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Comparative Study of Marine Cave Communities in a Protected Area of the South-Eastern Aegean Sea, Greece

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Abstract: Although more than 600 marine caves have been recorded so far along the Greek coasts of the Aegean Sea (Eastern Mediterranean), only a few have been systematically studied for their biodiversity. In this study, the benthic communities of six marine caves within a Protected Area of South-Eastern Aegean were studied for the first time, both qualitatively and quantitatively. The association of different geomorphological and topographical factors of the caves with the benthic community structure was investigated. A total of 120 photographic quadrats covering the entrance and semi-dark cave zones were analysed, with regard to coverage and taxon abundance, while motile taxa were qualitatively recorded by visual census. The ecological quality status of the caves was also assessed under an ecosystem-based approach. In total, 81 sessile and 45 motile taxa were recorded, including 12 protected and 10 non-indigenous species. Multivariate community analysis demonstrated that the geomorphological and topographical variables of the caves are significantly associated with the observed biotic patterns. The ecological quality of the caves was assessed as poor or moderate according to the CavEBQI index, highlighting the necessity for systematic monitoring. This study paves the way for similar studies in marine cave habitats aiming at the development of management and conservation actions.

Keywords: dark habitats; benthic communities; photoquadrats; visual census; scientific diving; Marine Protected Area; Eastern Mediterranean; non-indigenous species; habitat pressures; ecological quality

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1. Introduction

Mediterranean marine caves host rich biodiversity, including more than 2300 taxa, and provide shelter to several endemic, rare, and protected species [1,2]. They are characterised by steep environmental gradients [3] which generate a characteristic zonation of benthic communities succeeding one another on a scale of few meters [2–4]. Such patterns have been mainly studied in a qualitative manner, focusing specifically on sponges, which are the dominant colonisers on cave walls [5–7] while fewer studies involve quantitative analyses of benthic community structure [4,8–10].

Marine caves are characterized by a rich geomorphological variety. According to Riedl [3], six cave types exist in the Mediterranean Sea, depending on their level of submersion (submerged or semi-submerged), shape and number of openings (e.g., blind-ended or tunnel-shaped). Geomorphological and topographic features such as the cave depth and orientation, entrance area and cave type, affect the level of light diffusion and water renewal inside marine caves [3,7]. Such abiotic gradients also affect the structure of hard substrate benthic communities, resulting in biotic heterogeneity even among neighbouring marine caves, also known as "individuality" of each cave [2–4,9,11].

Marine caves constitute a typical ecosystem of the Mediterranean Sea and are protected by the European Union's Habitats Directive (92/43/EEC) and the Barcelona Convention under the Dark Habitats Action Plan [12]. So far, more than 3000 marine caves have been recorded across the Mediterranean rocky coastline [2,13], 622 of which are located on the Greek coasts of the Aegean Sea [14]. Although marine caves are known to be located in 33 out of 62 Mediterranean Marine Protected Areas (MPAs) [15], the exact number of marine caves in MPAs remains unknown. No specific management plans or regulations are implemented for marine caves in most countries [1,2,16].

Over the last years, various impacts have been detected in marine caves, such as the effects of climate change on their biota [17–21], coastal construction and marine pollution [13,22–24], as well as unregulated recreational activities [13,25,26]. In addition, more than 60 non-indigenous species (NIS) and cryptogenic taxa (i.e., those that cannot be reliably demonstrated as being either introduced or native) have been recorded in Mediterranean marine caves [27–30]. Particularly in the Eastern Mediterranean, marine caves may function as "stepping stones" for the expansion of sciaphilic NIS, such as invertebrates and fish of Indo-Pacific origin which shelter in caves and coral reef cavities within their natural range of distribution [28].

The current study aims to provide a quantitative description of hard-substrate benthic communities and a catalogue of motile taxa (including NIS) recorded in six marine caves in an MPA of the Eastern Mediterranean Sea using non-destructive methods. These data were used to assess the ecological status of the surveyed marine caves through an ecosystem-based index for the first time in the Eastern Mediterranean basin. In addition, it examines the association of benthic community patterns with distinctive geomorphological and topographic features of the studied caves. Through this study, three hypotheses were tested: (i) all studied caves are significantly differentiated mainly due to cave-specific features (individuality hypothesis); (ii) the examined geomorphological and topographic factors (cave type, entrance depth, entrance area, and entrance orientation) significantly affect the benthic community patterns, and (iii) equivalent ecological zones from different caves show higher similarity levels.

2. Materials and Methods

2.1. Study Area

Six marine caves were surveyed in October 2019 in the Marine Protected Area of North Karpathos and Saria Islands in the South-Eastern Aegean Sea (Greece), which is included in the Greek NATURA 2000 Network (code GR4210003). This Eastern Mediterranean marine area was studied for the first time regarding its marine cave biota. The six surveyed marine caves were selected according to representativeness criteria [12] among 76 cave formations recorded within the MPA during an extended exploration covering 45 km of coastline [31]. Out of the six caves examined, two were fully submerged, located at the north-eastern coast of Karpathos Island, while four semi-submerged caves were located along the northeast to western coastline of Saria Island (Figure 1, Table 1). The maximum seafloor depth of the examined caves ranged from 4 to 11 m for fully submerged and 9–16 m for semi-submerged caves, while the cave length ranged from 16 to 37 m. All examined caves were blind-ended (i.e., had a single opening/entrance).

Table 1. Geomorphological and topographic characteristics of the six studied marine caves. Sub., fully submerged; Semi-sub., semi-submerged.

Cave Name	Latitude (DD)	Longitude (DD)	Type	Depth (m)	Length (m)	Entrance Width (m)	Entrance Orientation
Alona	35.81969	27.23049	Sub.	1–4	24	11	E
Troulakas	35.81072	27.23314	Sub.	8–11	16	13	E
Giourious	35.86615	27.20269	Semi-sub.	0–14	17	10	W
Oxonisos	35.90087	27.21935	Semi-sub.	0–16	17	10	N
Palatia	35.88730	27.23276	Semi-sub.	0–9	17	4	S
Panteleimonas	35.85458	27.19273	Semi-sub.	0–15	37	30	W

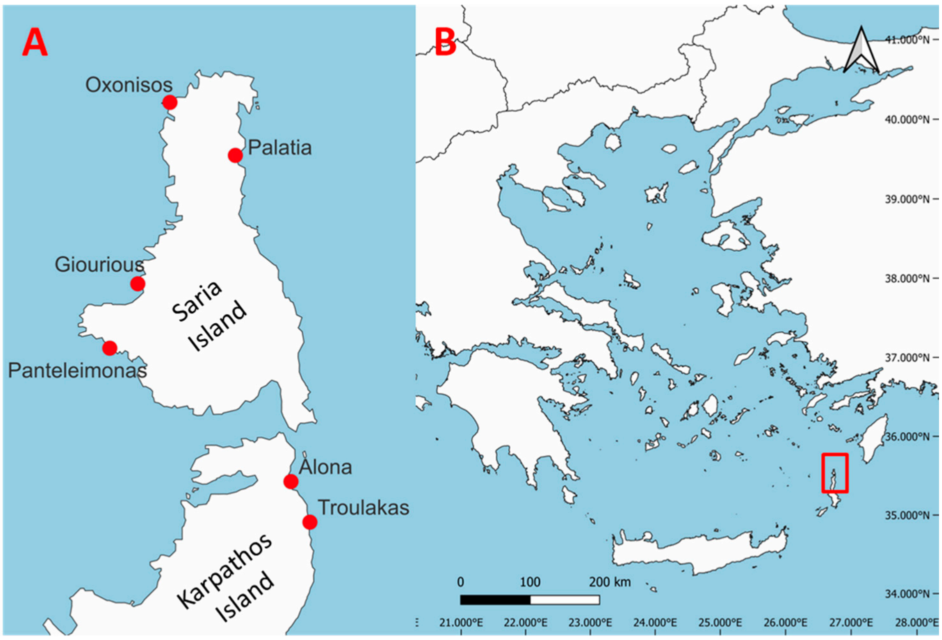

Figure 1. Location of the studied marine caves on the north coasts of Karpathos and Saria Islands (**A**) and their location in Greece, Eastern Mediterranean (**B**).

2.2. Sampling

SCUBA diving was used to approach the marine caves and perform the sampling. For the study of hard substrate benthos sets of five random standard replicate quadrats (25 × 25 cm) were photographed on the opposite walls of each cave zone [10,32,33]. Photographs were taken at a 4608 by 3456 pixel resolution with a digital camera coupled with two external underwater strobes. Cave zones were defined according to the bionomic model developed by Pérès [34]: (i) entrance zone, which is usually dominated by sciaphilic macroalgae (e.g., rhodophytes), and (ii) semi-dark zone, which is dominated by sciaphilic animals, mostly sponges in the Eastern Mediterranean Sea [2,27]. None of the studied caves had a distinct innermost completely dark zone, large enough for proper sampling. In total, 120 quadrats were collected from all caves. Additional close-up photos and qualitative samples were also collected for the identification of sessile taxa. Qualitative identification of motile species was performed visually with a special focus on protected taxa and NIS. Potential threats and pressures (e.g., necrosis of sessile taxa and litter) were also documented and photographed, when present.

2.3. Photoquadrats Processing

The percentage of biotic cover for sessile benthos was calculated using PhotoQuad, an advanced image processing software dedicated for marine biological applications [35]. Each photoquadrat was analysed by overlaying 100 uniformly stratified points. Each point was assigned to a sessile taxon or morpho-functional category (e.g., encrusting Rhodophyta, turf-forming algae). Identification was held to the lowest feasible taxonomic level. Taxa that were present in the photoquadrats but did not fall below a random assignment point were given an arbitrary value of 0.5% cover [36–39]. Supplementary close-up photographic material was used to assist identification of sessile species. Percent coverage of the identified species for every quadrat was automatically calculated by PhotoQuad software [35].

2.4. Ecological Quality Assessment

The ecological quality index CavEBQI, as proposed by Rastorgueff et al. [22] for the Western Mediterranean, was applied to assess the ecological quality of all the studied caves in terms of ecosystem structure and functioning. The identified sessile taxa, whose coverage was calculated through photoquadrat analysis, were assigned to different components of the cave ecosystem as 'Passive filter feeders', 'Large active filter feeders', and 'Small active filter feeders', while motile taxa were assigned as 'Detritus feeders and omnivores', 'Characteristic carnivores', and 'Associate carnivores' according to the model suggested by Rastorgueff et al. [22]. Accidental cave visitors (e.g., herbivores) and NIS were not considered in this assessment due to the lack of information regarding their habits in the marine cave environment [27,28]. Sessile filter feeders' stratification (with height of mm, cm, or dm) and the presence of cave-dwelling mysids were also taken into account. The Confidence Index of the Ecosystem-Based Quality Index (CI_{EBQI}), rescaled from 0 (worst confidence in the value of the EBQI) to 10 (highest confidence in the value of the EBQI), was also calculated for each studied cave [22].

2.5. Structure Assessment and Statistical Analysis

Multivariate, non-parametric resemblance analysis of the biotic coverage data was performed through the software PRIMER-6 [40]. Coverage data were transformed under the square root formula and a triangular similarity matrix was created based on the Bray-Curtis similarity index [41]. Non-metric multidimensional scaling (nMDS) [42] was used to investigate spatial patterns in the community structure. The association of geomorphological and topographic factor patterns with those of the benthic community was assessed using one-way analysis of similarity (ANOSIM) [43] for six fixed factors: Cave (six levels, one for each cave), Ecological Zone (two levels: Entrance, Semi-dark zone), Cave Type (two levels, fully submerged and semi-submerged), Entrance Area (three levels: 15–40 m^2, 110–230 m^2 and 630 m^2), Entrance Depth (max) (two levels: 0–10 m and 10–20 m) and Entrance Orientation (four levels: west (W), east (E), north (N) and south (S)). The contribution of different taxa to Bray-Curtis dissimilarity among the resulting sample groups was estimated through SIMPER (SIMilarity PERcentages) analysis [43].

3. Results

3.1. Sessile Community Structure

In total, 81 sessile taxa and morpho-functional categories were identified, classified into Porifera (37), Bryozoa (13), Macroalgae (10), Cnidaria (6), Ascidiacea (6), Brachiopoda (3), Mollusca (3), Foraminifera (1), Polychaeta (1), and Crustacea (1), listed in detail in Table S1 in Supplementary Materials. Sixty-eight taxa were recorded from the cave entrance, while 71 were recorded from the semi-dark zone. These taxa belonged to 47 species, 22 genera, 2 families, 2 orders, and 8 morpho-functional groups (Encrusting Rhodophyta, Green filamentous algae, Turf-forming algae, Orange encrusting sponge, White sponge, Yellow encrusting sponge, Bryozoan turf, Encrusting Bryozoa). The total number of taxa varied among the different caves, from 43 in Alona and Palatia caves to 59 in Troulakas cave (Oxonisos, Giourious, and Panteleimonas caves had 46, 48, and 50 taxa, respectively). Eleven taxa were recorded only at the entrance zone, while 16 taxa were found exclusively at the semi-dark zone of the studied caves (Table S1).

The percent coverage of sessile taxa was calculated separately for each ecological cave zone (Tables 2 and S1, Figure 2). Macroalgae, dominated at the entrance zone (CE) of all caves, reaching a maximum of 64% in the semi-submerged cave Palatia. Rhodophytes were dominant at the cave entrance of all caves with lower percent coverage at the submerged caves Troulakas and Alona (25% and 29%, respectively). Macroalgae covered up to 21% of the semi-dark walls of Giourious cave.

Sponges dominated at the semi-dark zone of all caves (range of 16.9 to 59.9%), followed by bryozoans, polychaetes and algae. For five out of the six examined caves, living sessile communities did not occupy the full extent of the wall substrate at the semi-dark zone, as manifested by the substantial percentages of non-living substrate (barren cave rock) in our results (Figure 2). These percentages were high for Palatia and Alona (58.3 to 58.5%) and lower for Oxonisos, Panteleimonas and Troulakas (14.7, 8.5, and 23.1%, respectively).

Table 2. Summary data with the average percentage of coverage (%) of all groups of sessile taxa and non-living substrate for each ecological cave zone. ALO: Alona, GIOU: Giourious, OXO: Oxonisos, PAL: Palatia, PANT: Panteleimonas, TROU: Troulakas, CE: entrance zone, SD: semi-dark zone, NLS: Non-living substrate.

Taxa/Categories	ALO		GIOU		OXO		PAL		PANT		TROU	
	CE	SD	CE	SD	CE	SD	CE	SD	CE	SD	CE	SD
Macroalgae	28.5	-	56.2	20.9	47.6	8.6	64.2	1.1	64.1	10.4	24.7	0.7
Foraminifera	0.1	0.2	0.4	1.2	4.0	1.5	1.0	0.7	0.1	4.3	-	0.9
Porifera	27.2	16.9	11.7	52.9	30.8	53.2	4.0	26.9	6.9	59.9	16.4	53.2
Cnidaria	0.1	-	0.5	1.0	-	1.0	-	-	1.8	0.2	6.5	0.6
Polychaeta	5.6	10.6	0.2	0.2	3.0	3.0	1.4	11.1	0.3	0.4	15.7	8.3
Mollusca	0.3	1.0	-	-	-	-	-	-	-	-	-	-
Crustacea	-	-	-	-	-	-	-	-	-	0.2	-	-
Bryozoa	19.3	12.8	29.9	22.7	16.9	18.0	10.2	1.9	25.9	6.1	17.2	13.2
Ascidiacea	0.1	-	0.1	-	-	-	-	-	0.2	-	-	-
NLS	18.8	58.5	1.0	1.1	4.0	14.7	20.1	58.3	0.7	18.5	19.5	23.1

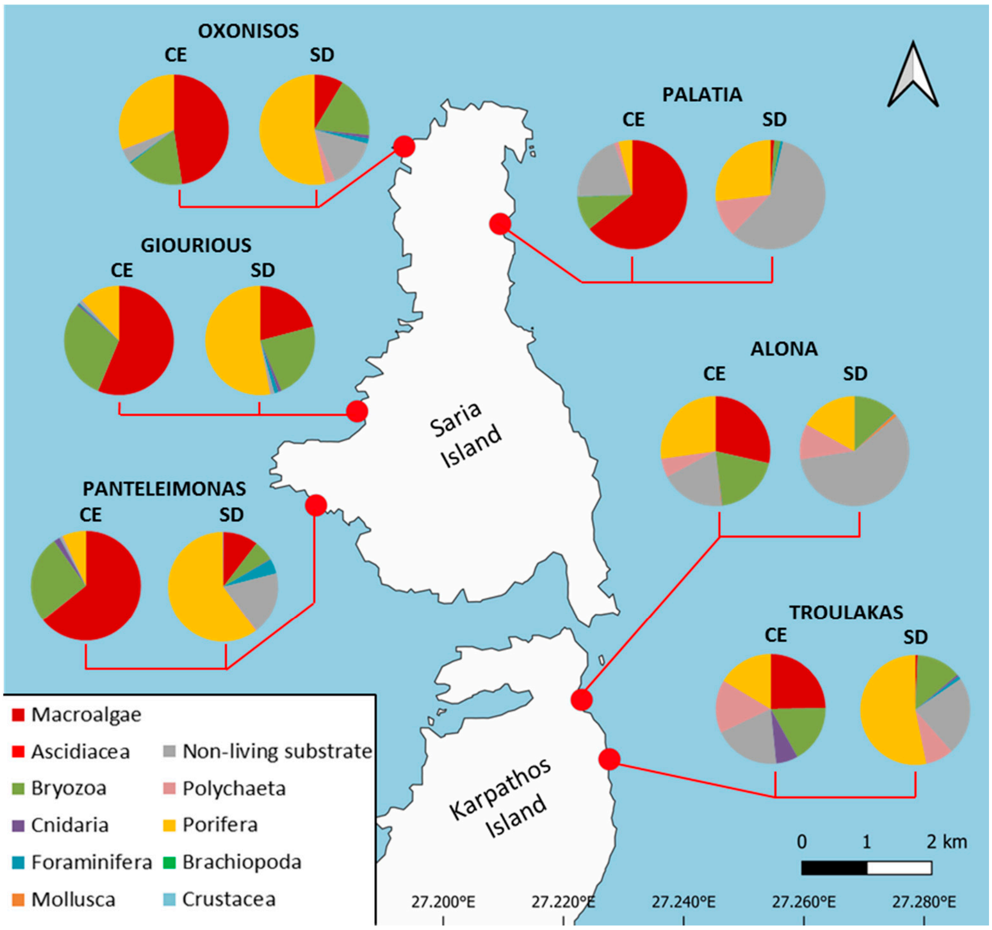

Figure 2. Location of the studied caves and percent of coverage of identified sessile taxa and non-living substrate is presented for each ecological cave zone (CE: cave entrance, SD: semi-dark zone).

The total number of sessile taxa varied among each ecological zone, from a minimum of 27 at the entrance zone of Oxonisos cave to a maximum of 40 at the entrance of Panteleimonas cave and from 17 to 44 at the semi-dark zone of Alona and Troulakas caves, respectively (Table 3 and Table S1). The total number of taxa increased from the cave entrance to the semi-dark zone for most caves except for Alona and Panteleimonas caves (Table 3). The same pattern was observed for Porifera, the group with the highest number of taxa in total.

Table 3. Summary data with the total number of taxa by sessile group for each ecological cave zone. ALO: Alona, GIOU: Giourious, OXO: Oxonisos, PAL: Palatia, PANT: Panteleimonas, TROU: Troulakas, CE: entrance zone, SD: semi-dark zone.

Taxa	ALO		GIOU		OXO		PAL		PANT		TROU	
	CE	SD	CE	SD	CE	SD	CE	SD	CE	SD	CE	SD
Macroalgae	6	-	5	3	4	5	5	1	6	2	7	1
Foraminifera	1	1	1	1	1	1	1	1	1	1	-	1
Porifera	10	6	15	16	14	22	15	22	14	9	17	23
Cnidaria	2	1	1	4	1	4	-	1	3	2	2	4
Polychaeta	1	1	1	1	1	1	1	1	1	1	1	1
Mollusca	2	1	1	1	-	-	-	-	1	-	-	-
Crustacea	-	-	-	1	-	-	-	-	-	1	-	-
Bryozoa	7	3	4	5	4	6	2	4	9	5	5	7
Brachiopoda	-	3	-	2	-	-	2	2	1	-	-	2
Ascidiacea	3	1	1	3	2	2	2	2	4	-	1	5
SUM	32	17	29	37	27	41	28	34	40	21	33	44

Among the identified sessile taxa, seven are protected according to the Bern and Barcelona Conventions and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Table S1). The circalittoral bivalve *Neopycnodonte cochlear* was reported from the entrance and semi-dark zone of the Alona cave with 0.3% and 1% coverage, respectively (Figure 3A, Table S1). Bioconstructions formed by the serpulid polychaete *Protula tubularia* (Figure 3B) as well as nodular formations of bryozoans were also recorded in the semi-dark zone of the Panteleimonas and Oxonisos caves, respectively.

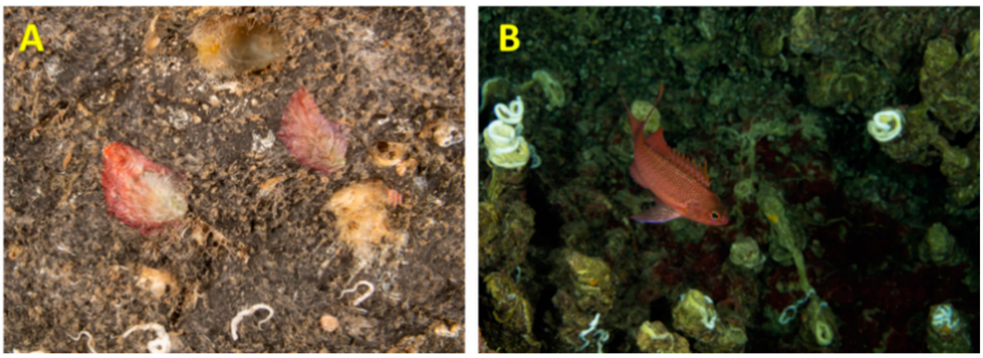

Figure 3. The bivalve *Neopycnodonte cochlear* (**A**), serpulid bioconstructions and a cardinal fish *Anthias anthias* individual (**B**) photographed in the semi-dark zone of Alona and Panteleimonas caves, respectively. Photos by T. Dailianis.

All studied marine caves were significantly differentiated. In addition, one-way ANOSIM analysis results indicated all examined geomorphological and topographic factors (cave type, entrance depth, entrance area, and entrance orientation) as having significant effects on the resemblance patterns of benthic community structure (p-value < 0.01 in all cases; Table S2), as supported by the nMDS analysis shown on Figure 4. This was also supported by the pairwise tests (*p*-value < 0.01 in all cases) (Tables S3–S5) verifying that the examined geomorphological and topographic factors significantly affect the benthic community patterns. This is particularly evident for the samples from different 'ecological zones' (Figure 4B), 'cave types' (Figure 4C), and 'entrance depth' (Figure 4E) which appear to be grouped in different clusters in the nMDS plots (i.e., cave entrance vs. semi-dark zone, semi-submerged vs. submerged caves and shallower vs. deeper caves, respectively). According to the results of SIMPER analysis, the average dissimilarity (based on the Bray-Curtis dissimilarity index) for different 'ecological zones' was 71.22% while for 'cave types' and 'entrance depth' was 68.70% and 69.82%, respectively. Among the studied caves, average dissimilarity ranged between 53.82% (Giourious vs. Oxonisos caves) and 76.50% (Alona vs. Panteleimonas caves).

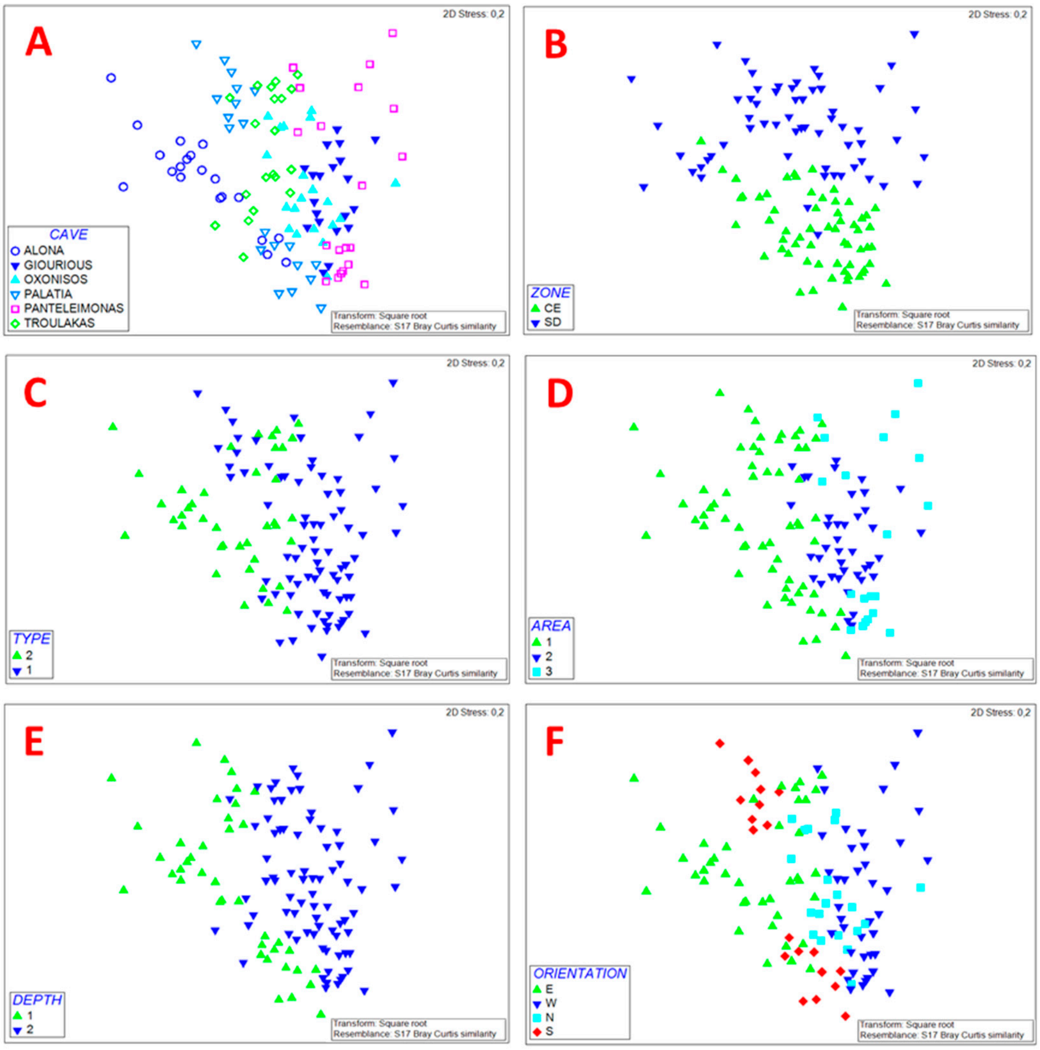

Figure 4. Non-metric multidimensional scaling (nMDS) plots showing the similarities among the analysed photoquadrat samples from all caves. Photoquadrats are coloured by different factors. (**A**) Cave; (**B**) Ecological Zone: entrance (CE) or semi-dark (SD); (**C**) Cave Type: semi-submerged (1) or submerged (2); (**D**) Entrance Area: 15–40 m^2 (1), 110–230 m^2 (2), or 630 m^2 (3); (**E**) Entrance Depth (max): 0–10 m (1) and 10–20 m (2); (**F**) Entrance Orientation: east (E), west (W), north (N), and south (S).

Regarding the factor 'entrance area', samples from the caves with wider entrance (group 2: 110–230 m^2 and 3: 630 m^2) seem to be grouped together and differentiated from those with narrower entrance (group 1: 15–40 m^2) in the nMDS plot (Figure 4D). SIMPER analysis showed lower dissimilarity between groups 2 and 3 (61.88%) than between 1 and 2 or 1 and 3 (66.43% and 73.18%, respectively).

According to SIMPER analysis for the factor 'ecological zone', the average similarity of equivalent 'ecological zones' from different caves is higher (46.01% for CE and 37.16% for SD) than the average similarity between the different zones (28.78%) verifying that equivalent ecological zones from different caves show higher similarity levels. The taxa which contributed the most to the average similarity between photoquadrats were *Peyssonnelia* sp., Bryozoan turf, and Encrusting Rhodophyta for the entrance zone (57%), and *Dendroxea lenis*, Serpulidae, Bryozoan turf and Encrusting Bryozoa for the semi-dark zone (53%) (Table S6). Different taxa showed different percent contribution to the average similarity for every studied factor (Tables S7–S11).

3.2. Threats and Pressures on the Sessile Community

Partial necrosis was observed for different sessile taxa. Rhodophyte necrosis was recorded at the entrance of Oxonisos and Troulakas caves (0.8% and 0.5%, respectively) and both entrance and semi-dark zones of Giourious (0.9% CE, 2.1% SD) and Panteleimonas caves (2.9% CE, 0.1% SD). Necrosis of the sponges *Agelas oroides* and *Spirastrella cunctatrix* were recorded in the entrance and semi-dark zone of the cave Oxonisos, with 0.2% coverage each. Partial necrosis of the sponge *Agelas oroides* and *Ircinia oros* were also recorded at the entrance of Panteleimonas, Giourious (Figure 5A), and Oxonisos caves (Figure 5B). Broken fragments of the coral *Leptopsammia pruvoti* and erect bryozoans (*Myriapora truncata* and *Reteporella* sp.) were also observed on the floor of the semi-dark zone of Troulakas cave (Figure 5C).

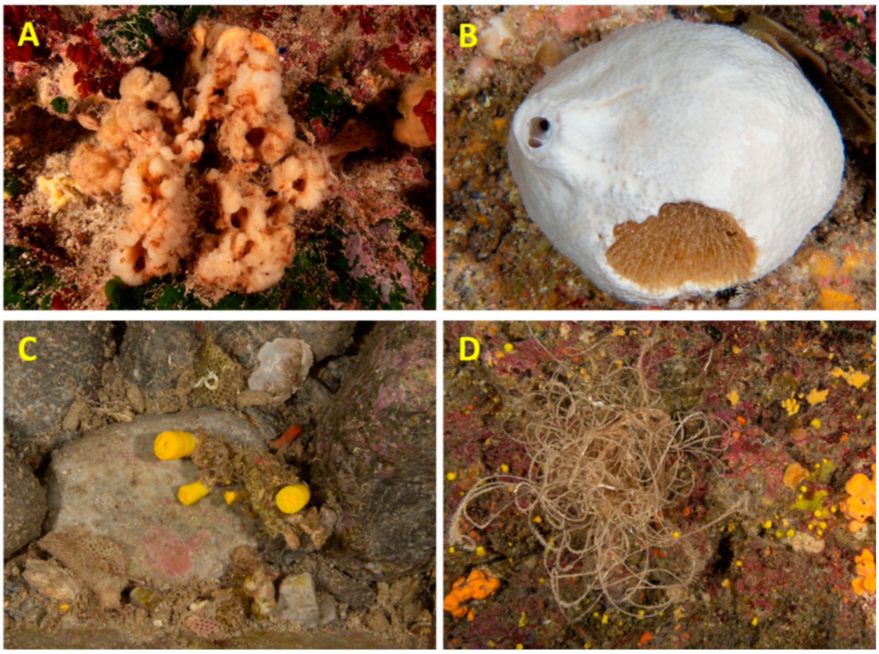

Figure 5. Partial necrosis of the sponges *Agelas oroides* (**A**) and *Ircinia oros* (**B**) from the entrance zone of Panteleimonas and Oxonisos caves, respectively; fragments of the coral *Leptopsammia pruvoti* and the erect bryozoans *Myriapora truncata* and *Reteporella* sp. (**C**); fishing line (**D**) attached to the walls at the semi-dark zone of Troulakas cave. Photos by T. Dailianis.

Another pressure observed in most of the studied caves (Alona, Oxonisos, Giourious, and Troulakas) was litter, mainly consisting of plastic waste such as fishing lines (Figure 5D and authors' personal observations). Higher concentrations were observed in Oxonisos cave, a semi-submerged cave, exposed to north winds and intense wave action.

3.3. Motile Fauna

In total, 45 motile taxa classified as Pisces (24), Crustacea (10), Echinodermata (6), Polychaeta (2), Mollusca (2), and Mammalia (1) were identified as species (41), genus (2), and family (2) ranks (Table S12). Among the recorded motile species, five are protected (*Palinurus elephas*, *Scyllarides latus*, *Epinephelus marginatus*, *Paracentrotus lividus*, and *Monachus monachus*) under the Bern and Barcelona Conventions (Annex II: List of endangered or threatened species and Annex III: List of species whose exploitation is regulated). Schools of the circalittoral fish *Anthias anthias* were visually recorded at the entrance and semi-dark zone of Oxonisos and Panteleimonas caves (Figure 3B).

In addition, 10 NIS were identified (Table S12). Non-indigenous species were reported at all studied caves varying from one for Giourious cave to seven for Troulakas cave (Table S12). Most of the NIS were detected only at the entrance zone of the caves (*Parupeneus forsskali*, *Siganus luridus*, *S. rivulatus*, *Torquigener flavimaculosus*, and *Diadema setosum*) (Figure 6A,B) while a few others were exclusively found at the semi-dark parts (*Urocaridella pulchella* and *Cerithium scabridum*) or at both zones (*Sargocentron rubrum*, *Pempheris rhomboidea*, and *Pterois miles*) (Figure 6C,D).

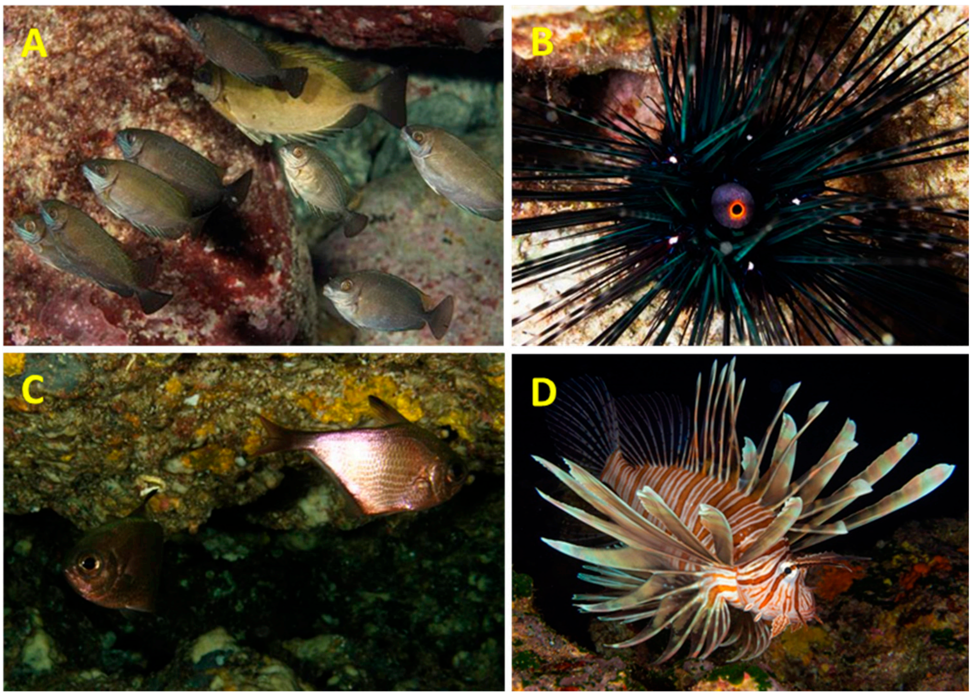

Figure 6. The NIS fish *Siganus luridus* (**A**) and the echinoderm *Diadema setosum* (**B**) from the entrance zone of Troulakas and Palatia caves, respectively. The non-indigenous fish species *Pempheris rhomboidea* (**C**) and *Pterois miles* (**D**) from the semi-dark zone of Panteleimonas and Oxonisos caves, respectively. Photos by T. Dailianis.

3.4. Ecological Quality Assessment

The ecological quality of the studied marine caves was assessed as poor or moderate, with values of CavEBQI ranging from 2.7 (poor) for Palatia cave to 5.2 (moderate) for Alona cave (Table 4). The highest values were calculated for the two fully submerged caves (i.e., Alona and Toulakas), which had a moderate quality status. The Confidence Index (CI_{EBQI}) was high in all cases (Table 4), since the overall assessment was based on recent data, following the recommended methodology [22]. Most marine caves showed extremely low percent cover of 'Passive filter feeders' (i.e., scleractinian corals), ranging between 0.5 and 3.7% (category 0–25%), while they were totally absent from Palatia cave. The group 'Large active filter feeders' (i.e., massive/erect sponges, large bryozoans, mollusks, and ascidians) had mean coverage between 0.9 and 10.2% (category 0–25%) in each cave. The group 'Small active filter feeders' (i.e., encrusting sponges, serpulids, and brachiopods) had mean cover between 28.3 and 55.7% (categories 25–50% and 50–75%, respectively). Volumetric stratification was low at the caves Alona, Giourious, and Palatia (centimetric-sized organisms) and moderate for Troulakas, Panteleimonas, and Oxonisos (decimetric-sized organisms) due to the presence of the massive sponge *Agelas oroides*, a few hydrozoans and bioconstructions formed by serpulids and bryozoans. As far as motile taxa are concerned, 'Cave-dwelling mysids' were observed in low numbers (a few individuals) only at the semi-dark interior of Alona and Troulakas caves (Figure S1). The highest numbers of 'Characteristic carnivores' were found in Alona cave (6 species) and 'Associated carnivores' in Panteleimonas cave (10 species), while the highest number of 'Detritus feeders and omnivores' were found at Troulakas cave (4 species) (Table S12).

Table 4. Results of ecological quality index CavEBQI and Confidence Index CI_{EBQI} for the six studied caves.

Cave	CavEBQI	Ecological Quality	CI_{EBQI}	Confidence Index
Alona	5.2	Moderate	10	High
Giourious	3.7	Poor	10	High
Oxonisos	3.8	Poor	10	High
Palatia	2.7	Poor	10	High
Panteleimonas	3.5	Poor	10	High
Troulakas	4.5	Moderate	10	High

4. Discussion

Although the number of studies focusing on marine caves of the Eastern Mediterranean Sea has increased over the last years, few studies quantitatively assess their benthic communities [10,32,33,44]. Herein, a quantitative description of sessile benthic communities and a catalogue of motile taxa (including non-indigenous species) recorded in six marine caves in the North Karpathos and Saria Islands MPA (Greece, Eastern Mediterranean Sea) is provided along with the first ecological quality assessment for this habitat in the Eastern Mediterranean Sea. The correlation of six different geomorphological and topographic cave factors (i.e., cave, ecological zone, cave type, entrance depth, entrance area, and entrance orientation) with the sessile community structure was also investigated. All studied marine caves were significantly differentiated verifying the individuality hypothesis of the current study (hypothesis i). Cave-specific (micro)topography with associated environmental gradients, modifications in larval or trophic supply as well as stochastic biological patchiness (e.g., several cave-exclusive and rare taxa recorded only from a few or a single marine cave) may lead to cave individuality [2,4,9,45,46].

Factors, such as 'cave type', 'entrance depth', 'entrance area', and 'entrance orientation', were found to be significantly associated with the benthic community patterns, verifying the hypothesis that the examined geomorphological and topographic factors significantly affect the cave community structure (hypothesis ii). Geomorphological features represent a proxy for other environmental features in caves, such as light availability or water chemistry [47]. For instance, the hydrodynamic regime and light exposure increase in semi-submerged caves, caves with lower entrance depth and/or wider entrance [2]. Orientation with respect to the cardinal points (i.e., aspect) and presence of multiple entrances can also affect the cave community patterns creating a variation on the level of light penetration and inner cave parts' isolation [2,3].

Marine caves showed higher resemblance when compared within equivalent 'ecological zones', mainly due to the dominance of rhodophytes and sponges in the entrance zone and semi-dark zone respectively [2], verifying that equivalent ecological zones from different caves show higher similarity levels (hypothesis iii). Taxa distribution patterns are in agreement with previous studies on marine caves of the Eastern Mediterranean Sea [10,33,48].

Although photographic methods provide advantages, such as the ability to collect high numbers of informative samples to characterize sessile assemblages within the limited time of diving-operated surveys, some limitations also occur [49,50]. For this reason, taxa whose identification is uncertain through external morphology and is only feasible through detailed morphological and/or molecular analysis (e.g., bryozoans, and rhodophytes) were grouped in morpho-functional categories (e.g., Bryozoan turf, Encrusting Rhodophyta). As a result, cave species richness is potentially underestimated at both ecological cave zones. Future sample analysis and monitoring, as well as quantitative visual census of motile species could complement and expand the biodiversity lists of the studied caves.

Most of the sessile species identified are commonly found in the interior of marine caves and other marine habitats of Greece while 10 species were reported for the first time as part of the marine cave fauna of the Aegean Sea [2,27]. These were the demosponge *Haliclona (Reniera) aquaeductus*, the gastropod *Cerithium scabridum*, the bryozoans *Caberea boryi*, *Reptadeonella violacea* and *Patinella radiata*, the echinoderm *Diadema setosum*, the ascidian *Pycnoclavella nana* and the fishes *Atherina* sp., *Parupeneus forsskali*, and *Torquigener flavimaculosus*, enlarging the existing list of taxa [27]. The protected calcarean sponge *Petrobiona massiliana* was recorded for the second time in Aegean marine caves [20].

Different sponges of the class Homoscleromorpha, categorised as Plakinidae and *Plakina* sp., were reported from the semi-dark zone of three caves (Table S1). Although four new species of the genus *Plakina* have recently been described from marine caves of Greece, they are still poorly known due to their small size and cryptic habit [51,52]. Therefore, targeted sample analysis and future studies on marine caves of the Aegean Sea may expand the known biodiversity of plakinid sponge species. Although brachiopods exhibit a particular preference for cryptic habitats they have rarely been studied in marine caves of the Eastern Mediterranean. The brachiopod species found in this study are among the most abundant in marine caves of the North Aegean Sea [53]. Two circalittoral or deep-water species were recorded in the studied caves, confirming the affinity of marine cave fauna with that of deeper waters [2]. The circalittoral bivalve *Neopycnodonte cochlear*, which was observed in one studied cave (Table S1, Figure 3A), has been reported to form thick encrustations on rocky walls in marine caves of Italy and Croatia [54,55]. The cardinal fish *Anthias anthias*, which formed schools in two marine caves (Table S12, Figure 3B), is a nocturnal fish, usually observed at depths exceeding 30 m [56].

Despite the fact that visual surveys for motile fauna did not follow a quantitative assessment protocol and they tend to underestimate small-sized and highly cryptic fauna [57], two cryptobenthic fish species were recorded in the study area (*Microlipophrys nigriceps* and *Tripterygion melanurum*) (Table S12). Further research using standardised protocols for the assessment of motile assemblages, including cryptobenthic taxa, is expected to increase the motile diversity of Aegean marine caves [57].

Seven out of 10 Decapoda species (*Dromia personata*, *Lysmata seticaudata*, *Palaemon serratus*, *Palinurus elephas*, *Plesionika narval*, *Scyllarides latus*, and *Stenopus spinosus*) identified from the studied caves are considered to be among the most common decapods in Mediterranean Sea caves [58]. The abundance of *Plesionika narval* in three marine caves (Alona, Giourious and Palatia) (Table S12 and authors' personal observations) indicates that the marine cave ecosystem can act as refuge for this species, which is highly fished in parts of the Aegean Sea. The endangered Mediterranean monk seal *Monachus monachus*, the population of which is well known and monitored in the area over the last years [59] was among the 12 protected species observed in the studied caves. Other interesting features of scientific interest and conservation concern are the small-sized serpulid bioconstructions observed in Panteleimonas cave (Figure 3B), which resemble those discovered in dark caves of other Greek islands and are relatively smaller compared to those from Apulia, Sicily and Cyprus [60–63].

Several threats were recorded at all studied caves. A total of 10 NIS were observed. All recorded NIS have Indo-Pacific origin, having reached the Eastern Mediterranean basin through the Suez Canal [64]. Although in the relevant literature there are no data that indicate any direct impacts of NIS on the diversity of marine caves, at least three of the observed NIS (i.e., *Pterois miles*, *Siganus luridus* and *S. rivulatus*) are considered as invasive with high impact on the native biodiversity of the Aegean Sea and the Eastern Mediterranean, while the remaining NIS have low or unknown impact [28,65]. Only two NIS were reported exclusively in the semi-dark cave zone (Table S3), suggesting that this habitat type could be unfavourable, at least to a certain point, for impacts related to opportunistic NIS [28]. However, the high abundance of the sweeper *Pempheris rhomboidea* at two caves (Oxonisos and Panteleimonas) (Table S12 and authors' personal observations) could probably have a high negative impact due to its predating behaviour [28], but further future investigation is needed. The cleaner shrimp *Urocaridella pulchella* was recently reported for the first time in Greek waters from several marine caves with the earliest confirmed record in 2018 in Crete [30]. The current study fills a distributional gap for this non-indigenous palaemonid, representing the first sighting from Karpathos Island. The presence of NIS at all studied caves indicates their possible establishment.

Partial necrosis was observed for different sessile taxa such as rhodophytes and sponges (*Agelas oroides* and *Spirastrella cunctatrix*). Such necrosis may be related with seasonal environmental fluctuations [66], or broader mortality events due to temperature rise in the Mediterranean Sea as it has been shown in previous studies [67–69]. Marine litter was also among the pressures observed in most of the studied caves. Until today, very few studies have focused on pollution in Mediterranean marine caves indicating our gap of knowledge on some threats that caves are continuously facing [2,70].

The assessment of ecological quality revealed poor ecological quality for most caves (all semi-submerged). Shallow semi-submerged caves are exposed to a higher hydrodynamic regime caused by wave action and are vulnerable to sea surface temperature rise, anthropogenic pressures (e.g., pollution) and higher numbers of NIS [2,13,23,24,28] which can affect their community structure and ecological quality. It should be noted that the ecological quality index (CavEBQI) applied in this study was developed for marine caves of the Western Mediterranean basin [22]. Therefore, it remains still to be explored if the abovementioned results are linked to the biogeographic heterogeneity of the Mediterranean Sea, indicating rather the oligotrophic conditions of the eastern basin than a possible decline in habitat quality [13,71]. For instance, a striking example of how this assessment can be affected is the notable absence of decimetric-sized passive filter feeders (e.g., gorgonians) from shallow marine caves in the Eastern Mediterranean Sea [2,27] which cause a reduction in volumetric stratification and thus underestimation of the ecological quality. In addition, the impact of NIS on the ecological quality of the marine cave ecosystem should be also considered and included in the assessment process [72]. Given the scarcity of risk assessments for marine cave ecosystems globally [73] and the general lack of information on the relationships between cave species [74], further trials and cross-calibration exercises are already under way in order to establish monitoring schemes in the Eastern Mediterranean Sea.

In conclusion, this quantitative and qualitative study revealed the rich biodiversity of six marine caves of Karpathos and Saria Islands MPA. The results of the study highlighted the spatial heterogeneity of hard substrate community composition among caves with different geomorphology and topography. This heterogeneity should be considered in future conservation and management actions [13,71]. In addition, monitoring and further research is needed to deepen scientific knowledge on eastern Mediterranean marine cave ecosystems.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/jmse10050660/s1: Table S1. Summary table with the average percentage of coverage (%) of all sessile taxa and morpho-functional groups recorded at the ecological zones of the six studied caves. Table S2. Results of one-way ANOSIM for six geomorphological and topographic factors of the studied marine caves. Table S3. *p*-values of one-way ANOSIM pairwise tests for the factor 'Cave'. Table S4. *p*-values of one-way ANOSIM pairwise tests for the factor 'Entrance Area'. Table S5. *p*-values of one-way ANOSIM pairwise tests for the factor 'Entrance Orientation'. Table S6. Similarity percentage analysis (SIMPER), showing the contribution of sessile taxa to the average similarity (%) in each ecological zone of the studied caves. Table S7. Similarity percentage analysis (SIMPER), showing the contribution of sessile taxa to the average similarity (%) in the six studied caves. Table S8. Similarity percentage analysis (SIMPER), showing the contribution of sessile taxa to the average similarity (%) in each cave type. Table S9. Similarity percentage analysis (SIMPER), showing the contribution of sessile taxa to the average similarity (%) in each cave entrance area range. Table S10. Similarity percentage analysis (SIMPER), showing the contribution of sessile taxa to the average similarity (%) in each entrance depth range. Table S11. Similarity percentage analysis (SIMPER), showing the contribution of sessile taxa to the average similarity (%) in caves with different entrance orientation. Table S12. Summary table of the presence of motile species recorded in the caves through visual census. Figure S1. Spider-web graphics representing the ecosystem-based ecological quality evaluation of each studied marine cave.

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