvos	–	42.3 ± 1.8	58
Palios	26.7 ± 1.5	24.8 ± 1.4	–
Kalloni	23.0 ± 4.8	32.6 ± 3.0	–

et al., 2015), as well as those dominated by the red coral *Corallium rubrum* in the NW Mediterranean (Kipson *et al*., 2011; Casas-Güell *et al*., 2016). Regarding perennial species alone (which represent the core community of coralligenous assemblages), a low variability was observed both at the level of sites (range: 23–33 taxa) and at the level of localities (range: 52–58 taxa). The values of α- and γ-diversity, based on perennial species, were also comparable to those reported from coralligenous assemblages at three localities of the NW Mediterranean Sea (Casas-Güell *et al*., 2015, 2016).

Coralligenous assemblages are intrinsically variable and identifying the scale at which variability is predominantly expressed is a focal issue in their study in order to meaningfully assess spatial patterns, e.g. in response to natural or anthropogenic stressors. As commonly documented (Garrabou *et al*., 2002; Piazzi *et al*., 2004, 2014), abiotic conditions and associated biotic interactions for limited resources (space, light and food) result to the patchy distribution of organisms, and hence, to an increased variability within the same assemblage. It is thereby not surprising that several studies have reported higher small-scale variability (even at the level of replicate sample) linked to physical habitat features, such as depth, orientation, substrate inclination and sedimentation (e.g. Balata *et al*., 2005; Virgilio *et al*., 2006; Bedini *et al*., 2014). Structural complexity and species composition of coralligenous assemblages in the N Aegean Sea presented consistent patterns at distinct spatial scales, and some degree of variability was found at all levels (from locality to replicate samples). However, statistical differences were mainly detected at the level of sites situated within the same geographic locality. These findings suggest that, despite localised differences, coralligenous assemblages of the N Aegean Sea are overall similar. This is in accordance with previous studies, which report a generalized homogeneity in community composition at large geographic scales (Piazzi *et al*., 2004, 2014; Casas-Güell *et al*., 2015).

At the locality level, assemblages presented a rather uniform structure. The upper stratum (>10 cm height; *sensu* Gatti *et al*., 2012) was dominated by the yellow gorgonian *E. cavolini*, which had a mean density range between 6 and 23 colonies per m^2 (Table 1), although the percent cover in the analysed images was low as only the basal part of the colonies was considered. Erect sponges of the genus *Axinella* also contributed to this upper stratum, thus enhancing structural complexity at certain sites. In the intermediate layer (1–10 cm height), Animal massive –especially massive sponges– prevailed in percent cover; the Animal tree group had a similar number of species with the Animal massive group, but their contribution to the percent cover was relatively low. The basal layer (<1 cm height) presented an increased cover of turf-mixture, which, along with Algae encrusting and Animal encrusting species, had an overall mean cover of more than 60%. The remaining morpho-functional groups (Algae turf, Algae erect, Animal borer, Animal cup, Animal epibiont) were relatively low both in species number and area cover, and hence had a small contribution to the overall variability. Again, these results indicate a comparative similarity in structural complexity between the *E. cavolini* dominated assemblages of the N Aegean Sea and those characterised by the presence of *P. clavata* in the NW Mediterranean (Casas-Güell *et al*., 2015). Moreover, community composition displayed a similarity level of 44% across the N Aegean localities, most of which (approximately 80%) was explained by 16 perennial taxa (Table 3). On the other hand, a significant between-localities variability was detected in β-diversity, which was also reflected in the SIMPER analyses. These differences were mainly due to a higher percentage of unshared species between Lesvos and the remaining localities, and the prevalence of prostrate or erect algal species (especially *P. squamaria* and *F. petiolata*) in Chalkidiki compared to Pelio or Lesvos localities; the latter had a greater number of encrusting and massive animal species.

At the site level, significant differences were observed between the two sites of Pelio (i.e. Ag. Vasso and Lefteris) and the two sites of Lesvos (i.e. Palios and Kalloni), while no differences were detected between the Chalkidiki sites. As in previous reports (e.g. Ferdeghini *et al*., 2000; Tamburello *et al*., 2012; Bedini *et al*., 2014; Bevilacqua *et al*., 2018), these differences can be related to variations in environmental factors, disturbance levels, and the associated species interactions, which generate different aspects of the coralligenous. Regarding the differences observed within the Pelio locality, Lefteris reef is a north-facing vertical wall that is characterised by high substrate rugosity, whereas Ag. Vasso is composed of numerous small rocky outcrops with small inclination and a southeast orientation. Because of these somewhat different physiognomic profiles, Lefteris reef is shadier than Ag. Vasso, despite that the former is located in shallower waters (20–30 m and 30–50+ m, respectively). For this reason, the coralligenous assemblage at Lefteris site had a lower cover of chlorophytes than that of Ag. Vasso, and supported a very diverse animal community, particularly sponges and anthozoans. This observation is in line with previous studies which have indicated that coralligenous assemblages of vertical walls are mainly composed of sponges and scleractinians (Ros *et al*., 1985; Cocito *et al*., 2002).

Within Lesvos locality, Kalloni differed significantly from Palios site. Overall, community composition at Palios reef was similar to the coralligenous assemblages found in other localities, and was characterised by a high cover of encrusting coralline algae (particularly *N. mamilosum* and *L. stictaeforme/cabiochiae*) along with a high diversity of sponge species. On the contrary, coralligenous assemblages of Kalloni had a high dissimilarity compared to all other investigated sites, as in the former, the cover of encrusting coralline algae was particularly low and replaced by a high cover of encrusting sponge and tunicate species. As these results reflect differences in the percent cover of perennial species alone, it is suggested that the observed dissimilarity in community structure is due to factors other than seasonal variations. Kalloni is situated within a narrow channel that connects a large highly-productive enclosed bay with the open sea, and is characterised by high turbidity, increased levels of naturally-induced sedimentation, and high current velocities generated by tidal and wind forces (Millet & Lamy, 2002). Hence, the notable divergence of Kalloni from the rest of the investigated sites is possibly due to the extreme environmental conditions dominating the specific area, which promote the growth of coralligenous assemblages and gorgonian populations in shallower waters (15 m) than those of the rest of the Aegean Sea (Sini *et al*., 2015). While further investigation of the abiotic factors is essential to better understand the observed community patterns, it is possible that the increased cover of animal species in Kalloni is due to a competitive advantage of animal versus coralline algal species under the reduced light conditions induced by the high turbidity and sedimentation levels (Irvin & Connell, 2002; Balata *et al*., 2005), and the prevalence of strong currents that enhance the growth of large suspension feeders (Zabala & Ballesteros, 1989). Next to the prevalent effects of natural factors, Kalloni is also more exposed to human-induced disturbances. Considering its shallow depth range, stressors include direct mechanical damage caused by fishing gear (especially long-lines, traps and nets) that were scattered over most parts of the site, recurrent periods of nutrient loads which have been previously recorded in the wider area (Pavlidou *et al*., 2005; Spatharis *et al*., 2007, 2009), and potential thermal anomalies of the water column. It is important to note that, during this study, assessment of gorgonian populations at Kalloni indicated the occurrence of a mass mortality episode. Specifically, *E. cavolini* colonies showed extensive tissue loss and overgrowth by other organisms (Sini *et al*., 2015), while in shallower, more illuminated parts of the site (<15 m) a dense population of the white gorgonian *E. singularis* almost disappeared within approximately two years. Although necrosis of other benthic organisms was not systematically measured in the photoquadrat samples, individuals of several sponge species in Kalloni displayed visible signs of partial damage or were overgrown by turf and filamentous mucilaginous algae. Given the lack of regular monitoring, neither the causes that triggered this outbreak, nor the time of initiation and duration of the stressor/s involved can be directly addressed through this study. However, it is possible that the distinctive composition of coralligenous assemblages at Kalloni site is a result of a large disturbance that led to a shift in community structure and caused the prevalence of encrusting animal forms. A similar observation of a shift from erect to encrusting forms was also observed by Di Camillo & Cerrano (2015), following two consecutive mass mortality outbreaks in the NW Adriatic.

At the remaining sites, the common presence of damaged nets and fishing lines in all investigated areas highlights the widespread occurrence of the threats posed by ghost fishing and marine debris, the effects of which require long term monitoring to assess. The invasive species *Womersleyella setacea* was observed at both sites of Chalkidiki, while *Caulerpa cylindracea* was recorded at Palios site (Lesvos locality); however, their benthic cover was more pronounced in the shallower parts of the sampling sites, and neither of them was present in the photographic samples. The presence of these two species has previously been reported at a similar depth range from sites located close to our respective investigated areas (Antoniadou & Chintiroglou, 2007; Gerovasileiou *et al*., 2009). Moreover, filamentous mucilaginous algal aggregates were observed to periodically flourish at several sampled sites and to fully cover gorgonian colonies. Although no apparent ecological damage was detected, their potentially harmful effects on benthic organisms (mainly caused through starvation or suffocation) may be exacerbated under conditions that enhance their prolonged persistence (Giuliani *et al*., 2005; Schiaparelli *et al*., 2007; Piazzi *et al*., 2018b).

This study represents the first quantitative assessment of the shallow coralligenous assemblages of the N Aegean Sea, and directly addresses the need for baseline data regarding their diversity and conservation status (UNEP-MAP-RAC/SPA, 2008; UNEP-MAP-RAC/SPA, 2015). By focusing on assemblages that are dominated by the yellow gorgonian *E. cavolini*, this work contributes to the better understanding of one of the most characteristic coralligenous facies across the Mediterranean, and provides important reference data that can serve as a basis for future comparisons at a local and regional scale. It further highlights the need for additional sampling efforts in space and time and the implementation of systematic monitoring. These will improve our understanding of current trends, reinforce the evaluation of conservation status in different parts of the Aegean Sea, and help mitigate potential disturbances or threats through effective conservation planning and management.

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