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Assessment of macroalgal communities on shallow rocky reefs in the Aegean Sea indicates an impoverished ecological status

Andrei SAVIN[1], Maria SINI[1], Ioanna XYNOGALA[1], Vasiliki LIOUPA[1], Konstantina VOUGIOUKALOU[1], Konstantinos STAMATIS[1], Simona NOÈ[1,2], Michail RAGKOUSIS[1], Vasilis GEROVASILEIOU[1,3,4], Thanos DAILIANIS[1,4] and Stelios KATSANEVAKIS[1]

[1]Department of Marine Sciences, University of the Aegean, 81100 Mytilene, Greece
[2] Department of Animal Conservation and Public Engagement, Stazione Zoologica Anton Dohrn, 80121 Naples, Italy
[3] Department of Environment, Faculty of Environment, Ionian University, 29100 Zakynthos, Greece
[4] Hellenic Centre for Marine Research (HCMR), Institute of Marine Biology, Biotechnology and Aquaculture (IMBBC), 71500 Heraklion Crete, Greece

Corresponding author: Maria SINI; mariasini@marine.aegean.gr

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Abstract

Mediterranean rocky reefs are undergoing regime shifts, from a structurally complex and diverse state dominated by canopy-forming macroalgae to a degraded one characterised by low-lying turf or encrusting macroalgal species, due to increased anthropogenic pressure and climate change. Using data gathered from 89 sites across the entire Aegean Sea, this study aims to provide the most comprehensive health status assessment of shallow rocky reefs in the area, based on macroalgal community structure. Overall, 2520 benthic images were collected through photoquadrat sampling at 0, 5 and, 15 m depth. Five macroalgal and seven invertebrate morphofunctional groups, along with four substrate categories, were considered for community structure description. Health status was assessed using the reef-EBQI and EEI-c indices. Results indicate turf as the most widespread macroalgal group (36.8% average area cover), followed by encrusting calcareous (16.6%), shrubby (12.7%), articulated calcareous (8.9%), and canopy-forming algae (3.7%). Bare rock also occupied a substantial surface area (9.0%) with highest cover (13.8%) at 5 m. The area cover of canopy-forming algae was particularly low, ranging from 10% at 0 m to 0.1% at 15 m depth, on average. All depths pooled, according to the reef-EBQI index, the ecological status of the Aegean Sea was estimated to be 'Bad', mainly due to the bad ecological status of the 5 and 15 m stations. At 0 m depth, the status of the Aegean Sea was ranked 'Moderate' according to the reef-EBQI index and 'Good' according to the EEI-c index. The results underline the importance of considering a wide depth range when assessing the health status of rocky reef communities.

Keywords: Hard substrate; community structure; ecological status; biotic indices; photoquadrat sampling; regime shift; Mediterranean Sea.

Introduction

Rocky bottoms represent one of the most widespread, diverse, and productive coastal ecosystems in the Mediterranean Sea, playing a pivotal ecological role in the structure and function of marine communities and offering multiple services to human societies (Bevilacqua *et al.*, 2021). In the infralittoral zone, rocky reef communities are generally dominated by a high diversity of macroalgal species, whose distribution and abundance are controlled by the dynamic interplay of bottom-up (e.g., light and nutrient availability, substrate lithology) and top-down (e.g., herbivory) processes (e.g., Sala *et al.*, 1998; Garrabou *et al.*, 2002; Airoldi *et al.*, 2003; Guidetti *et al.*, 2004; Medrano *et al.*, 2020). Overall, rocky reef macroalgal assemblages display high seasonality. The best-preserved sites are characterised by perennial canopy-forming species, namely of the genera *Cystoseira*, *Ericaria*, *Gongolaria*, and *Sargassum* (class Phaeophyceae, order Fucales). These species act as autogenic ecosystem engineers and form dense stands (also known as macroalgal forests), which provide habitat to highly speciose animal assemblages and support rich food webs (Piazzi *et al.*, 2018).

However, Mediterranean rocky reefs are threatened by various human-induced stressors (Sala *et al.*, 2012; Bevilacqua *et al.*, 2021). The Mediterranean Sea has been classified as one of the most threatened marine areas of the world due to the increasing levels of anthropogenic pressures (Halpern *et al.*, 2008; Dailianis *et al*., 2018). At the same time, it is considered a climate change hot spot, as surface waters have been shown to warm up 3-6 times faster than the global ocean warming rate (Cramer *et al.*, 2018; Pisano *et al.*, 2020), while marine heatwaves drive recurrent mass mortalities of rocky reef biota (Garrabou *et al.*, 2019, 2022).

Increased pressures exerted on nearshore rocky reefs have led to regime shifts, from a complex and highly diverse state, dominated by canopy-forming macroalgae, to a degraded one with less diverse and structurally simplified communities (Benedetti-Cecchi *et al.*, 1998; Sala *et al.*, 2011; Rindi *et al.*, 2018). Over the years, canopy-forming macroalgal species have suffered substantial declines in species diversity, area cover, and biomass, in different parts of the Mediterranean (Thibaut *et al.*, 2005; Tsiamis *et al.*, 2013b; Blanfuné *et al.*, 2016; Rindi *et al.*, 2020). The ultimate state of degradation is the total disappearance of macroalgae and the persistence of rocky barrens or areas dominated by encrusting and turf-forming algal species (Sala *et al*., 2011, 2012; Boudouresque & Verlaque, 2013; Vergés *et al.*, 2014a). This decline in abundance and coverage of macroalgal forests has generally been attributed to several ongoing pressures, such as habitat destruction, pollution, overgrazing, and sea surface temperature rise (e.g., Soltan *et al.*, 2001; Thibaut *et al.*, 2005; Rilov, 2016). Moreover, overfishing is known to play a crucial role in this gradual loss of macroalgal forests, and hence rocky reef health status reduction, through a cascading top-down regulation effect, as the decline of predatory fish has led to an increase in sea urchin populations and to the subsequent overgrazing of canopy-forming algal species (Guidetti, 2006; Sala *et al.*, 1998, 2012; Ling *et al.*, 2015; Tsirintanis *et al.*, 2018). In turn, the loss of macroalgal forests, which provide essential habitats for reproduction and growth of other organisms, inhibits the replenishment of predatory fish populations (Cheminée *et al.*, 2013). The expansion of herbivorous alien fishes *Siganus luridus* (Rüppell, 1829) and *S. rivulatus* Forsskål & Niebuhr, 1775, is also known to amplify the overgrazing problem and contribute to the increase of rocky barrens in the eastern Mediterranean (Sala *et al.*, 2011; Vergés *et al.*, 2014b). As a result of this large-scale degradation, Mediterranean rocky reef photophilous communities with canopy-forming algae have been classified as an endangered habitat type in the European Red List of Habitats (Gubbay *et al.*, 2016).

With regards to recovery potential, as in the case of certain fish (especially fisheries-targeted species; Giakoumi *et al.*, 2017), a positive response to protection measures has been observed for canopy-forming species of the genus *Cysoseira sensu lato* at sites located in Marine Protected Areas - MPA (e.g., Fraschetti *et al*., 2012; Medrano *et al*., 2020; Di Franco *et al*., 2021). However, only 0.23% of the total Mediterranean Sea surface is subject to strict protection against human impacts on biodiversity (Claudet *et al*., 2020), while the overall recovery of benthic assemblages from extreme phase shifts may be very difficult or particularly slow even under strict protection regimes (Parravicini *et al*., 2010; Ling *et al*., 2015; Boada *et al*., 2017). Several factors are presumed to be responsible for this slow recovery, including (i) the abiotic features that modulate the post-disturbance benthic habitat and the associated assemblages (e.g., substrate rugosity, oceanographic circulation, nutrient availability; Fraschetti *et al*., 2012; Boada *et al*., 2017; Di Franco *et al*., 2021); (ii) the complex biotic dynamics that may retain the newly-formed rocky reef assemblages at an alternative stable state for a long time (Knowlton, 2004; Parravicini *et al*., 2010; Ling *et al*., 2015), (iii) the idiosyncratic (i.e., species-specific) responses of different organisms to the new conditions (Fraschetti *et al*., 2012; Medrano *et al*., 2020), and (iv) the ongoing disturbances that cannot be removed or eliminated in an MPA, such as climate change or invasive species (Parravicini *et al*., 2013; Medrano *et al*., 2019; Montero-Serra *et al*., 2019; Dimitriadis *et al*., 2021).

Despite this alarming situation, assessments regarding the composition and health status of rocky reefs and macroalgal communities beyond the north-western part of the Mediterranean basin are scarce and spatially restricted. Located in the north-eastern Mediterranean, the island-dominated Aegean Sea is characterised by an extensive rocky coastline supporting a plethora of marine habitats and species (Coll *et al*., 2010; Sini *et al*., 2017). However, only 25% of rocky reefs are included in the Natura 2000 network of MPAs (Sini *et al.*, 2017), while according to the criteria set by the EU Habitats Directive (92/43/EEC - Article 17; EU, 1992), rocky reefs in the Natura 2000 network have been evaluated to be in a bad ecological state over the period 2013-2018 (EUNIS, 2022). Moreover, no regular large-scale, long-term monitoring program is being implemented outside the marine Natura 2000 network of the Greek Seas, whereas available assessments of key biotic components provide indications of an overall degraded ecosystem (Sala *et al.*, 2012; Sini *et al.*, 2019b; Bevilacqua *et al.*, 2020).

Among the main challenges for marine biodiversity assessment, conservation, and management is the acquisition of sufficient quantitative information on the past and present distribution of marine species and habitats, and their spatiotemporal variability. Such information is essential for identifying early signs of ecosystem change, and setting measurable thresholds and management targets (Jackson & Jacquet, 2011; Gerovasileiou *et al*., 2019; Fraschetti *et al*., 2022). Given the limited access to detailed long-term biodiversity data in several regions (such as the Aegean Sea), biotic indicators have traditionally been used as diagnostic tools for assessing ecosystem health status, and macroalgae are one of the main biotic elements used as such (e.g., Ballesteros *et al.*, 2007; Orfanidis *et al.*, 2001, 2011; Thibaut *et al.*, 2017). Their ecological importance in the structuring of benthic communities, sedentary lifestyle, which keeps them continuously exposed to local pressures, and their varying sensitivity to stress, render macroalgae good indicators for the assessment and monitoring of ecosystem status (EU, 2000; Ballesteros *et al.*, 2007; D'Archino & Piazzi, 2021). Several biotic indicators use macroalgae, either in isolation or in combination with other species groups, to describe the ecological status of different bathymetric zones or habitat types of Mediterranean rocky reefs, from the littoral and upper-sublittoral photophilous communities (e.g., CARLIT - Ballesteros *et al.*, 2007; EEI - Orfanidis *et al.*, 2001, 2011; reef-EBQI - Thibaut *et al.*, 2017) to the lower sublittoral and upper circalittoral coralligenous assemblages (e.g., ESCA - Cecchi *et al.*, 2014; Piazzi *et al.*, 2017a,b). Moreover, several field techniques have been used to assess macroalgal assemblages, such as destructive sampling through scraping, or non-destructive visual estimates that are carried out either *in situ* or through photoquadrats (D'Archino & Piazzi, 2021). Photoquadrat sampling is a commonly used method as it is fast, cost-effective, and easy to apply in the field, allowing the collection of many samples. It is handy for ecological monitoring as it causes minimal to no disturbances, thus ensuring the integrity of the natural habitats and eliminating physical damage caused to the investigated organisms. Although photoquadrat sampling does not always allow the identification of taxa to species level (Balata *et al.*, 2011), the grouping of species into surrogate morphofunctional (i.e., based on shared morphological and ecological traits - Littler & Littler, 1980; Steneck & Dethier, 1994) or trophic groups (Thibaut *et al.*, 2017) is a common approach applied when assessing the ecological status of an ecosystem (D'Archino & Piazzi, 2021).

In the current study, photoquadrat images obtained from a large number of sites across the entire Aegean Sea were used to acquire quantitative information on the structure and health status of macroalgal communities in the region. Moreover, two different biotic indices were applied, the reef-EBQI (Thibaut *et al.*, 2017) and EEI-c (Orfanidis *et al.*, 2011), and their outputs were compared in order to evaluate their efficiency and potential limitations.

Material and Methods

Study Area

The study covers the entire Aegean Sea (Fig. 1), an area characterised by great geomorphological and ecological diversity. Given its geophysical variability, the Aegean Sea is commonly divided into two broad geographic subregions, namely the North (N) and the South (S) Aegean sectors (Sini *et al.*, 2017). The N Aegean is significantly influenced by the cold, brackish waters of the Black Sea, entering through the Bosporus and the Dardanelles straits, and the nutrient-rich freshwater discharge of several major rivers of mainland Greece. In contrast, the S Aegean is influenced by the northward-flowing warm waters of the Levantine Sea, characterised by high salinity and considerably lower productivity (Lykousis *et al.*, 2002; Zervakis *et al.*, 2004).

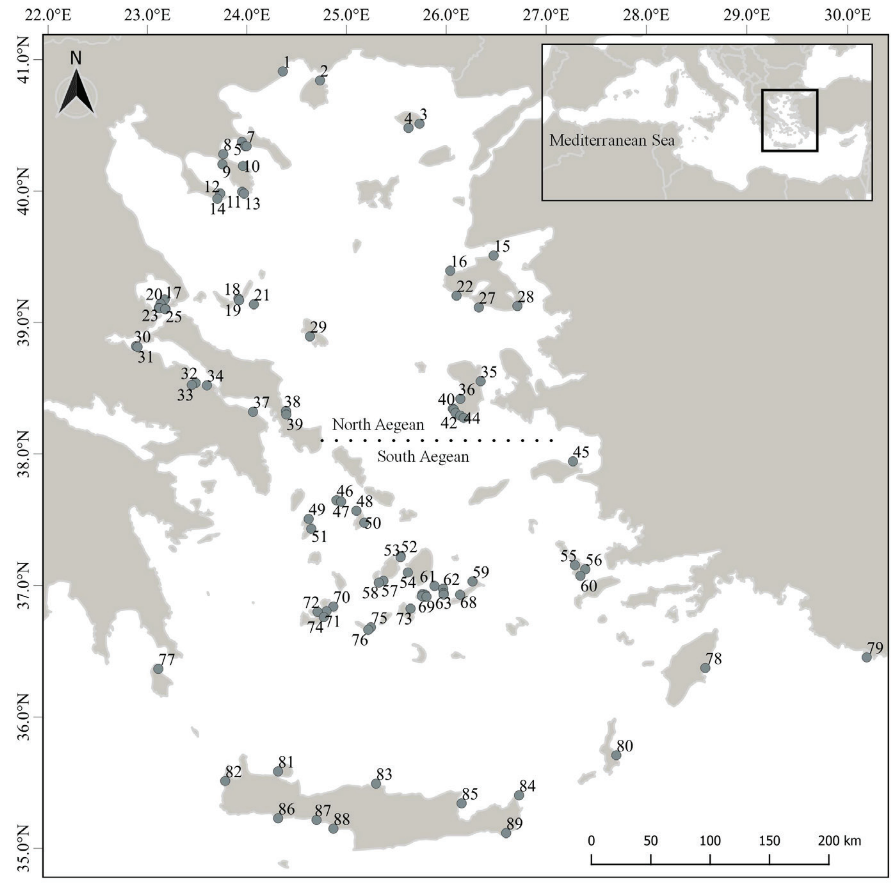

Fig. 1: Map of the Aegean Sea, showing the distribution of the 89 sampling sites. The dashed line indicates the division point between the North (N) and the South (S) Aegean sectors.

Data Collection and Field Protocols

Data collection took place in 2016 and 2020. We aimed to cover as many parts of the Aegean Sea as possible in a representative manner. However, the final choice of sampling sites was dictated by logistic constraints, weather conditions, and the availability of extensive rocky substrates. Overall, 89 sites were sampled throughout the Aegean Sea (Fig. 1, Supplementary Table S1), of which 44 were located in the N and 45 in the S Aegean.

Benthic image samples were obtained using a 25x25 cm quadrat frame at three distinct depths of 0-1 (hereafter referred to as 0 m), 5 and 15 m, for good representation of all the bathymetric zones of the upper sublittoral rocky reefs, and to enable between-depth comparisons. Quadrat size and number of samples per depth were decided based on the recommendations regarding the minimum representative sampling area for Mediterranean rocky benthic communities (Kipson *et al*., 2011; Sant *et al*., 2017), and also in accordance with previous research in the region, in order to obtain comparable results (Orfanidis *et al*., 2011; Salomidi *et al*., 2016). At 0 m depth, eight images were collected per site. The first image was taken at a randomly selected point; the remaining seven were obtained every 5 m while swimming in one direction, in a straight line, along the specific depth contour, i.e., a systematic random sampling approach was followed (Acharya *et al*., 2013). At 5 and 15 m depth, 18 images were collected per site along three consecutive line transects positioned several meters apart. At each transect, the first image was taken at a randomly selected point; the remaining images were successively obtained every 5 m while moving in one direction along the transect line. The choice of the location and number of replicate images was dictated by the overall objectives of the sampling expeditions, and also based on previous research in the area. Specifically, the 5 and 15 m transect lines were also used to assess fish and sea urchin biomass (not presented here); the 0 m sampling applied the field methodology of Salomidi *et al*. (2016). Overall, 89 depth stations were sampled at 5 m, 52 stations at 0 m, and 29 stations at 15 m depth. Out of a total number of 2520 image samples, 17% were taken at 0 m, 63% at 5 m, and 20% at 15 m, while the number of photographic samples from the N and the S stations was almost equal, 52% and 48% respectively (Supplementary Table S2).

Image Analysis

The percentage area cover of the different components in the benthic images was estimated using the point count tool of the photoQuad software (Trygonis & Sini, 2012). A total of 100 points were uniformly spawned per image and assigned to eleven different macroalgal categories (Table 1), seven categories of sessile benthic invertebrates, and four substrate categories (Supplementary Table S3 and S4, respectively).

Data Analysis

The biotic elements (algae and invertebrates) were further aggregated into morphofunctional groups (Table 1, Supplementary Table S3). The percentage area cover and standard error of the different morphofunctional groups and substrate categories were estimated per sampling station. To assess the variability in the structure of macroalgal assemblages, a three-way PERMANOVA (Permutational Multivariate ANOVA) analysis was applied using data from the five macroalgal morphofunctional groups and bare rock. PERMANOVA was run using geographic location (two levels: N and S) and depth (three levels: 0, 5, 15 m) as fixed factors, and station as a random factor nested within geographic location, applying 9999 permutations. To visualise the spatial patterns of similarity among stations found at different geographic locations and depths, a cluster analysis and a non-metric multidimensional scaling (nMDS) were carried out using a Bray-Curtis similarity index based on average values per station. Similarity percentage (SIMPER) analysis was used to investigate the contribution of each of the six data categories (five macroalgae morphofunctional groups and bare rock) to the spatial patterns observed. All multivariate analyses were run using PRIMER® version 6.1.16 (Clarke & Gorley, 2006) with the PERMANOVA+ add-on (version 1.0.6).

Two indices were used to estimate the ecological status per station: the reef-EBQI (Thibaut *et al.*, 2017) and EEI-c (Orfanidis *et al.*, 2011). The reef-EBQI index is an ecosystem-based index developed in response to the Marine Strategy Framework Directive (EU, 2008) call for more robust and holistic approaches to biodiversity assessment. It has been applied in several areas of the Mediterranean and at some sites of the Aegean Sea (Thibaut *et al.*, 2017; Bevilacqua *et al.*, 2020). This index incorporates all major tropho-functional groups of the photophilous subtidal rocky reef communities. In the current study, the application of the reef-EBQI index was restricted to the vegetal components of the upper sublittoral. According to the index requirements, the initial macroalgal categories were merged into three broad groups (arborescent perennial, shrubby, and turf/encrusting algae), corresponding to the presence of different strata of multicellular photosynthetic organisms. As proposed by Thibaut *et al.* (2017), in each photographic sample, only the area cover of the highest stratum present was considered for the estimation of reef-EBQI, as the lower strata are expected to develop underneath. Based on the area cover of the highest stratum, samples were attributed a reef-EBQI grade from 4 to 0, corresponding to a decreasing ecological status (Supplementary Table S5). The scores were then converted (rescaled) into a scale from 0 to 10 and averaged to yield the final reef-EBQI value per depth and site (Supplementary Table S5), which Thibaut *et al*. (2017) link to five categories of ecological status, i.e., Bad, Poor, Moderate, High and Very High (Supplementary Table S6).

The application of EEI-c is limited to the <1 m depth zone. It strictly focuses on vegetal elements and is

Table 1. Name and description of macroalgal categories belonging to different morphofunctional groups. The description of selected algal groups is adopted from Littler *et al.* (1983) and Orfanidis *et al.* (2011).

Morphofunctional group	Macroalgal category	Description	Examples
Algal turf	Seasonal algal turf	Low-lying macroalgae with thin and delicately branched soft thalli	*Cladophora* sp.
Algal turf	Mucilaginous algae	Mucus-like phenotype	*Chrysophyceae*
Encrusting calcareous algae	Encrusting calcareous algae	Heavily calcified thalli with stone-like texture and prostrate growth, forming flat, but sometimes multi-layered epilithic crusts	*Lithophyllum* spp., *Mesophyllum* spp., P*eyssonnelia rosa-marina*
Articulated calcareous algae	Articulated calcareous algae I	Heavily calcified, branched thalli	*Amphiroa* spp., *Corallina* spp., *Jania* spp., *Liagora* spp.,
Articulated calcareous algae	Articulated calcareous algae II	Semi-calcified, erect thalli	*Flabellia petiolata*, *Halimeda tuna*, *Peyssonnelia rubra*
Shrubby algae	Shrubby algae	Upright, well developed thalli of moderate height, forming bushy aggregations	*Laurencia* spp., *Halopteris* spp.
Shrubby algae	Foliose algae I	Thin thalli forming pseudo-canopies	*Dictyota* spp., *Dictyopteris* spp.
Shrubby algae	Foliose algae II	Large thalli forming pseudo-canopies	*Padina pavonica*, *Zonaria tournerfortii*, *Stypopodium schimperi*
Shrubby algae	Massive algae	Wide cauloid	*Codium bursa*
Canopy algae	Canopy-forming macroalgae I	Perennial stems, upright, tree-like thalli with thick blades and branches, forming dense canopies found primarily in pristine environments	*Cystoseira* spp., *Gongolaria* spp.
Canopy algae	Canopy-forming macroalgae II	Perennial stems, upright, tree-like thalli with thick blades and branches, forming dense canopies. Present high adaptive plasticity and can survive in adverse conditions; found in pristine and moderately degraded environments	*Cystoseira compressa, Sargassum* spp.

intended for rocky reefs with a macroalgal area cover of >10%. This index was developed for monitoring within the context of the Water Framework Directive (EU, 2000) and has been implemented in several areas of the central and eastern Mediterranean Sea (e.g., Cyprus - Carletti & Heiskanen, 2009; Greece - Panayotidis *et al.*, 2004; Orfanidis & Panayotidis, 2005; Italy - Falace *et al.*, 2009; Slovenia - Orlando-Bonaca *et al.*, 2008). In order to apply the EEI-c index, the initial macroalgal categories were merged into five Ecological Status Groups (Supplementary Table S7) according to specific functional traits (Orfanidis *et al.*, 2011). For each station, the mean EEI-c value of all samples was estimated. These values were then converted into a scale from 0 to 10 (Orfanidis *et al.*, 2011) and linked to the five-level classification of ecological status, i.e., Bad, Low, Moderate, Good and High (Supplementary Table S8).

Both indices were applied at depth station, site, sub-basin (N versus S Aegean) and whole basin (Aegean as a whole) level. Based on the results of the reef-EBQI and EEI-c indices, maps displaying the ecological status per depth station and site were created with QGIS 3.18.3-Zürich.

To quantify the scale and sign of differences between the outputs of the two distinct indices, direct comparisons were applied to the EEI-c and the reef-EBQI results (on an ordinal scale) using data from the 0 m stations alone. A heatmap was created to visualise the scale of differences. A Spearman's ρ (rho) correlation coefficient was calculated to quantitatively assess the type and strength of the relationship between the reef-EBQI and EEI-c output values. This was conducted in R (R Core Team, 2022).

Results

According to the analysis of the morphofunctional groups (Figs. 2-4), macroalgal groups (78.7% ± 1.7%, average ± S.E.) appeared to be more abundant in terms of area cover than the invertebrate (8.3% ± 0.6%) and substrate (13.1% ± 0.01%) groups. Of all macroalgal groups, turf algae were the most abundant, followed by encrusting calcareous algae, shrubby algae, articulated calcareous algae and, finally, canopy algae (Table 2). Articulated calcareous algae were more prevalent in the N than in the S Aegean. Canopy algae were predominantly detected at 0

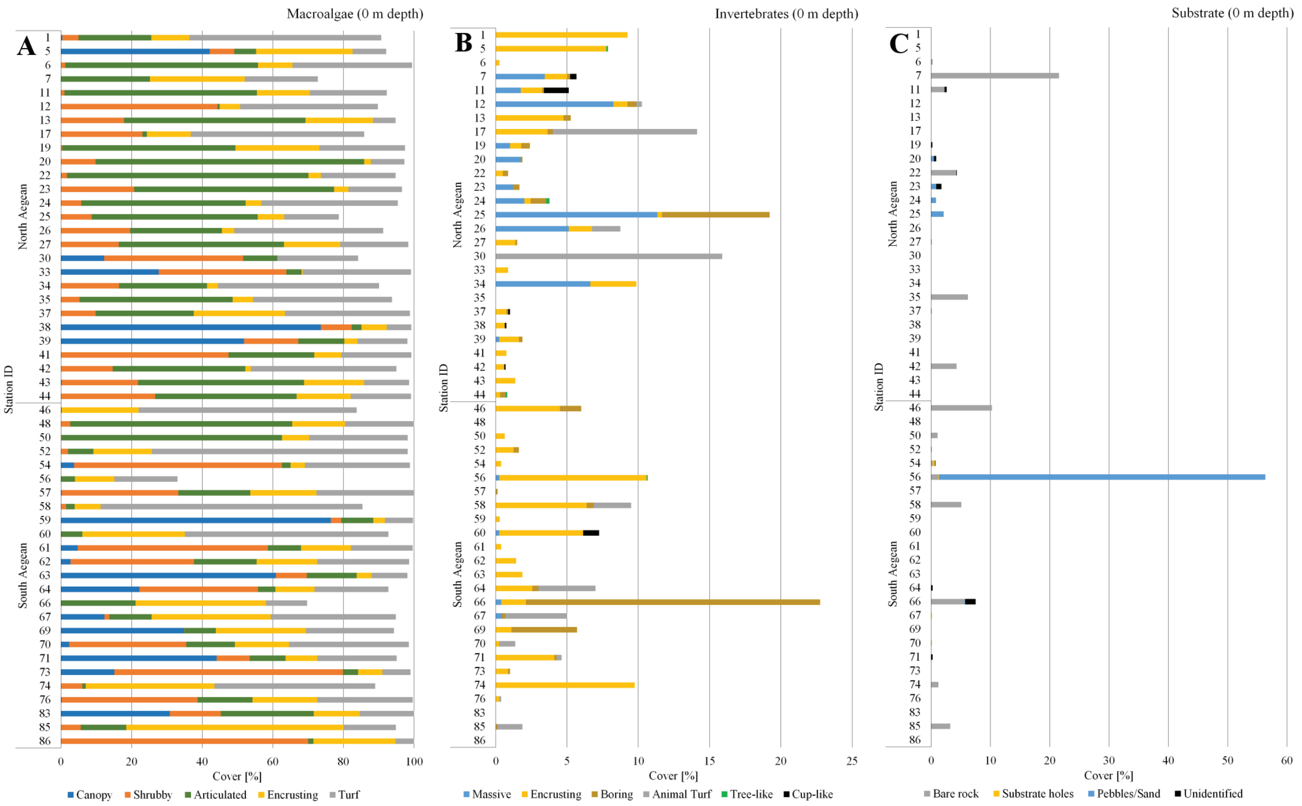

Fig. 2: Percentage area cover of macroalgal and invertebrate morphofunctional groups, as well as substrate categories, per site at 0 m depth. Sites are ordered from the highest (top) to the lowest (bottom) latitude.

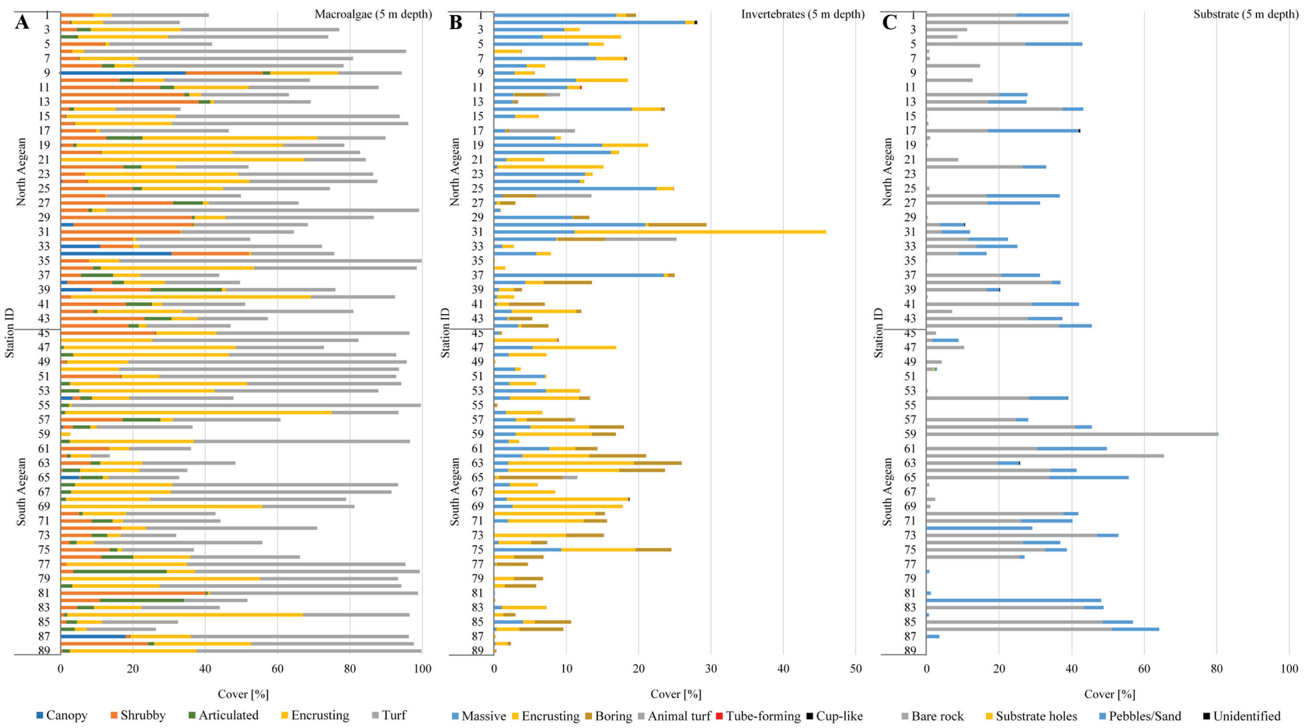

Fig. 3: Percentage area cover of macroalgal and invertebrate morphofunctional groups, as well as substrate categories, per site at 5 m depth. Sites are ordered from the highest (top) to the lowest (bottom) latitude.

m depth, and their coverage declined with depth. Overall, the canopy-forming algal cover was similar at the N and S Aegean stations. At 15 m depth, there was a marked (almost complete) absence of macroalgae other than turf and encrusting calcareous algae in the S Aegean, while shrubby algae covered 18.7% ± 3.5% in the N Aegean (Fig. 4).

Among the invertebrate morphofunctional groups recorded, the most abundant were the perennial massive (3.4% ± 0.3%) and the perennial encrusting (2.9% ± 0.2%) forms. Perennial massive had a higher area cover at 5 m (4.6% ± 0.5%) and 15 m (3.9% ± 0.7%) compared to 0 m depth (0.9% ± 0.1%), while this group was more

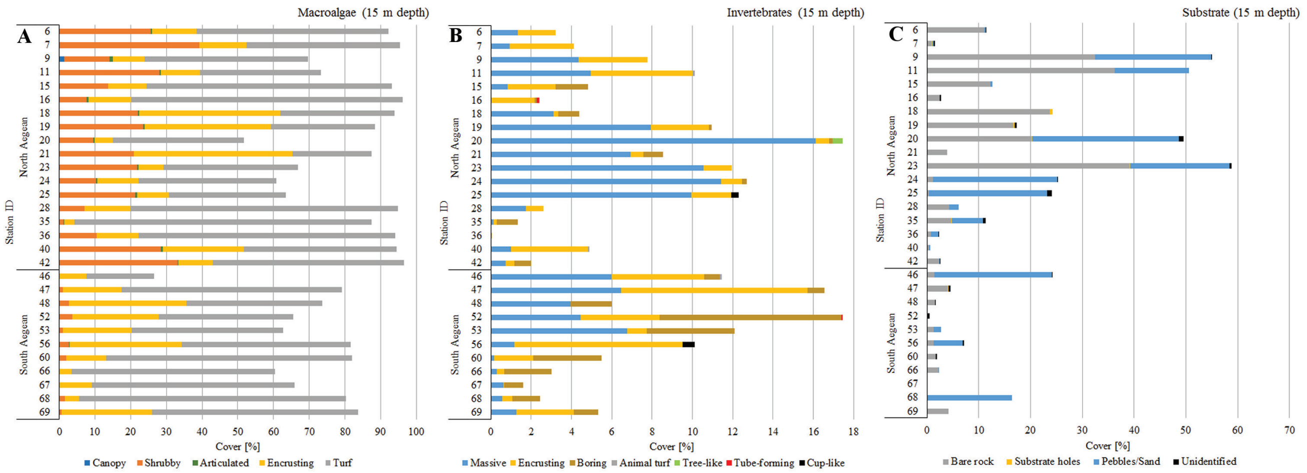

Fig. 4: Percentage area cover of macroalgal and invertebrate morphofunctional groups, as well as substrate categories, per site at 15 m depth. Sites are ordered from the highest (top) to the lowest (bottom) latitude.

Table 2. Percentage area cover range and mean values of the five macroalgal morphofunctional groups for the Aegean Sea, per geographic location and depth level; ± denotes standard error.

	Range [%]	Mean ± Standard error [%]					
Morphofunctional group	**Aegean Sea**	**Aegean Sea**	**N Aegean**	**S Aegean**	**0 m**	**5 m**	**15 m**
Algal turf	0 - 96.4	36.8 ± 1.5	36.0 ± 2.0	37.8 ± 2.4	27.3 ± 2.3	38.2 ± 2.1	49.5 ± 3.2
Encrusting calcareous algae	0 - 73.7	16.6 ± 1.2	14.5 ± 1.6	18.9 ± 1.8	14.2 ± 1.6	18.1 ± 2.0	16.1 ± 2.1
Articulated calcareous algae	0 - 76	8.9 ± 15.8	11.4 ± 2.0	6.2 ± 1.2	24.1 ± 3.0	2.9 ± 0.5	0.2 ± 0.0
Shrubby algae	0 - 70	12.7 ± 1.1	15.8 ± 1.3	9.2 ± 1.7	17.3 ± 2.6	10.1 ± 1.2	12.1 ± 2.2
Canopy algae	0 - 76.4	3.7 ± 0.9	3.4 ± 1.3	4.1 ± 1.4	10.0 ± 2.8	1.3 ± 0.6	0.1 ± 0.1

Table 3. PERMANOVA analysis based on percentage area cover of macroalgal morphofunctional groups in relation to geographic location and depth; numbers in bold indicate significant differences ($p < 0.05$); df: degrees of freedom, SS: sums of squares, MMS: mean square estimates of variation based on within-group distances, Variance components (square root): sums of squared effects divided by degrees of freedom.

Source	**df**	**SS**	**MS**	**Pseudo-F**	**p-value**	**Variance components**	
						Estimate	Square root
Geographic location	1	23401	23401	2.4	**0.0496**	23.05	4.8
Depth	2	395080	197540	22.8	**0.0001**	368.5	19.2
Site (Geographic location)	89	1649400	18532	22.7	**0.0001**	710.2	26.7
Geographic location x Depth	2	73965	36983	4.3	**0.0009**	110.4	10.5
Depth x Site (Geographic location)	76	652510	8585.6	10.5	**0.0001**	583.2	24.2
Residuals	2365	1935200	818.26			818.3	28.6
Total	2535	4972800					

prevalent in the N (5.1% ± 0.5%) than in the S Aegean (1.4% ± 0.2%). Perennial encrusting invertebrates had the highest abundance at 5 m depth (4.1% ± 0.4%), with lower values at 0 m depth (1.9% ± 0.3%) and 15 m depth (1.1% ± 0.2%).

With regard to the substrate groups, the most dominant one was bare rock (9.0% ± 1.1%), with an area cover of 1.3% ± 0.5% at 0 m, 13.8% ± 1.8% at 5 m, and 8% ± 2.1% at 15 m depth. Overall, bare rock exhibited a greater area cover in the S Aegean Sea (9.5% ± 1.9%) than in the N (8.6% ± 1.2%).

According to the PERMANOVA analysis, the structure of macroalgal communities was found to be significantly different at all spatial scales considered, but differences were more significant at the smaller scales (Table 3). Specifically, according to the estimated components of variation, the highest variability was observed at the level of residuals, which reflects a high within-station variability, followed by the among-stations variability. On the other hand, geographic location had the lowest variability and a marginally significant p-value. Depth also appeared to have an important overall effect on data variability, while the pairwise analysis indicated significant differences between all depth levels, with the 5 and 15 m depth displaying a higher between-group similarity compared to the 0 m depth (Table 4).

The effects of geographic location and depth on the macroalgal community structure are visualised through the cluster analysis (Supplementary Fig. S1) and the nMDS plot (Fig. 5). In the nMDS, a segregation of stations located at 0 m depth from those at 5 and 15 m depth is evident, while the 15 m stations display lower variability. On the other hand, there is no apparent segregation of stations in response to geographic location. These results agree with the PERMANOVA analysis, which highlights the overall stronger effect of depth over that of geographic location on macroalgal community structure.

The SIMPER analyses on the area cover of the different macroalgal morphofunctional groups and bare rock indicate that the N and S Aegean Sea stations displayed an average dissimilarity of 59.2%, with turf algae, encrusting calcareous algae, and bare rock, having a cumulative percentage contribution of 69.6%, whereas the more complex shrubby, articulated calcareous, and canopy-forming algae had a respective cumulative contribution of 30.5% (Table 5).

Algal turf was also a top contributor to the observed dissimilarities across all depths (Table 6). This group alone contributed 24.8% of the 0 and 5 m dissimilarity, 29.6% of the 0 and 15 m dissimilarity, and 35.6% of the 5 and 15 m depth dissimilarity. The increased average cover of articulated calcareous and shrubby algae at 0 m were also two of the main contributors to the observed dissimilarity between this depth zone and the 5 or 15 m zones, whereas encrusting calcareous algae and bare rock had a cumulative contribution of >43% to the observed dissimilarity between 5 and 15 m depth.

The reef-EBQI index was calculated for all depth stations separately (Supplementary Fig. S2-S4, Supplementary Table S9), and as the average of all depth stations per site (Fig. 6, Supplementary Table S9). The average ecosystem health status across the entire Aegean Sea (all depth stations pooled) is Bad (average reef-EBQI score = 2.5 ± 1.6), with no difference between the N Aegean (2.8 ± 1.6) and the S Aegean (2.2 ± 1.6). Of the 89 surveyed sites, the ecological status of 71 sites (ca. 80%) was found to be Bad, that of six Poor, 11 Moderate, and only one station (namely station 39) was classified as High, while no stations were found to be Very High status. At 0 m depth, the ecosystem status of the whole Aegean Sea according to the reef-EBQI index was estimated to be Moderate (4.6 ± 2.3), with no substantial difference between the N Aegean (4.6 ± 1.8) and the S Aegean (4.7 ± 2.8). Out of the 52 stations for which data were available at 0 m

Table 4. Results of PERMANOVA pairwise tests based on percentage area cover of macroalgal morphofunctional groups in relation to depth; numbers in bold indicate significant differences ($p < 0.05$).

Groups	t	p-value	Average similarity between groups (%)
0, 5	5.3	**0.0001**	33.8
0, 15	4.7	**0.0001**	36.8
5, 15	4.7	**0.0001**	46.4

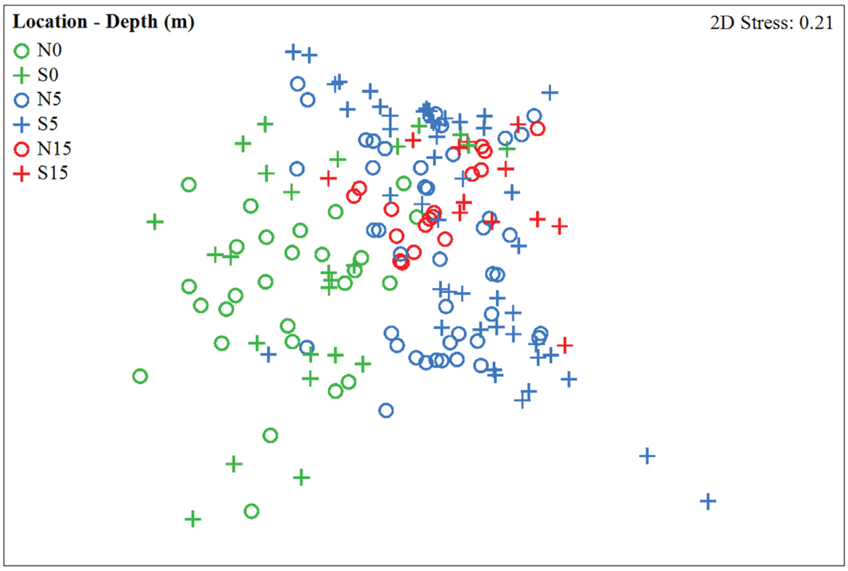

Fig. 5: Non-metric multidimensional scaling (nMDS) plot of the macroalgal morphofunctional groups, data from the N and S Aegean regions at 0, 5 and 15 m depth.

Table 5. Summary of similarity percentage analysis (SIMPER) indicating the dissimilarity level of all sampled stations of the Aegean Sea based on percentage area cover of macroalgal morphofunctional groups. Av Diss: average dissimilarity; Diss/SD: dissimilarity to standard deviation ratio; Contrib %: percent contribution; Cum %: cumulative percent contribution.

Morphofunctional group	Average dissimilarity: 59.2%					
	Av Cover (%)	**Av Cover (%)**	**Av Diss**	**Diss/SD**	**Contrib (%)**	**Cum (%)**
	N Aegean	S Aegean				
Turf algae	38.5	38.8	18.1	1.3	30.5	30.5
Encrusting calcareous algae	14.4	20.0	12.8	1.0	21.6	52.2
Bare rock	7.3	14.0	10.3	0.8	17.4	69.6
Shrubby algae	15.0	7.3	9.6	1.0	16.2	85.7
Articulated calcareous algae	7.6	4.4	5.8	0.6	9.8	95.5
Canopy algae	2.6	2.3	2.7	0.3	4.5	100.0

Table 6. Summary of similarity percentage analysis (SIMPER) indicating the dissimilarity level between the 0, 5 and 15 m depths based on percentage area cover of macroalgal morphofunctional groups. Av Cover: average cover; Av Diss: average dissimilarity; Diss/SD: dissimilarity to standard deviation ratio; Contrib %: percent contribution; Cum %: cumulative percent contribution.

Morphofunctional Group	Av Cover (%)	Av Cover (%)	Av Diss	Diss/SD	Contrib (%)	Cum (%)
	0 m	**5 m**				
Turf algae	27.3	38.1	16.5	1.3	24.8	24.8
Articulated calcareous algae	24.4	3.0	13.3	0.9	20.1	44.9
Encrusting calcareous algae	13.9	18.4	11.7	1.0	17.6	62.6
Shrubby algae	17.0	9.3	10.5	0.9	15.8	78.4
Bare rock	1.3	14.0	8.4	0.7	12.7	91.1
Canopy algae	9.8	1.3	5.9	0.5	8.9	100.0
	0 m	**15 m**				
Turf algae	27.3	49.7	18.7	1.4	29.6	29.6
Articulated calcareous algae	24.4	0.2	13.6	0.9	21.5	51.1
Shrubby algae	17.0	12.2	10.9	1.0	17.3	68.4
Encrusting calcareous algae	13.9	16.1	9.8	1.1	15.5	83.9
Canopy algae	9.8	0.1	5.4	0.4	8.6	92.4
Bare rock	1.3	7.9	4.8	0.5	7.6	100.0
	5 m	**15 m**				
Turf algae	38.1	49.7	19.1	1.4	35.6	35.6
Encrusting calcareous algae	18.4	16.1	12.6	1.0	23.5	59.1
Bare rock	14.0	7.9	10.6	0.8	19.7	78.8
Shrubby algae	9.3	12.2	8.7	1.0	16.3	95.1
Articulated calcareous algae	3.0	0.2	1.8	0.4	3.4	98.5
Canopy algae	1.3	0.1	0.8	0.2	1.5	100.0

depth, only 15 stations were characterised Bad, 12 Poor, 13 Moderate, four High, and the remaining eight Very High. With regard to the ecological status at 5 m depth, the overall Aegean Sea status was estimated as Bad (1.8 ± 1.5), with the N Aegean (2.3 ± 1.7) and S Aegean (1.3 ± 1.1) displaying similar scores. As for the status of the 89 stations sampled at 5 m depth, 82 were characterised as Bad, two Poor, three Moderate, and two Very High. At 15 m depth, the overall status of the Aegean Sea was Bad (1.3 ± 1.2), with a higher average score in the N Aegean (2.0 ± 0.8) than in the S Aegean (0.1 ± 0.2) sites. Of the 29 stations sampled at this depth, the status of 28 was found to be Bad, and that of one Poor. Hence, as reflected by the reef-EBQI scores, ecological status declined with depth in both the N and S Aegean.

According to the EEI-c index, the average ecological status across the entire Aegean Sea (only 0 m depth stations considered) is Good (EEI-c score = 6.5 ± 2.5) (Fig. 7, Supplementary Table S10). Both the N Aegean (6.9 ± 2.3) and the S Aegean (6.1 ± 2.5) stations, on average, fall within the limits of the Good ecological status category. Station 39 scored the highest ecological status (9.9 ± 0.4

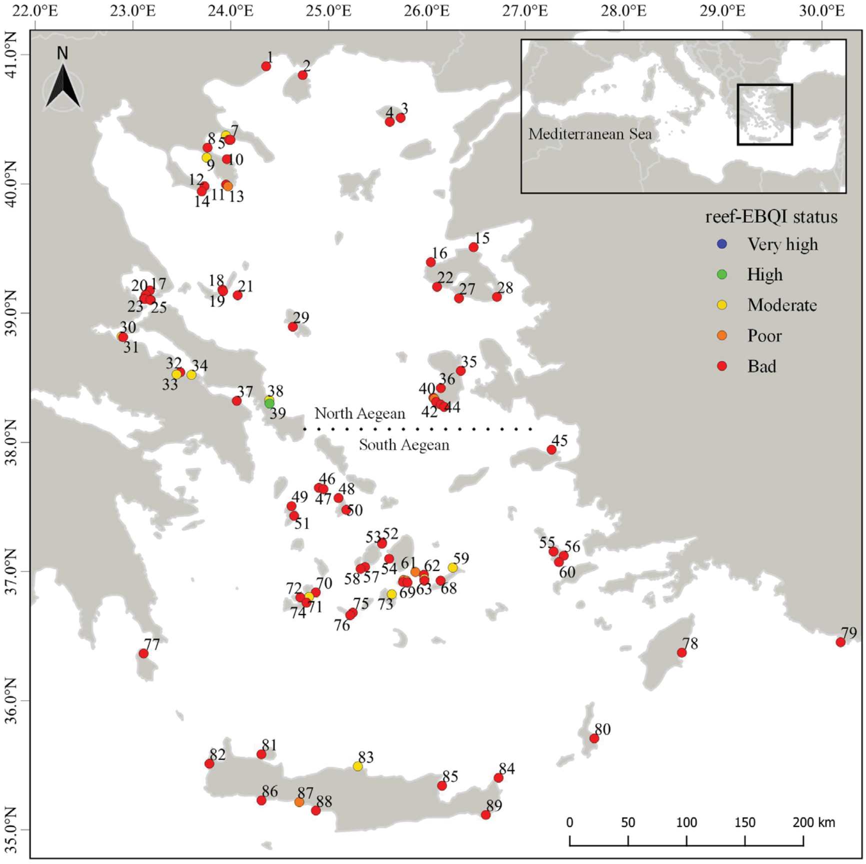

Fig. 6: Map of the Aegean Sea displaying the average reef-EBQI values per site (all depths pooled).

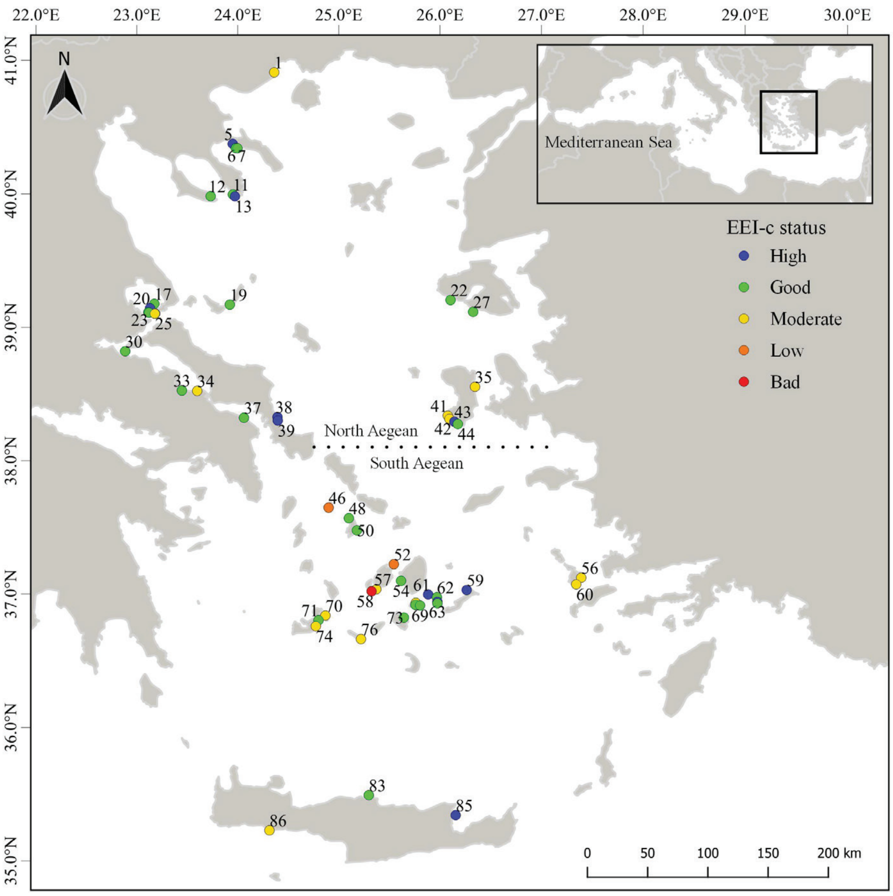

Fig. 7: Map of the Aegean Sea displaying the EEI-c values per site (0 m depth only).

- High), while nine other stations were classified as High status (stations 60, 64, 5, 20, 62, 44, 40, 86, and 13 in decreasing order of their scores). Additionally, the status of 25 stations was Good, that of 14 Moderate, and that of two Low. Station 59 scored the lowest ecological status (1.8 ± 0.7 - Bad).

When only the 0 m values were used for estimating the reef-EBQI index, the divergence between the two indices was not as large as when all depth levels were considered for estimating reef-EBQI. Specifically, the status of the Aegean Sea as a whole and the N and S Aegean sectors was assessed as Moderate by reef-EBQI index. Of the 52 stations surveyed at 0 m depth (Supplementary Table S10), 36 rated higher according to the EEI-c, four stations ranked higher according to reef-EBQI, and the remaining 12 were rated equally by both indices (Fig 8).

Spearman's ρ (rho) indicated that there is a positive correlation between the reef-EBQI (restricted to 0 m depth data) and the EEI-c ecosystem status scores (ρ = +0.50). However, there is an apparent tendency for the Low to Moderate stations to be ranked higher by the EEI-c index than by the reef-EBQI index, i.e., below the diagonal of the heatmap in Figure 8. On the contrary, four of the 12 stations ranked "High" and "Very High" by the reef-EBQI index were assessed more modestly by the EEI-c index.

Discussion

Sublittoral photophilous communities of the Aegean Sea present a relatively poor community structure, dominated by turf and encrusting algal forms, with a low abundance of sessile invertebrates. Although no quantitative analysis of the past structure of macroalgal communities over a similar spatial scale is publicly available, sporadic reports indicate that several localities of the Aegean Sea used to host highly speciose macroalgal assemblages, including a large number of canopy-forming and other structurally important species (e.g., Tsiamis *et al*., 2013a; Bianchi *et al*. 2014), which presented a high cover even in impacted areas (e.g., Orfanidis *et al*., 2001). In turn, the low abundance of sessile invertebrates recorded herein may result from the simplified macroalgal assemblages, as lower habitat complexity has been shown to reduce the diversity and abundance of epibenthic communities (Sala *et al*., 1997a; Bianchi *et al*. 2014).

Despite the distinct abiotic (Androulidakis *et al*., 2022) and biotic characteristics (Lykousis *et al*., 2002; Voultsiadou, 2005; Ragkousis *et al*., 2023) that differentiate the N from the S Aegean Sea, the structural complexity of shallow rocky reef macroalgal assemblages across the Aegean Sea displays a relatively low (yet significant) variability, while higher variability is observed at smaller spatial scales, i.e., among samples of the same station (the residuals in this study) or among different depth stations of the same site. Higher variability at small spatial scales – even at the level of replicate samples – is commonly reported for Mediterranean rocky reef communities (e.g., Balata *et al*., 2008; Casas-Güell *et al*., 2015; Sini *et al*., 2019a), and is mainly linked to the small-scale variability of the natural habitat due to depth, substrate rugosity, orientation, inclination, or other abiotic factors, and the associated interactions between benthic organisms for limited resources (i.e., space, light, and food), which result in their patchy distribution, and thus, increased within-assemblage variability (Garrabou *et al*., 2002; Duran *et al*., 2018).

Moreover, the complexity of macroalgal community structure displays a decreasing trend with depth. At 0 m, turf-forming algae are dominant, but shrubby and articulated calcareous algae are also abundant, while canopy-forming species are frequent at many stations and, in some cases, occupy a relatively large surface area (>30%). At the deeper stations (5 and 15 m), turf algae, encrusting calcareous algae, and bare rock have a cumulative average cover of more than 70%. On the contrary, the area cover of the more complex algal forms appears remarkably reduced, with shrubby and articulated calcareous algae almost absent at 15 m. This type of community structure, where the cover of structurally important macroalgal species drops substantially below the first few meters from the surface, possibly reflects the grazing effects caused by either herbivorous fish or sea urchins (Salomidi *et al*., 2016; Tsirintanis *et al*., 2018). Herbivorous fish consume the palatable fronts of bushy and canopy-forming algae and enhance the more opportunistic, low-lying turf species, whereas sea urchins are responsible for the creation of rocky barrens (i.e., stretches of bare rock and encrusting coralline algae) (Bulleri *et al*., 2002; Hereu *et al*., 2006; Sala *et al*., 2011). The abundance of these grazers is assumed to be lower at 0 m

EEI-c \ reef-EBQI	Bad	Poor	Moderate	High	Very High
Bad	1	0	0	0	0
Low	2	0	0	0	0
Moderate	7	3	3	1	0
Good	4	7	8	3	3
High	1	2	2	0	5

Fig 8: Heatmap depicting the number of stations (at 0 m depth) that were assessed by both ecological indices (reef-EBQI on the X-axis and EEI-c on the Y-axis) and their ecosystem status ranking according to each index; stations assessed higher by EEI-c are depicted in shades of blue, stations ranked similarly by both indices are shown in shades of green; stations assessed higher by reef-EBQI are displayed in shades of orange.

given the risks of feeding in shallow waters, such as predation by seabirds and dislodgement due to wave action, whereas deeper waters (in the 0-15 depth range) remain exposed to increased levels of grazing pressure (Salomidi *et al*., 2016). Other pressures, such as habitat destruction and climate change, may also be responsible for the decline of macroalgal forests in the region (e.g., Thibaut *et al*., 2017; Bevilacqua *et al*., 2021; Garrabou *et al*., 2022). However, the presence of more diverse and structurally complex macroalgal assemblages in the shallower areas of rocky reefs supports the hypothesis that this deterioration in community structure with depth is due to overgrazing. Other factors would have affected a wider depth range (e.g, pollution or habitat destruction due to coastal infrastructure), or predominantly the shallower parts of the reefs (e.g., ocean warming). Besides, the pattern of healthier macroalgal communities in the upper sublittoral zone was found to be more pronounced in the S Aegean, where the alien herbivorous fishes *Siganus luridus* and *S. rivulatus* (voracious grazers of canopy-forming algae; Vergés *et al*., 2014a) are well-established. On the contrary, at the time of the sampling surveys, these fish were either absent or recently introduced with very low densities in the N Aegean (Evagelopoulos *et al*., 2015; Sini *et al*., 2017; Katsanevakis *et al.*, 2020b).

At a more local scale, a predominance of turf-forming algae and a decline in the abundance of canopy-forming species have been reported in past studies carried out in the Cyclades Archipelago (S Aegean; Giakoumi *et al*., 2012; Salomidi *et al*., 2016). However, in the current study, the area cover of canopy-forming algae in the Cyclades Archipelago appears to be 69, 96 and 98% lower than the values reported for 0, 5, and 15 m depth, respectively, at Santorini Island in 2012 (Salomidi *et al*., 2016), possibly indicating further deterioration of rocky reefs at this location over time. Nevertheless, with the exception of few localised studies, the lack of data on the previous condition of rocky reefs in the Aegean Sea constitutes a critical obstacle for the evaluation of the magnitude of this decline. For instance, a semi-quantitative comparison of rocky reef assemblages (to ca. 10 m depth) between 1981 and 2013 in the S Aegean (Kos Island), revealed dramatic changes in their structure, and an overall biotic homogenization, which is attributed to seawater warming, several types of human pressures, and biological invasions (Bianchi *et al*., 2014).

The estimation of the ecological status of the Aegean Sea using the reef-EBQI index per depth reflects a marked decline of macroalgal assemblages with depth, from Moderate ecological status at 0 m to Bad at 5 and 15 m depth, regardless of the geographic location. However, with all three depths pooled, the reef-EBQI estimate for the whole Aegean Sea is Bad, given that the status of approximately 80% of the sampling stations is, on average, Bad regardless of the geographic location (N versus S Aegean Sea). This finding agrees with previous ecological assessments, which have indicated that the ecological status of the subtidal rocky reefs of the Aegean Sea is Bad or Poor (EUNIS, 2022; Bevilacqua *et al*., 2020), with a substantial degradation of fish communities (Sini *et al*., 2019b). On the other hand, applying the EEI-c index at the 0 m depth provided an estimate of Good ecological status both for the Aegean Sea as a whole and for the N and S Aegean sectors separately.

Differences in the outputs of the two indices are due to the distinct approaches followed, and hence to the differential allocation of certain species to groups of different ecological statuses. EEI-c was designed to detect the response of macroalgal species in the 0-1 m zone to different levels of nutrient enrichment by grouping algal species according to their morpho-physiological characteristics, life history traits, and assumed abundance across eutrophication gradients (Orfanidis *et al*., 2011). In this way, the EEI-c index ranks the ecosystem status of encrusting coralline algae as relatively high (i.e., IC) compared to the reef-EBQI ranking which positions this morphological group in the lowest status category due to its inferior structural role in this habitat type. As a result, EEI-c tends to upgrade sites ranked as Bad to Moderate according to reef-EBQI. On the other hand, reef-EBQI is built to address a wider depth range, and hence a broader spectrum of stressors based on the grouping of macroalgal species into coarse morphological groups of decreasing height and structural complexity (i.e., arborescent, shrubby, turf/encrusting; Thibaut *et al*., 2017). Still, it lacks the taxonomic resolution required to assess the sensitivity/tolerance of certain structural species of the arborescent and shrubby algal groups, such as *Cystoseira compressa* (Esper) Gerloff & Nizamuddin and *Sargassum* spp., to specific stressors. This is perhaps why it tends to upgrade stations classified as Moderate to Good according to the EEI-c. Such variability in the outputs of different indices is commonly reported in the literature, as the results are essentially affected by the different goals and methods used to collect and analyse data, as well as by the sensitivity of distinct indices to different environmental or anthropogenic pressures (García-Sánchez *et al*., 2012; Bermejo *et al.*, 2014; Piazzi *et al*., 2017a). For this reason, in addition to acquiring long-term monitoring data, there is also an urgent need to produce comparable results. To do this, we need to advance the knowledge gained from existing indices, agree on a minimal set of standard metrics, decide on the taxonomic resolution needed, harmonise sampling designs and data reporting according to common standards, and develop improved indices that follow a more integrative, ecosystem-based approach (Duffy *et al*., 2019; D' Archino & Piazzi, 2021). Moreover, data should be readily available for further analysis through centrally accessible, open-access repositories (Duffy *et al*., 2019).

In the current study, the results of the reef-EBQI index regarding the deterioration of health status with depth, highlight the importance of considering different depth levels when assessing the health status of rocky reefs in a given area, as communities found at different depth zones may be exposed to different types and levels of stress (Bell, 1983; Sini *et al*., 2019b; Angiolillo & Fortibuoni, 2020; Garrabou *et al*., 2022). This is particularly true for marine habitat types such as the Mediterranean photophilous communities with canopy-forming algae, as they expand over a wide depth range from 0 m to the upper circalittoral zone (Gubbay *et al*., 2016; Sant & Ballesteros, 2021). Other geomorphological and topographical characteristics, such as substrate type in terms of lithological properties, rock rugosity, inclination, orientation, and exposure to wave action, are already incorporated in some of the existing biotic indices, as they represent important descriptors of the physical habitat and complement its bionomic characterisation (Ballesteros *et al*., 2007; Gatti *et al*., 2015). Moreover, integrating other food-web compartments, as proposed by Thibaut *et al.* (2017), is essential for obtaining more holistic estimates of ecosystem status and a more comprehensive understanding of the multiple pressures exerted on its constituent components. Allocating sensitivity factors to different species or groups of species for the detection of different types of pressure would also be useful (e.g., Sartoretto *et al*., 2017), while the incorporation of alien species in such indices would provide important information and possibly some early warning signals of ecosystem change in areas that are alien species hotspots. All of the above would improve the monitoring tools that are now available and enhance the prioritization of management and conservation actions.

Although the status of the Aegean Sea rocky reefs appears alarming, certain localities still harbour rich macroalgal forests, especially in the 0 m depth, but even up to 15 m or beyond at some exceptional sites. These areas represent valuable pockets of biodiversity and, in some cases, potentially form contemporary climatic refugia (Verdura *et al*., 2021) that should be protected and managed immediately. Conservation actions should include detailed mapping and systematic monitoring, fisheries restrictions to increase the biomass of higher predators, especially sea bream and groupers, eliminate the overgrowth of grazers (Sala, 1997b; Shapiro Goldberg *et al*., 2021), and reduce all potential activities causing habitat destruction and pollution. Moreover, the application of long-term restoration actions in the more degraded areas, such as transplantation, *ex situ* out-planting, recruitment enhancement of canopy-forming macroalgae and other structural organisms, along with complementary actions of turf removal and herbivory management, are also needed to promote growth and recovery of these communities (Gianni *et al*., 2013; Verdura *et al*., 2018; De La Fuente *et al*., 2019; Guarnieri *et al*., 2020; Cebrian *et al*., 2021; Orlando-Bonaca *et al*., 2021). Yet again, to restore rocky reef communities as a whole, it is essential to increase scientific understanding regarding the mechanisms that determine the responses of different taxonomic and trophic groups to protection (Di Franco *et al*., 2021).

The CBD Global Biodiversity Framework and the European Union have committed to ambitious but challenging biodiversity recovery plans, focusing on extending the network of protected areas, restoring degraded habitats, and improving management effectiveness (Hermoso *et al*., 2022). With recent improvements in our knowledge regarding the restoration of algal forests, restoration activities need upscaling and require baseline information (Tamburello *et al*., 2019). Such information includes large-scale assessments of the current state of macroalgal communities and continuous monitoring to support efficient conservation planning and prioritization of restoration efforts (Katsanevakis *et al*., 2020a). This work provides essential reference data for management decisions to support the conservation and restoration efforts of reef ecosystems in the Aegean Sea.

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Supplementary Data

The following supplementary information is available online for the article:

Table S1. List of all sampling stations, ordered from the highest to the lowest latitude.

Table S2. Number of photographic samples taken per depth.

Table S3. Name and description of the invertebrate morphofunctional groups.

Table S4. Name and description of the substrate categories.

Table S5. Reef-EBQI strata of multicellular photosynthetic organisms (MPOs), their corresponding macroalgal/substrate categories of the current study, MPOs percentage area cover, reef-EBQI grades and related scores (Thibaut et al., 2017).

Table S6. Ecological status characterisation and range values of the reef-EBQI index (Thibaut *et al*., 2017).

Table S7. The EEI-c ecological status groups (ESGs) and their functional traits according to Orfanidis *et al*. (2011) , along with the corresponding macroalgal categories of the present study.

Table S8. Ecological status characterisation and range values of EEI-c (Orfanidis *et al*., 2011).

Table S9. Reef-EBQI values and corresponding ecological status per depth , and per site. ID = station ID. Colours denote different ecological status. Red: Bad, Orange: Poor, Yellow: Moderate, Green: High, Blue: Very high. Blank: no sampling carried out at the specific depth.

Table S10. EEI-c values per site (0 m depth stations only) and Reef-EBQI values per site (0 m depth stations only), along with the corresponding ecological status according to each index. Reef-EBQI values are the same as in Table S9, but are also provided here for direct comparisons. Colours denote different ecological status. Red: Bad, Orange: Poor, Yellow: Moderate, Green: Good (EEI-c) / High (reef-EBQI),Blue: High (EEI-c) / Very high (reef-EBQI). Blank: no sampling carried out at the specific depth. ± denotes standard deviation.

Fig. S1: Cluster analysis based on area cover data of the macroalgal morphofunctional groups found at 0, 5 and 15 m depth in the Aegean Sea.

Fig. S2: Map of the Aegean Sea depicting reef-EBQI values per site at 0 m depth.

Fig. S3: Map of the Aegean Sea depicting reef-EBQI values per site at 5 m depth.

Fig. S4: Map of the Aegean Sea depicting reef-EBQI values per site at 15 m depth.