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Contribution to the Special Issue: Marine Animal Forest of the World (MAF WORLD)

Advancing knowledge on red coral *Corallium rubrum* (Linnaeus, 1758) populations and associated mesophotic communities in the Aegean Sea, Eastern Mediterranean

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Abstract

This study presents the first quantitative analysis of live red coral (*Corallium rubrum*) populations in Greek waters (North-Western Aegean Sea) and contributes to the limited knowledge of mesophotic benthic assemblages in the Eastern Mediterranean Sea. Utilizing ROV and stereo-video SCUBA surveys at two previously harvested sites (47-60 m depth), we quantified red coral density and morphometric parameters. Associated benthic communities, comprising 101 taxa with Porifera as the dominant group, were characterized, and the Mesophotic Assemblages Conservation Status (MACS) index was applied for the first time in this region, revealing an overall “Good” ecological status despite locally degraded facies. While red coral entanglement by widespread ghost fishing gear appeared low, high frequencies of necrosis and epibiosis were observed in the larger canopy-forming gorgonian *Paramuricea clavata*, potentially indicating current and past mechanical damage, although the synergistic effects of other physical stressors cannot be excluded. This research offers crucial baseline data on red coral populations and associated mesophotic communities in an under-studied region and ecological zone. Our findings are discussed in the context of existing national management frameworks and conservation measures, emphasizing the need for further monitoring and research to inform effective management and conservation strategies in view of increasing anthropogenic and environmental pressures.

Keywords: North Western Aegean Sea; Mesophotic benthic assemblages; coralligenous; Marine Animal Forests; population assessment; Ecological status; management and conservation; scientific diving.

Introduction

Although an emblematic species since antiquity (Vielzeuf *et al*., 2022) and still occasionally exploited to date (Chintiroglou *et al*., 1989; Dounas *et al*., 2010), populations of the precious red coral *Corallium rubrum* (Linnaeus, 1758) (Octocorallia, Scleralcyonacea) in Greek seas and the wider Eastern Mediterranean Sea have received limited scientific attention. Earlier studies provided only rough information on presence and morphometry, the latter mostly based on a few live colonies collected from the North Aegean and Cretan seas (Chintiroglou *et al*., 1989; Vafidis *et al*., 1994), or on dead material from the Levantine basin (Zibrowius, 1979; Çinar *et al*., 2018). Nevertheless, *in situ* assessments of living red coral stocks remain challenging due to the typically deep (>50 m) distribution of the species in the Eastern Mediterranean (Dounas *et al*., 2010) as compared to the western basin, where *C. rubrum* populations can be encountered as shallow as 10 m depth (Espinosa *et al*., 2019).

Later scientific attempts to locate *C. rubrum* facies in coralligenous formations in the Aegean, Ionian and Cretan seas using Remotely Operated Vehicles (ROVs) and submersible dives yielded limited evidence of its occurrence at the investigated sites and depths (30-120 m) (Salomidi *et al*., 2009). Indeed, among 22 explored sites, 10 exhibited well-developed gorgonian forests (i.e., *Eunicella cavolini* (Koch, 1887) and *Paramuricea clavata* (Risso, 1872)), yet only one small, isolated patch of *C. rubrum* was detected within a *P. clavata* forest at the 60-65 m depth zone of the West Aegean Sea. Similarly, a single, small *C. rubrum* colony was detected in a crevice at only one out of five coralligenous sites studied by SCUBA diving in the National Marine Park of Alonnisos and

Northern Sporades (North-Western Aegean Sea, Greece) (Chimienti *et al.*, 2023).

Conversely, the harvesting, processing and trade of the precious red coral boast a longstanding tradition in Greece, dating back to ancient times (Tsounis *et al.*, 2010). At European and international levels, *C. rubrum* has been listed among the animal species whose exploitation may be subject to management measures in the European Union's (EU) Habitats Directive (92/43/EEC, Annex V), the list of protected animal species of the Bern Convention (Annex III) and among species whose exploitation is regulated according to the Protocol Concerning Specially Protected Areas and Biological Diversity (SPA/BD) of the Barcelona Convention (Annex III). Recognizing the species as a national natural asset, the Greek State has included *C. rubrum* in its 1981 catalogue of species of conservation interest, whose taking in the wild should be subject to management (Presidential decrees PD 67/1981, PD 256/1987).

Greek law, refined over time, initially established a rotating harvest system for specific geographical zones (Fig. 1), limiting permits (maximum 10 per year) and requiring a 20-year closure after 5 years of exploitation. It has also banned destructive dragging gear, allowing only manual collection by divers. Although regulations mandated reporting of location, depth, red coral density, fishing effort, and production per exploited bank to the appropriate authority, only bulk information on total production per licensed boat across three successively activated harvest zones has been made officially available to date (Dounas *et al.*, 2010). Since 2019, further EU regulations (e.g., minimum size, yearly quota) have been adopted. However, owing to the absence of officially active coral divers since 2006, no relevant data has been collected, and no further precautionary measures have been deemed necessary.

In the absence of baseline or explicit catch and effort data, the current status of live red coral stocks is effectively unknown and assessing the efficacy of *ad hoc* designated management schemes remains highly problematic. This knowledge gap is even more critical when aiming to implement an ecosystem-based management approach, which necessitates the identification of conservation species as vital components of broader ecosystem structures, functions, and services (Marine Strategy Framework Directive - MSFD; 2008/56/EC). In this context, detailed *in situ* surveys are essential to improve our knowledge of the distribution, population structure, and habitat characteristics of *C. rubrum*. As a key structuring species in the mesophotic zone, the status of *C. rubrum* can also serve as an indicator of environmental quality and health of associated coralligenous communities (Ferrigno *et al.*, 2020). Therefore, such surveys provide a necessary foundation for assessing current ecological conditions and informing interpretations of both historical baseline data and future trends.

This study represents a first step toward investigating the present status of *C. rubrum* populations on Eastern Mediterranean coralligenous banks by quantifying density and key morphometric parameters (i.e., height, width, basal diameter). Additionally, the ecological status of the associated mesophotic coralligenous communities was assessed by applying the MACS index (Enrichetti *et al.*, 2019), aiming to achieve a more comprehensive understanding of red coral facies in Greek national waters and contributing to the broader exploration of the largely unknown Marine Animal Forests (MAFs) (Rossi *et al.*, 2022; Rizzo *et al.*, 2025) of the Eastern Mediterranean Sea.

Fig. 1: Red coral harvest zones as designated for Greek territorial waters, according to Ministry Decision 240102/1995. The red polygon indicates exclusion of the Marine Protected Area of the National Marine Park of Alonnisos and Northern Sporades.

Methods and Materials

Site Selection

Within the context of the "GFCM Research Programme on Mediterranean Red Coral" aiming to improve knowledge on the status of harvested red coral populations in the Mediterranean, a comprehensive *in situ* survey was conducted on previously exploited red coral banks of the Aegean Sea, Greece.

Given data deficiency, acquiring detailed information on the occurrence of important red coral banks in the Greek seas still largely relies on collaboration with experienced coral divers or crew operators. For this purpose, collaboration with a former coral crew operator (Mr. H. Gazinakis) provided accurate information regarding locations of previously harvested red coral banks within suitable normoxic trimix diving depths (50-60 m).

The field survey was conducted at two sites in the North-Western Aegean Sea (Fig. 2) in March-April 2022, following the acquisition of appropriate research permits. Licensing was granted by the competent Greek administrative authorities (Decentralized Administration of Thessaly and Central Greece), in accordance with the legal guidelines for Scientific Research, as issued by the General Directorate of Fisheries of the Greek Ministry of Rural Development and Food (Protocol Number 2179/157832, 28-09-2021).

ROV exploratory surveys and data analysis

To verify the presence and distribution of *C. rubrum* populations and associated communities at the indicated locations, exploratory ROV surveys were initially performed over a depth range of 40 to 70 m. DEEP TREKKER DTG3 (max depth range 200 m) and QYSEA FIFISH V6 (max depth range 100 m) ROVs were used, equipped with underwater lights and video cameras recording at 4K resolution. During dives, ROV movement was predominantly perpendicular to the substrate, following the reef morphology and extending horizontally over several dozens of meters. In the subsequent analysis, each dive was divided into consecutive sampling units (SUs) of 5 m in length, each corresponding to a surveyed area of approximately 7.5 m^2, based on an estimated Field of View (FOV) of 1.5 m. Within each SU, average depth and dominant substrate type were noted. All visible specimens were identified to the lowest possible taxonomic rank, and their occurrence was categorized using three abundance classes: 1 (low), 2 (medium), and 3 (high), with the exception of the main structuring species (i.e., megabenthic species forming a proper canopy with high influence on the community structure) which were individually counted. Marine litter was also recorded and classified according to the Joint List of Litter Categories for Marine Macrolitter Monitoring (Fleet *et al*., 2021).

The Mesophotic Assemblages Conservation Status (MACS), which was developed by Enrichetti *et al*. (2019) to evaluate and monitor the environmental status of temperate mesophotic reefs over time, was applied for the first time in the Eastern Mediterranean Sea. The MACS includes two independent components: the Index of Status (Is) and the Index of Impact (Ii), each based on six metrics (12 metrics in total) and associated with three MSFD descriptors (Biological Diversity, Seafloor Integrity and Marine Litter). The MACS index ranges from 0 to 100 and is categorized into five ecological quality classes: Bad, Poor, Moderate, Good, and High. Metrics were evaluated directly from the video analysis or using the open-source ImageJ (v. 1.54d) software package, following the methodology described in Enrichetti *et al*. (2019).

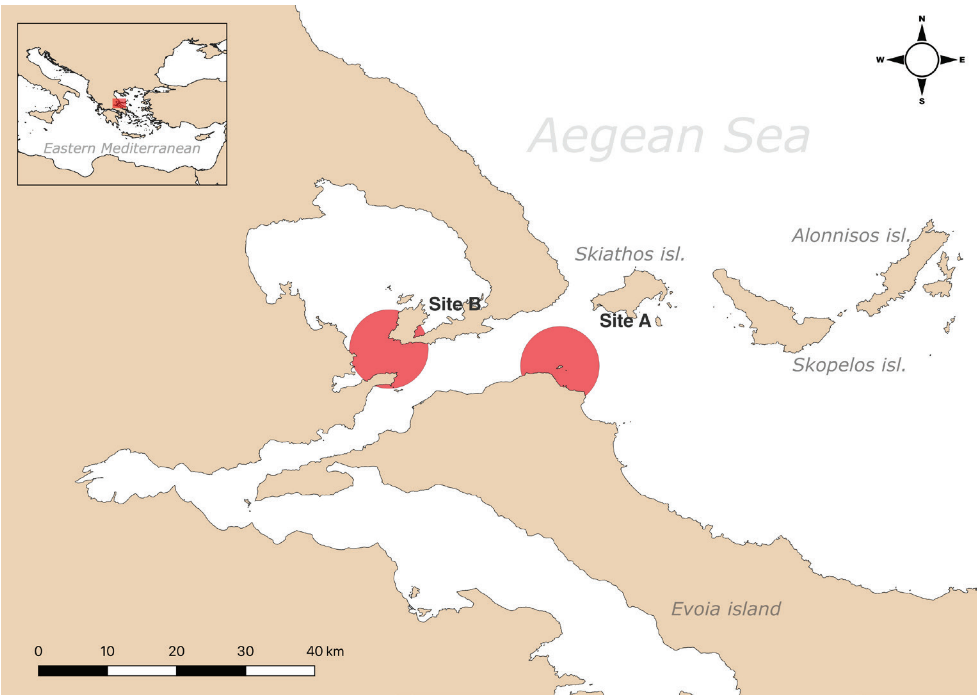

Fig. 2: Location of study sites (generalized) in the North Aegean Sea, Greece.

Five of the eight ROV video dives met the minimum area requirement of 100 m^2 for the MACS application and were therefore selected for further analysis. During each of these dives, 13 consecutive SUs containing coralligenous habitat were selected, excluding blue-water footage and periods of inactivity.

SCUBA surveys and data analysis

Deep SCUBA diving sessions using mixed gases (normoxic trimix) were implemented at two suitable locations (Sites A and B; Fig. 2) with dense *C. rubrum* facies at 50-60 m depth.

Non-destructive visual measurements of the *C. rubrum* colony density and morphology (i.e., height, width, and basal diameter) were conducted using a diver-operated stereo-video (stereo-DOV) system along 30-meter continuous transects at a depth of 55-57 m. The stereo-camera setup and calibration board were designed following the guidelines of Neuswanger *et al*. (2016) and Goetze *et al*. (2019), with custom modifications to accommodate the close-range measurements required for coral colonies.

Specifically, the system consisted of two GoPro HERO7 Black cameras in aluminium underwater housings; the distance between the cameras was set at 40 cm with a converging inward angle of 18°, recording at 4K resolution and 60 fps. Illumination was provided by two underwater video lights (8,000 lumens each), mounted on either end of the camera rig. To ensure high-quality imaging, the diver maintained a steady swimming speed of approximately 5-10 m/min while holding the stereo-DOV setup at ~50 cm above the substrate. The camera was visually swept horizontally covering a width of approximately 2 meters along each 30-meter transect. System calibration and distortion correction were conducted *in situ*, achieving a measurement accuracy of ± 0.5 mm at a working distance of 50 cm, verified using targets of known dimensions.

Coral colony measurements were performed using VidSync software (Neuswanger *et al*., 2016), and only colonies with a clearly visible basal diameter in the recorded footage were included in the analysis. To estimate colony density, 30 frames were systematically extracted from each video transect, and all visible coral colonies within a stereo-video estimated 50 × 50 cm field of view were counted.

Results

To acquire data on *C. rubrum* major habitat features (i.e., distribution, associated diversity, and population parameters), more than three hours of video footage from both ROV and SCUBA surveys were analysed. In total, ROV video coverage over the studied habitat spanned a total estimated length of 615 m and an estimated area of 922 m^2.

Red coral colonization and distribution patterns

In general, red coral presented a rather erratic, alternating patchy and continuous distribution across the study area. It typically colonized steep vertical coralligenous walls, overhangs, caverns or caves, apparently occupying all orientations, in both exposed and cryptic spaces, and formed either monospecific or mixed facies with other cnidarians, sponges or bivalve molluscs (Fig. 3).

The species' vertical distribution in the study area ranged between 47-58 m at Site A, and 54-60 m at Site B. In both cases, the species appeared considerably sparser at its upper limit, while its lower limit was clearly determined by the availability (lack thereof in this case) of suitable hard substrate, given that sedimentary bottoms succeeded the surveyed rocky slopes in deeper horizons.

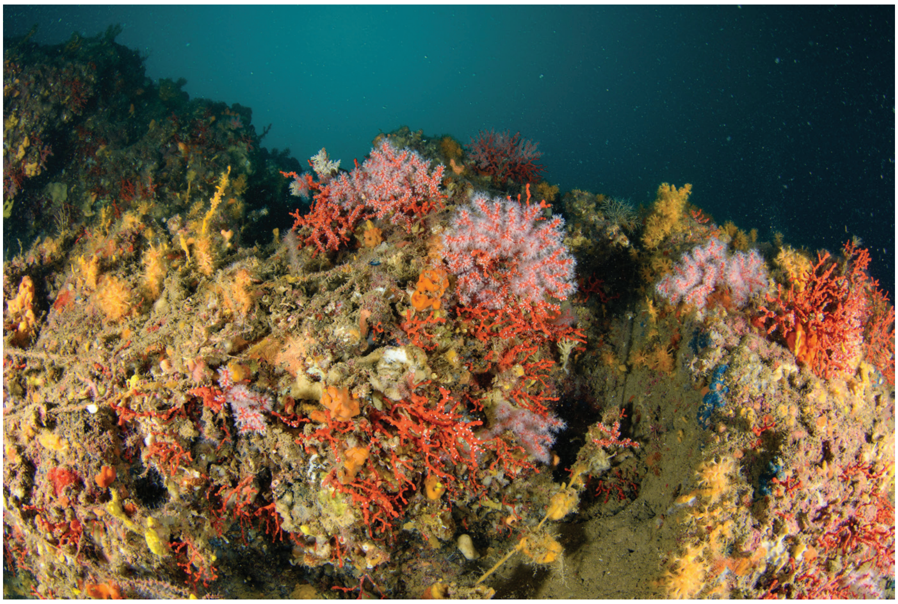

Fig. 3: Red coral colonies in exposed rocky faces at site B. Photo credits: Yannis Issaris/HCMR.

Red Coral Population Structure

According to the stereo-video analysis performed at the standard depth of 55-57 m at the two study sites:

Site A: The *C. rubrum* population presented a fairly continuous distribution with a mean density of 13.5 ± 2.8 colonies/m^2 (mean ± SE). The basal diameter of the colonies ranged between 5.6 and 18.5 mm (Fig. 4A), with a mean value of 9.7 ± 0.6 mm. Colony height ranged between 29.2 and 124.0 mm (Fig. 4B), with a mean value of 68.9 ± 5.2 mm.

Site B: The *C. rubrum* population occurred in two distinct patches, with a mean density of 114.7 ± 17.5 colonies/m^2 (mean ±SE). The basal diameter of the colonies ranged between 5.3 and 20.0 mm (Fig. 4C), with a mean value of 10.4 ± 0.4 mm. Colony height ranged between 35.6 and 337.0 mm (Fig. 4D), with a mean value of 87.7 ± 6.8 mm.

Associated diversity

According to both deep-diving and ROV video surveys performed, sites with *C. rubrum* presented a rich diversity of associated species. A total of 101 taxa were identified at the two study sites, among which 75 down to species level, 19 down to genus level, and the rest within higher taxonomic or morphological groups (morphotaxa or species complexes) (Tables S1, S2 in the Supplementary Material). Biodiversity structure (Fig. 5) revealed an overall dominance of the phylum Porifera (28 taxa), followed by Chordata (19 taxa – 6 Tunicata and 13 Teleostei), and the phyla Cnidaria (13 taxa) and Echinodermata (13 taxa). A comprehensive breakdown of all taxa recorded (per site and means of observation), along with their current protection and conservation status, is provided in Table S2.

Different numbers of taxa were recorded with different sampling scales (66 by SCUBA diving and 84 by ROV surveys) and at different sites (69 at Site A and 78 at Site B). Specifically, at Site A, a total of 38 taxa were identified with SCUBA diving, among which 25 down to species level and the rest within higher taxonomic or morphological groups. Porifera were the most species-rich group (12 taxa), followed by Anthozoa (5 taxa including *C. rubrum*) and Annelida (4 taxa). A checklist of all conspicuous benthic species associated with *C. rubrum*, as identified through diver-based high-resolution video recordings, is presented in Table S3.

At a larger scale, analysis of available 54 min ROV footage across the wider study site revealed even higher biodiversity, consisting of 63 taxa (Table S4). Again, Porifera was the most species-rich group (20 taxa), followed by Chordata (13 taxa – 5 Tunicata and 8 Teleostei), Anthozoa (8 taxa including *C. rubrum*), and Echinodermata (7 taxa).

In terms of frequency of occurrence, using both SCUBA and ROV acquired material, the most common records were various species of Hydrozoa, the anthozoans *Leptopsammia pruvoti* Lacaze-Duthiers, 1897 and *Parazoanthus axinellae* (Schmidt, 1862), the demosponges *Axinella verrucosa* (Esper, 1794), *Axinella polypoides* Schmidt, 1862 and *Agelas oroides* (Schmidt, 1864), the ascidian *Halocynthia papillosa* (Linnaeus, 1767), and the echinoderm *Hacelia attenuata* Gray, 1840. The encrusting Corallinaceae, the canopy forming sponges *Aplysina* sp., *Axinella* spp., and the gorgonian *Paramuricea clavata*, as well as the reef-building bivalve *Neopycnodonte cochlear* (Poli, 1795) also formed notable facies, but with a patchier distribution. Other common encounters were the various ephemeral turf algae and the non-commercial

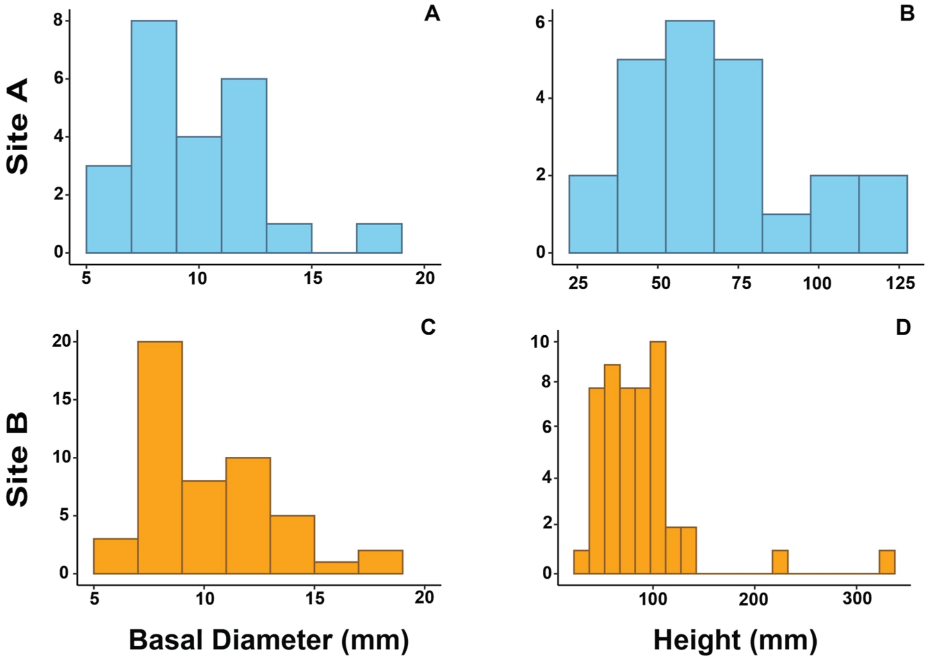

Fig. 4: Histograms of basal diameter and height of the observed colonies; blue for site A (graphs A, B) and orange for site B (graphs C, D).

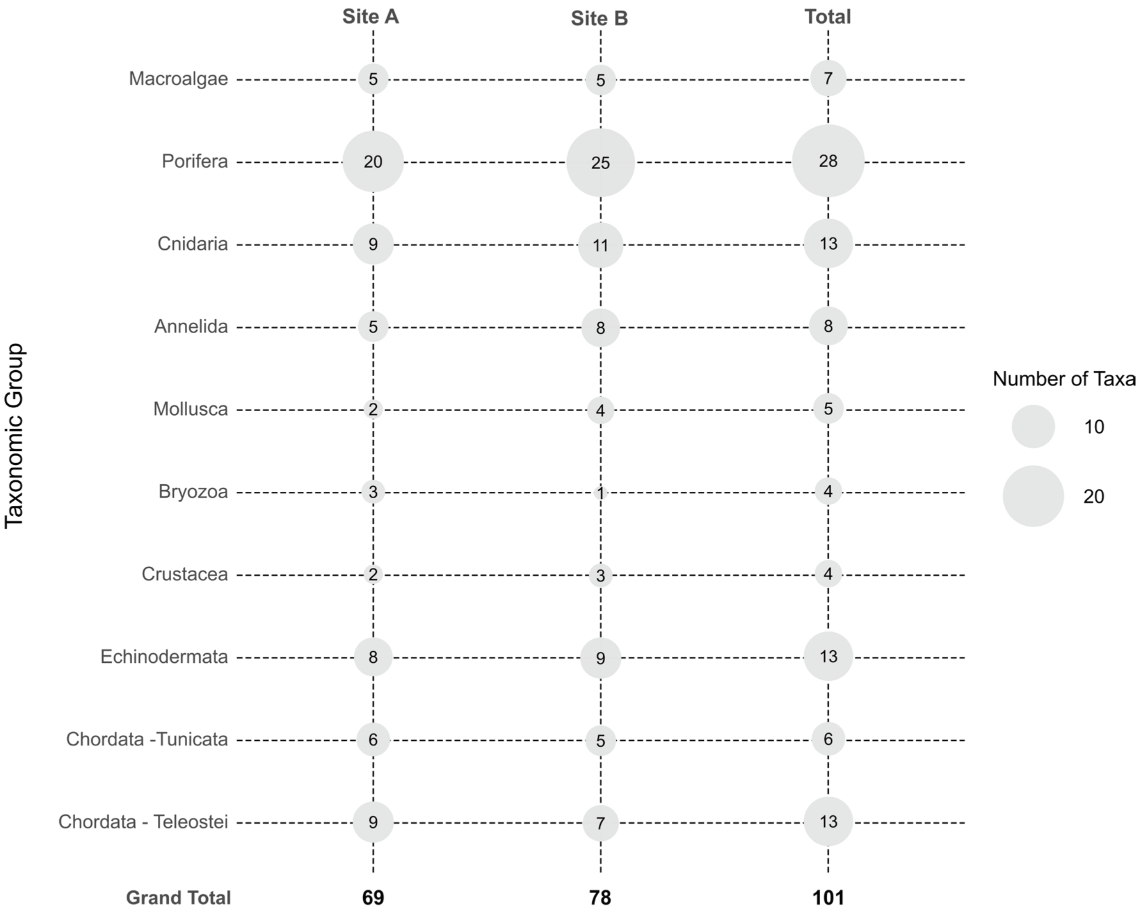

Fig. 5: Bubble plot of the biodiversity distribution among different taxonomic groups at Site A, Site B, and in total area of study.

swallowtail sea perch *Anthias anthias* (Linnaeus, 1758).

At Site B, a total of 51 taxa were identified with SCUBA diving, among which 37 down to species level and the rest within higher taxonomic or morphological groups. Porifera was the most species-rich group (20 taxa), followed by Chordata (7 taxa – 3 Tunicata and 4 Teleostei), Echinodermata (6 taxa), and Annelida (6 taxa), while Anthozoa (including *C. rubrum*) accounted for 4 species. A checklist of all conspicuous benthic species associated with *C. rubrum*, as identified through diver-based high-resolution video recordings, is presented in Table S5**.**

At larger scale, an analysis of available ~21 min ROV video footage across the wider study site recorded a total of 60 taxa (Table S6), among which 18 Porifera, 10 Anthozoa, and 10 Chordata (4 Tunicata and 6 Teleostei). Frequency of occurrence was highest for various unidentified Hydrozoa*,* the demosponges *Axinella verrucosa*, *Agelas oroides*, *Petrosia ficiformis* (Poiret, 1789), *Aplysina* sp. and *Terpios gelatinosus* (Bowerbank, 1866), the anthozoans *C. rubrum*, *L. pruvoti* and *P. axinellae*, various serpulids, and the encrusting red algae *Lithophyllum* spp. and *Peyssonnelia* spp.

The dominant taxa in the examined ROV transects from both Sites A and B are shown in Table 1, where occurrence values represent the number of sampling units (SUs, each 7.5 m²) in which a given taxon was observed, and dominant taxa are identified based on their frequency of occurrence across SUs.

Habitat Assessment

Pressures and threats

Ghost fishnets and long-lines, at places smothering protruding biota, were common and locally abundant across sites and transects studied (Fig. 6A), with a slightly more pronounced finding at Site A (41 longlines vs. 33 at Site B). Partial or full necrosis of *P. clavata* colonies (Fig. 6B) occasionally presenting various epibionts (i.e., hydrozoans, serpulids, turf algae) were also recorded at Site A.

Based on the estimated area observed (ROV Survey), the density was calculated for each type of item. The results for the total area at both investigated sites are presented in Table 2.

The percentage of entangled and necrotic anthozoan colonies, as well as those colonized by epibionts, was evaluated for each transect used in the MACS application. *C. rubrum*, the most abundant anthozoan, showed a low level of entanglement, with a maximum value of 3% of colonies entangled in one spot at Site B. Less than 0.5% of *P. clavata* colonies at Site A presented clear entanglement, but signs of necrosis (79%) and epibiosis (66%) were common. Although the analysis of MACS video footage did not reveal any necrosis or epibiosis in red coral colonies, when considering all dives at Site A (including shorter video footage unsuitable for the systematic application of the MACS index), the percentage of *C. rubrum* necrosis and epibiosis reached 19.6% and 23.9%, respectively.

Table 1. Dominant taxa from major phyla at Sites A and B based on ROV imagery. Values indicate the occurrence of a certain taxon, intended as the number of sampling units (7.5 m² each) in which the specific taxon was recorded.

Taxa	Occurrence	
	Site A	Site B
Porifera		
Agelas oroides (Schmidt, 1864)	59	41
Aplysina sp.	29	27
Axinella spp.	107	73
Haliclona sp.	-	18
Spirastrella cunctatrix Schmidt, 1868	33	-
Cnidaria		
Corallium rubrum (Linnaeus, 1758)	17	11
Hydrozoa spp.	47	28
Leptopsammia pruvoti Lacaze-Duthiers, 1897	47	20
Parazoanthus axinellae (Schmidt, 1862)	68	37
Echinodermata		
Hacelia attenuata Gray, 1840	30	8
Holothuria forskali Delle Chiaje, 1824	18	-
Holothuria spp.	-	9
Chordata		
Anthias anthias (Linnaeus, 1758)	16	-
Halocynthia papillosa (Linnaeus, 1767)	44	8
Serranus cabrilla (Linnaeus, 1758)	-	5

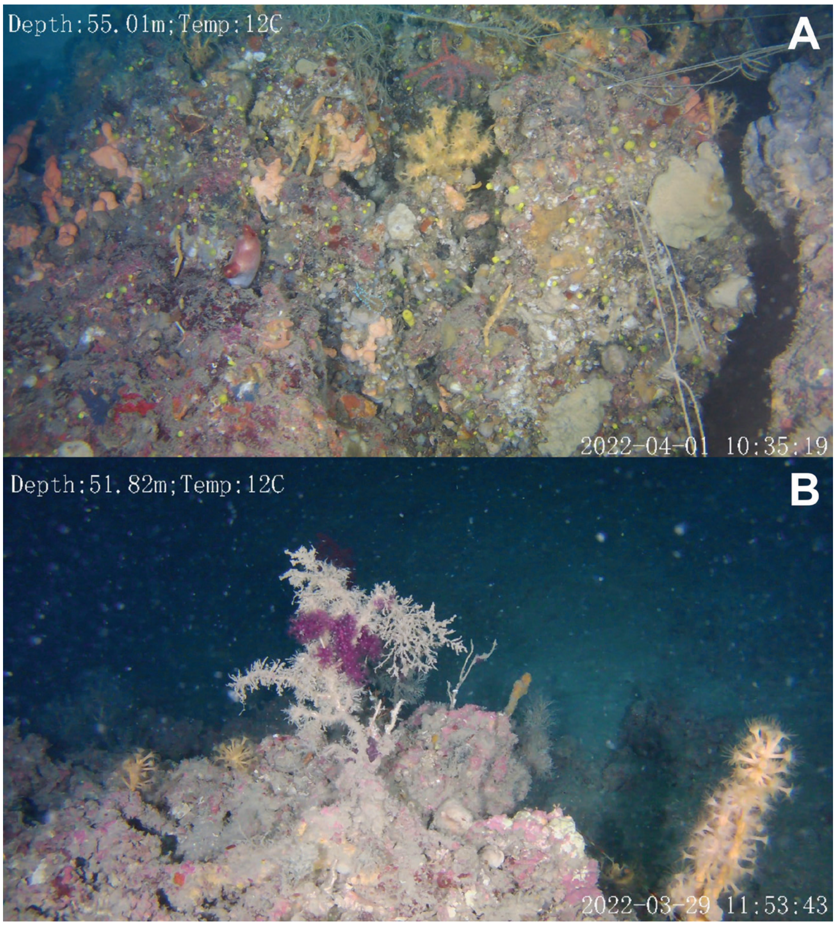

Fig. 6: A) Longlines near red coral colonies (Site B) Photo credits: V. Gerakaris/HCMR; B) Necrosed *Paramuricea clavata* covered by epibiotic hydrozoans and sediment (Site A) Photo credits: V. Gerakaris/HCMR.

Table 2. Type and density of marine litter for total area and each site investigated (ROV Survey).

Total Area				
G-Code	**Type**	**Description**	**N°**	**Density (item/m^2)**
G54	Artificial polymers	Net and net fragments > 50 cm	8	0.009
G56	Artificial polymers	Plastic tangled nets/cord	3	0.003
G59	Artificial polymers	Plastic fishing line	74	0.080
Site A				
G-Code	**Type**	**Description**	**N°**	**Density (item/m^2)**
G54	Artificial polymers	Net and net fragments > 50 cm	7	0.012
G56	Artificial polymers	Plastic tangled nets/cord	3	0.005
G59	Artificial polymers	Plastic fishing line	41	0.072
Site B				
G-Code	**Type**	**Description**	**N°**	**Density (item/m^2)**
G54	Artificial polymers	Net and net fragments > 50 cm	1	0.003
G56	Artificial polymers	Plastic tangled nets/cord	0	0
G59	Artificial polymers	Plastic fishing line	33	0.101

Density of structuring species

The three main structuring species identified in the study area were the sponge *A. polypoides* and the anthozoans *C. rubrum* and *P. clavata*. A total of 1918 structuring specimens/colonies were recorded in the examined ROV video material: 1182 *A. polypoides*, 644 *C. rubrum* and 92 *P. clavata*. The sponge *A. polypoides* presented the highest density in all but one dive, where *C. rubrum* prevailed instead. *Paramuricea clavata* was present at a few dive spots, but most colonies were heavily impacted, with diffuse necrosis and epibiosis (mainly by hydrozoans and serpulids of the *Salmacina/Filograna* complex). Density was evaluated per assemblage (only in SUs where the species was present) (Tables 3-5) and over the entire site (Tables 6-8).

Table 3. Assemblage density of structuring species in the total area explored by ROV. SD: standard deviation, SE: standard error.

Species	Abundance	Presence	Average Density (individuals or colonies / m^2)	SD	SE
Axinella polypoides	1182	96	1.642	1.185	0.121
Paramuricea clavata	92	19	1.642	0.503	0.115
Corallium rubrum	644	28	1.656	5.383	1.017

Table 4. Assemblage density of structuring species at site A. SD: standard deviation, SE: standard error.

Species	Abundance	Presence	Average Density (individuals or colonies / m^2)	SD	SE
Axinella polypoides	838	20	1.894	1.347	0.301
Paramuricea clavata	92	19	0.646	0.503	0.115
Corallium rubrum	142	17	1.114	1.114	0.270

Table 5. Assemblage density of structuring species at site B. SD: standard deviation, SE: standard error.

Species	Abundance	Presence	Average Density (individuals or colonies / m^2)	SD	SE
Axinella polypoides	344	37	1.240	0.717	0.118
Corallium rubrum	502	11	6.08	7.729	2.330

Table 6. Density of structuring species in total area explored by ROV. SD: standard deviation, SE: standard error.

Species	Abundance	N of SUs	Average Density (individuals or colonies / m²)	SD	SE
Axinella polypoides	1182	123	1.347	1.245	0.112
Paramuricea clavata	92	123	0.092	0.292	0.026
Corallium rubrum	644	123	0.641	2.729	0.246

Table 7. Density of structuring species in total area explored by ROV at site A. SD: standard deviation, SE: standard error.

Species	Abundance	N of SUs	Average Density (individuals or colonies / m²)	SD	SE
Axinella polypoides	838	76	1.397	1.426	0.159
Paramuricea clavata	92	76	0.153	0.366	0.041
Corallium rubrum	142	76	0.237	0.680	0.076

Table 8. Density of structuring species in the total area explored by the ROV at site B. SD: standard deviation, SE: standard error.

Species	Abundance	N of SUs	Average Density (individuals or colonies / m²)	SD	SE
Axinella polypoides	344	47	0.849	0.829	0.113
Corallium rubrum	502	47	1.240	4.170	0.567

Ecological Quality Status

Both study sites were found to be in Good ecological status according to the MACS index (Table 9). The application of the index across surveyed sites revealed Poor status for one dive spot at Site A, mainly based on the degree of sedimentation and necrosis of structuring species. Good or High ecological status was assessed for the remaining four spots at both sites (Table 10).

Discussion

While *Corallium rubrum* exhibits a broad depth distribution from 10 to 1000 meters (Knittweis *et al*., 2016), quantitative data on populations occurring deeper than 50 meters remain generally scarce (Rossi *et al*., 2008; Toma *et al*., 2022). This research constitutes the first quantitative analysis of live red coral populations in Greek waters and contributes to the limited body of knowledge on mesophotic benthic assemblages in the Eastern Mediterranean Sea.

Overall, the red coral colony height (mean 68.9-87.7 mm) and basal diameter (9.7-10.4 mm) observed during this study are in line with the ranges reported for shallow (< 60 m) populations in the North-Western Mediterranean, where mean heights of approximately 40-90 mm and basal diameters of 5-12 mm are common at sites characterised by moderate to low harvesting pressure (Rossi *et al*., 2008; Priori *et al*., 2013; Bramanti *et al*., 2014;

Table 9. MACS application for each Study Site. Is: Index of Status, Ii: Index of Impact.

Site	Is	Ii	MACS	Ecological Status
A	54	43	56	Good
B	58	28	65	Good

Table 10. MACS application for each single dive (Is: Index of Status, Ii: Index of Impact).

Dive Spot	Site	ROV platform	Is	Ii	MACS	Ecological Status
1	A	DEEP TREKKER DTG3	50	33	58	Good
2	A	QYSEA FIFISH V6	44	72	36	Poor
3	A	QYSEA FIFISH V6	67	22	72	High
4	B	DEEP TREKKER DTG3	61	33	64	Good
5	B	QYSEA FIFISH V6	56	22	67	High

Mallo *et al*., 2019). Similarly, the mean colony densities recorded at Site A (13.5 ± 2.8 colonies/m²) and Site B (114.7 ± 17.5 colonies/m²) are within the range reported for shallow red coral populations elsewhere in the North-Western Mediterranean, where densities commonly vary from a few colonies per m² up to more than 100 colonies/m², depending on depth, biotope, and harvesting intensity (Rossi *et al*., 2008; Priori *et al*., 2013; Bramanti *et al*., 2014; Mallo *et al*., 2019). However, it should be noted that despite the high accuracy of size estimates obtained through stereo-video analysis, the biometric parameters measured herein (colony height and basal diameter) are likely biased towards larger sizes, since smaller colonies (<30 mm in height) growing within cracks and crevices were rarely visible in the video footage and therefore excluded from this analysis.

According to a Length-Based Spawning Potential Ratio Analysis applied to the pooled dataset, the Greek red coral population exhibited a Spawning Potential Ratio of 18% (Bitetto *et al*., 2022), considerably lower than the 40% threshold commonly considered risk-averse for stocks with low resiliency (Clark, 2002). This implies a significantly reduced mature fraction, typical of overexploited populations. Although poaching events cannot be entirely ruled out, it is notable that our study area (Greek Harvest Zone I: North Aegean Sea) has not been officially open to coral harvesters since at least 1998, which may account for the presence of numerous large colonies observed at both study sites (approximately 90% exceeding the minimum harvestable size of 7 mm basal diameter).

The lack of a rigid historical baseline, however, limits our understanding of the actual evolution of these populations over time, making it impossible to determine whether these specific patches have successfully recovered from past harvesting or simply represent facies that were either below harvestable size or otherwise escaped the attention of harvesters at that time. The latter assumptions may be further supported by studies that explicitly focus on age-size relationships for shallow red coral populations from the Western Mediterranean, which suggest an age of 30-35 years for colonies to reach the minimal harvestable size (Bramanti *et al*., 2014). However, considering the potential for significant regional variations in growth rates, and given that our study focuses on deeper populations in the Eastern Mediterranean, the direct application of these temporal growth estimates requires careful interpretation. Targeted *ad hoc* studies are therefore necessary to gain a better understanding of the complex dynamics of these populations and consistently evaluate their conservation and management status (Santangelo *et al*., 2007; Bramanti *et al*., 2009; 2014).

In agreement with the ecological importance of red coral as a habitat former, our surveys revealed a diverse associated community. A species-rich assemblage was found to be associated with red coral facies in both study areas, including 12 protected species (Table S2). These included three sponges (*Aplysina* sp., *Axinella cannabina* (Esper, 1794) and *A. polypoides*), five anthozoans (*C. rubrum* and the scleractinians *Caryophyllia (Caryophyllia) inornata* (Duncan, 1878), *Phyllangia americana mouchezii* (Lacaze-Duthiers, 1897) *and Polycyathus muellerae* (Abel, 1959), two crustaceans (*Palinurus elephas* Fabricius, 1787 and *Scyllarides latus* (Latreille, 1803), one echinoderm (*Ophidiaster ophidianus* (Lamarck, 1816)) and one fish (*Sciaena umbra* Linnaeus, 1758). In addition to the endangered red coral, three species have been categorised as Vulnerable (*P. clavata*, *P. elephas* and *S. umbra*) and two as Near Threatened (*Eunicella cavolini* and *E. verrucosa* (Pallas, 1766)) on the IUCN Red List of species at the Mediterranean or Global level (Table S2). However, the actual number of species of conservation interest is likely far greater than currently recognized, since the existing protective schemes inadequately address the full spectrum of vulnerable and key MAF-forming or MAF-associated species (Rizzo *et al*., 2025).

An analysis of the biodiversity, based on SCUBA diving and ROV-acquired footage, revealed limited occurrence and relatively low abundance of species of commercial interest, mainly the crustaceans *S. latus* and *P. elephas* (the latter being one of the most targeted species by small-scale fisheries on coralligenous and rhodolith beds in Greece - Kampouris *et al*., 2022), as well as four fish species of lesser commercial interest (*S. umbra*, *Scorpaena scrofa* Linnaeus, 1758, *Serranus cabrilla* (Linnaeus, 1758) and *S. hepatus* (Linnaeus, 1758)).

At community level, sponges (Porifera) were the dominant phylum, as observed in other coralligenous reefs of the Eastern Mediterranean Sea (e.g., Idan *et al*., 2018; 2021; Sini *et al*., 2019; Çinar *et al*., 2020), while anthozoans exhibited local dominance at smaller spatial scales (e.g., *Paramuricea* and *Corallium* facies). The main structuring taxon at both sites was *Axinella* spp.; at least four species were identified, namely, *A. cannabina*, *A. damicornis* (Esper, 1794), *A. polypoides* and *A. verrucosa*, although visual limitations prevented reliable species assignment for small individuals, as early developmental stages of the genus *Axinella* share a similar short, unbranched morphology. Among Porifera, *Agelas oroides* was one of the dominant massive-tubular species, in agreement with reports from other low-light habitats in the Aegean Sea (Gerovasileiou *et al*., 2016; Sini *et al*., 2019; Çinar *et al*., 2020). The tubular sponge *Aplysina* sp. reached remarkably high abundances, particularly in association with *Neopycnodonte cochlear* bioconstructions (Fig. 7A). Moreover, the presence of the sponge *Haliclona* cf. *poecillastroides* (Vacelet, 1969) was notable, often recorded in high numbers (up to nine individuals per sample) or high surface coverage (Fig. 7B). To the best of our knowledge, this is the first record of this species in the Aegean Sea (Voultsiadou *et al*., 2016), although a few additional unpublished observations are known to us (V. Gerovasileiou, personal observations).

In terms of density, the main structuring sessile species varied considerably among the three species examined (*A. polypoides*, *C. rubrum* and *P. clavata*). For the red coral, the number of colonies per sample ranged between 1 and 175 occurrences, although most dive sites were devoid of colonies. Consequently, mean densities differed depending on the spatial scale considered, with 1.656 colonies/m² at assemblage level and 0.641 col-

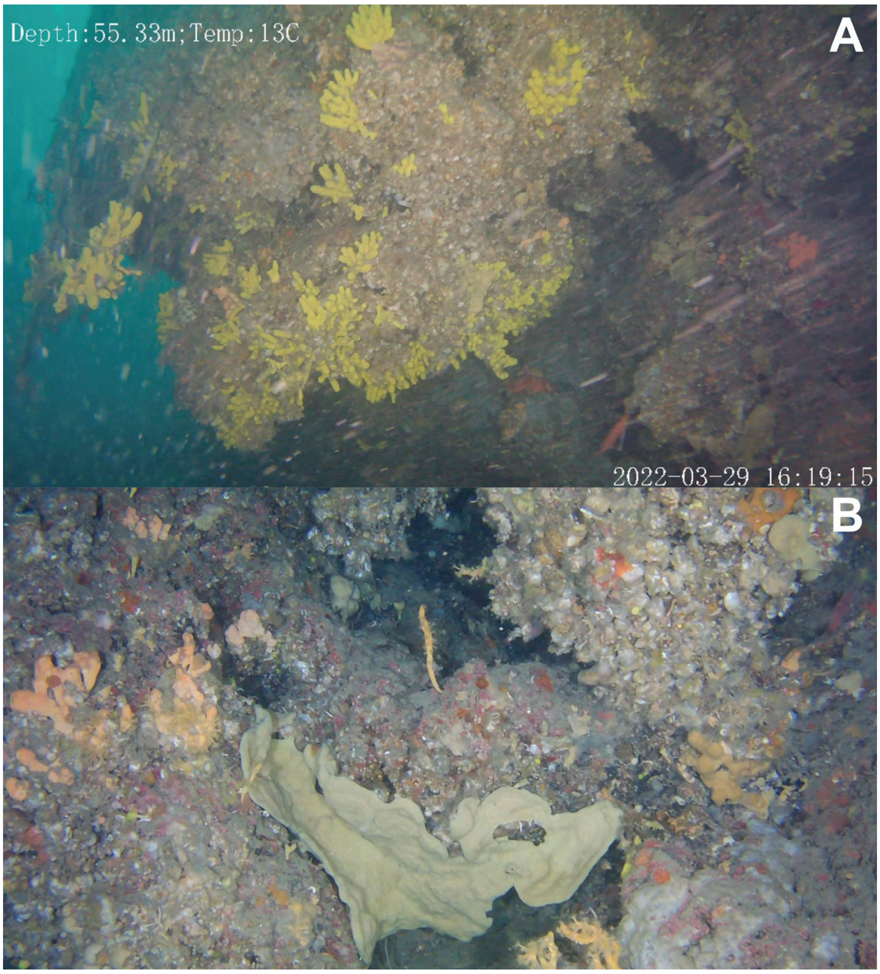

Fig. 7: The tubular sponge *Aplysina* sp. presenting high density in association with *Neopycnodonte cochlear* bioconstructions. Photo credits: V. Gerakaris/HCMR; B) *Haliclona* cf. *poecillastroides* at site A. Photo credits: T. Dailianis/HCMR.

onies/m² across the total surveyed area, both showing high variability due to differences in colony numbers and cluster sizes within sampling units. A similar pattern was observed for the densities of the anthozoan *P. clavata* and the sponge *A. polypoides* (Tables 3-8).

Other associated fauna varied between sites, but dense aggregations of the zoanthid *Parazoanthus axinellae* and various unidentified hydrozoans were consistently common across the surveyed locations. Although typical components of Mediterranean coralligenous assemblages, these taxa are characterized by relatively rapid or ephemeral growth. Their frequent primary colonization of substrate in our study area may indicate past impacts from either legal (pre-1995) or illegal use of highly destructive gear (such as the ingegno), which may have affected significant portions of these fragile bioconstructions.

The MACS index was applied to assess the ecological status of red coral assemblages; however, it is important to acknowledge that the study focused on two rather pristine and well-structured red coral facies within a broader region visibly impacted by anthropogenic activities, most notably fishing. In line with these localized conditions, the index generally indicated a good ecological status. At Site A, however, one of the dive spots was assigned a Poor value for the Index of Status (Is), and a Bad value for the Index of Impacts (Ii), largely reflecting the widespread presence of heavily impacted *P. clavata* colonies. Although a very low level of entanglement was observed, high levels of necrosis and epibiosis revealed a suffering population, with 66% of the observed specimens hosting at least one epibiont and 80% exhibiting partial necrosis. While the most frequent epibionts in our study (Hydrozoa spp. and *Filograna/Salmacina* complex) are also commonly found on *P. clavata* elsewhere, notable differences emerged compared to the findings of Canessa *et al.* (2023): a lower diversity of epibiont taxa and contrasting proportions between the two main groups (lower prevalence of Hydrozoa spp. and higher prevalence of *Filograna/Salmacina* spp.). Although our methodology does not allow for a detailed investigation of epibiotic community composition, nor to ascertain whether differences between our results and those of Canessa *et al.* (2023) reflect broader patterns between the Eastern and Western Mediterranean basins, the high incidence of epibiosis observed herein may further suggest a high frequency of mechanical damage in the examined *P. clavata* population. Tissue injuries caused by non-entangling fishing gear are known to enhance colonization by epibionts (Bavestrello *et al.*, 1997; Mortensen *et al.*, 2005; Bo *et al.*, 2014; Ferrigno *et al.*, 2018; Betti *et al.*, 2020). However, other large-scale stressors cannot be discounted, including: (a) increased sedimentation linked to severe wildfires on the adjacent land forests during the year preceding this study; (b) a persistent algal bloom that spread across the wider North

Aegean Sea during spring-summer 2021; or (c) unreported mass mortality events (MMEs), which are increasingly affecting this species in recent decades (Garrabou *et al*., 2022). Given the considerably deeper occurrence of the necrosed gorgonians observed herein, the assumption of MMEs would challenge the depth refuge hypothesis proposed for the *P. clavata* populations (Bramanti *et al*., 2023), at least in the Eastern Mediterranean context.

Signs of direct anthropogenic impact and habitat degradation were common and at places intense. At these sites, as well as in many other coralligenous formations across Greece (Salomidi *et al*., 2009; Chimienti *et al*., 2023; authors' personal observations), both direct and indirect mechanical impact caused by net and longline fishing was prevalent. This is in direct conflict with Council Regulation (EC) No 1967/2006 that prohibits any destructive fishing over "sensitive habitats" such as the Mediterranean coralligenous communities.

Coralligenous walls, overhangs and marine caves are known to constitute the primary habitats for red coral populations in the Mediterranean (Ballesteros, 2003). According to the latest (2013-2018) national habitat assessments under Article 17 (https://nature-art17.eionet.europa.eu/article17/) of the Habitats Directive (92/43/EEC), Habitat Type 1170 (Reefs, including coralligenous) presents an Unfavourable - Bad Conservation Status, while Habitat Type 8330 (marine caves, including deep submerged ones) has been assessed in an Unfavourable - Inadequate Conservation Status in Greece. Given that no conservation targets or *ad hoc* management measures have yet been established to mitigate imminent pressures exerted on these vulnerable habitats, the overall assessment of the Conservation Status of *C. rubrum* (Annex V of the Habitats Directive) has been assessed as Unfavourable - Inadequate and deteriorating.

In addition to coralligenous formations, marine caves and overhangs, Greek coral harvesters also report the sporadic presence of dense red coral populations on rocky outcrops within otherwise flat sedimentary seabeds (Mr. E. Baramatis & Mr. K. Baramatis, personal communication). Similar occurrences documented elsewhere from the Mediterranean (Cau *et al*., 2016), are of particular interest given that such formations are highly prone to anthropogenic disturbance; despite their recognized fragility, such habitats remain largely unmapped and unprotected from the impacts of highly destructive practices such as bottom trawling and bottom-set gillnets, contrary to the requirements of Council Regulation (EC) No 1967/2006 and the corresponding national legislation.

While the current inactivity of the coral harvesting sector in Greece might appear beneficial for conservation, significant issues persist. These include a reported increase in illegal harvesting by unauthorized vessels using destructive dragging methods (Dounas *et al*., 2010), opportunistic poaching by deep divers, as well as allegations of collaboration between officially inactive Greek coral divers and foreign poaching crews. In addition, the deep distribution of red coral, inaccessible to routine recreational and scientific diving, results in a near-complete lack of knowledge regarding the overall population status of the species in Greek seas.

Considering the findings of this study combined with escalating fishing pressure, blue growth demands, climate change, and the increasing vulnerability of sessile benthic species to MMEs, a deeply concerning scenario emerges. In addition, recent genetic analyses performed on samples collected during this study suggest that these red coral populations exhibit low genetic diversity (Aurelle *et al*., in prep), which further highlights a reduced capacity to adapt to change, increased vulnerability to various threats, and a higher risk of extinction (e.g., Frankham, 2005; Ledoux *et al*., 2010). Conservation efforts must move beyond single-species, single-threat approaches and embrace ecosystem-based management strategies, as foreseen by the European Common Fisheries Policy. In addition to long-term temporal closures (such as the current 20-year periods implemented in Greece), well-enforced, no-take Marine Protected Areas (MPAs) with confirmed *C. rubrum* presence are essential for meaningful conservation and monitoring (Mallo *et al*., 2019), particularly given escalating anthropogenic and climate-driven threats to both exploited and non-exploited populations. This need is particularly pertinent for the Aegean Sea and probably the wider Eastern Mediterranean basin, where general protective measures targeting populations shallower than 50 m remain largely ineffective due to the scarcity of well-developed *C. rubrum* assemblages in that zone (Dounas *et al*., 2010).

Greek coral divers remain a valuable source of information regarding the distribution and historic state of red coral populations in the Greek Seas. Given that most are now retired or approaching retirement, establishing red coral monitoring programs that bring together scientists and former coral divers would help capture crucial traditional ecological knowledge on red coral and other mesophotic assemblages across the Greek Seas, creating a much-needed historical baseline for this data-deprived region. Furthermore, any future coral harvesting licenses should be granted based on a robust management scheme that incorporates real-time monitoring and observer programs, similar to those successfully established in other Mediterranean countries such as Italy, Spain, and France within the framework of the General Fisheries Commission for the Mediterranean (GFCM) recommendations.

By delivering vital site-specific data on red coral populations and associated communities, this study sheds light on a previously understudied marine region, particularly within a persistently overlooked depth zone. Nevertheless, the extensive potential distribution of coralligenous communities across the North-Eastern Mediterranean Sea (Martin *et al*., 2014) underscores the urgent need for extended surveys aimed at gaining a better understanding of the status and trends characterising these unique and vulnerable ecosystems, as well as providing valuable information required for improving future management and conservation efforts.

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Supplementary Data

The following supplementary information is available online for the article:

Table S1. Number of taxa detected using both deep-diving and ROV surveys.

Table S2. Taxa recorded at study sites with deep SCUBA diving and ROV surveys. Their protection and conservation status (IUCN Red List) are also provided. Bern: Bern Convention, Barc: Barcelona Convention, CITES: Convention on International Trade in Endangered Species of Wild Fauna and Flora, HD: Habitats Directive, II: Annex/Appendix II, III: Annex/Appendix III, V: Annex/Appendix V, EN: Endangered, VU: Vulnerable, NT: Near Threatened, LC: Least Concern, DD: Data Deficient.

Table S3. Checklist of taxa detected through diver-based high-resolution video footage at Site A.

Table S4. Checklist of taxa detected through ROV footage at Site A.

Table S5. Checklist of taxa detected through diver-based high-resolution video footage at Site B.
Table S6. Checklist of taxa detected through ROV survey footage at Site B.