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RESEARCH ARTICLE

Photogrammetric survey of macro-invertebrates inside the marine caves in Karaburun-Ildır SEPA (Aegean Sea, Türkiye)

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Abstract

Benthic macro-invertebrates in three marine caves (MCs) located in the Special Environmental Protected Area (SEPA) of Karaburun-Ildır Bay (Aegean coast of Türkiye) were surveyed via Structure-from-Motion photogrammetry (SfM-p). This approach enabled the digital modelisation of 171.92 m^2 of marine habitats. Faunal cover was 13.07-38.48%, while epifaunal surface ranged between 3.37 and 14.96 m^2, depending on the sections of MCs. The quantitative assessment revealed the dominance of the phyla Porifera (28.72-99.81%), Cnidaria (≤71.04%, mostly scleractinians) and Mollusca (≤18.67%). The most abundant species were *Phorbas tenacior*, *Spirastrella cunctatrix*, *Hoplangia durotrix* and *Madracis pharensis*, while other species were cave-specific (e.g., *Lithophaga lithophaga*, *Pseudosuberites* sp. and *Halisarca dujardinii* in Ayı Balığı cave and *Mycale (Mycale) lingua*, *Agelas oroides* and *Axinella polypoides* in Eşendere cave). SfM-p was not suitable for MCs with sandy bottoms, such as Yatak Odası cave. Statistical analyses underlined the significant effects of MCs' geomorphology and level of submersion on most of ecological indices, with the highest indices observed for blind-ended and entirely submerged MCs. Height and depth of MCs' entrance were the most important factors affecting communities of macro-invertebrates. MCs within the SEPA of Karaburun-Ildır Bay had larger sponges/corals surfaces when compared to other MCs in the Northern Aegean and Marmara Seas, along the Turkish coastline.

Keywords: Karaburun-Ildır SEPA, Eastern Mediterranean Sea, underwater marine caves, Structure from Motion photogrammetry, benthic cover.

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Introduction

Marine caves (MCs) are entirely or partially submerged semi-enclosed subterranean systems below the sea surface with diverse shapes and significant volumes (Gerovasileiou and Bianchi 2021). These underwater cavernous habitats are wide enough to allow the exploration by one adult SCUBA diver (Gunn 2004; Romero 2009), although other numerical criteria can be employed to differentiate MCs from other cave-like underwater structures (Bianchi *et al.* 1996). Due to their relative seclusion from open-water environments, MCs are viewed as aphotic, oligotrophic enclaves most often devoid of halocline and with variable hydrodynamic regimes depending on their configurations (Keith *et al.* 2022). Even though their isolation is not systematic, MCs are considered as extreme habitats known to harbour assemblages from dark environments, which are distributed along different zones within the cave (entrance, semi-dark and dark areas) (Pérès and Picard 1964; Pérès 1967). Famous for being non-resilient refuges, reservoirs and hotspots for biodiversity (Riedl 1966; Gerovasileiou and Voultsiadou 2012; Derrien *et al.* 2024; Iluz *et al.* 2025), MCs enable the preservation of species such as the red coral *Corallium rubrum* and the Mediterranean monk seal *Monachus monachus*, which are included in the IUCN Red List of Threatened Species (Garrabou *et al.* 2015; Dede and Tonay 2019; Ouerghi *et al.* 2019; IUCN 2024).

The protection of MCs goes hand in hand with the creation of a robust baseline datasets on assemblages from dark environments through monitoring programs and diversity surveys. However, MCs are notoriously difficult to access—even for experienced divers. Despite these limitations, several methods can still be used inside MCs to study marine biodiversity, such as approaches based on transects, photoquadrats and video surveys (Benedetti-Cecchi *et al.* 1996; Bianchi *et al.* 2004; Cardone *et al.* 2022; Spaccavento *et al.* 2022). Technological innovations in miniaturisation also allowed the usage of hand-held echosounders, remotely operated/autonomous vehicles and photogrammetry (Gerovasileiou *et al.* 2013; Chemisky *et al.* 2015; Vallicrosa *et al.* 2020; Pulido Mantas *et al.* 2023).

Structure from Motion photogrammetry (SfM-p) or multi-image photogrammetry is an optical-based innovative approach in the field of marine imaging research (Price *et al.* 2019; Bayley and Mogg 2020; Prado *et al.* 2020). It can be described as the production of high-resolution three-dimensional (3D) models of the epibiotic cover on the seafloor, based on overlapping real-scaled two-dimensional (2D) images taken at different angles or following a boustrophedon pattern. Between each overlapping images, points sharing similarities are determined in the 3D space. A dense point cloud is produced at the end of this process, encompassing all similarities or common features between pictures (Snavely *et al.* 2008; Westoby *et al.* 2012; D'Urban Jackson *et al.* 2020). Recurrent concepts in SfM-p such as automation and auto-calibration of geometric features perception were introduced thanks to digital progress since the 1960s, through computational vision, feature-matching algorithms, geographical information systems (GIS) and digital terrains models (Lochhead and Hedley 2020; Russo *et al.* 2023).

Although it was initially developed and applied on land, SfM-p has since then become an important tool for creating 3D models in underwater settings for bathymetric surveys (Abadie *et al.* 2018), marine archaeology (Skarlatos *et al.* 2012; McCarthy and Benjamin 2014; Beltrame and Costa 2017), ecological monitoring (Fukunaga *et al.* 2019), morphometric analysis (Gutierrez-Heredia *et al.* 2016; Napolitano *et al.* 2019; Irschick *et al.* 2022), benthic mapping (Burns *et al.* 2015; Leon *et al.* 2015; Pizarro *et al.* 2017; Bayley *et al.* 2019) and chronological trends assessments (Bennecke *et al.* 2016; Piazza *et al.* 2018). The method also is already used in a wide variety of underwater environments such as tropical coral reefs, temperate-polar-deep waters and oyster reefs (Bridge *et al.* 2014; Ferrari *et al.* 2016; Bryson *et al.* 2017; Kim *et al.* 2018; Fukunaga *et al.* 2019; Piazza *et al.* 2019; De Oliveira *et al.* 2021; Menna *et al.* 2022; Spyksma *et al.* 2022).

SfM-p produces spatial information about seafloor depth, shape and texture, which in turn permits marine biologists to quantify habitat complexity, epibenthic biomass, benthic cover, growth rates, bioerosion and coral diseases contamination (Raoult *et al.* 2016; Palma *et al.* 2018; Ríos *et al.* 2020; Combs *et al.* 2021; Prado *et al.* 2021; Aston *et al.* 2022; Morais *et al.* 2022; Marlow *et al.* 2024). Hence this approach provides a comprehensive understanding about ecological dynamics through benthic maps (Roach *et al.* 2021; Morsy *et al.* 2023). Therefore, photogrammetric products can be critical to Marine Protected Areas (MPAs) conservation and management.

Nowadays, software tools such as VisualSFM, Agisoft Metashape and Pix4D are widely used with numerous benefits (Remondino *et al.* 2012). Photogrammetry is a versatile research tool. The approach can easily be coupled with other image acquisition methods such as underwater photography, towed camera, ROV (Remotely Operated Vehicle) and AUV (Automated Underwater Vehicle) (Bryson *et al.* 2013; Bonin-Font *et al.* 2016; Burns and Delparte 2017; Mizuno *et al*. 2017; Robert *et al.* 2017; Ríos *et al.* 2020). Systems based on multiple cameras can increase the likelihood of obtaining accurate photogrammetric products, which can later be analysed through machine-learning algorithms, artificial intelligence (AI) assisted software tools for automatic species identification and benthic imagery automatic analysis (Mohamed *et al.* 2020; Pavoni *et al.* 2021).

Photogrammetry appears to be an optimal methodological match for studies in MCs. But despite these benefits, only a few studies employed photogrammetric approaches (Díez *et al.* 2022; Quiles-Pons *et al.* 2022; Pulido Mantas 2022, 2023; Pulido Mantas *et al.* 2023) among the 488 articles available in the scientific literature about Mediterranean MCs (based on open sources made available online). Furthermore, to the best of our knowledge, no quantitative photogrammetric surveys have been performed yet on the benthic biodiversity of MCs in the Eastern Mediterranean Sea, at least along the Turkish coastline. To date, a total of 169 MCs has been reported in the Sea of Marmara, Aegean and

Levantine coasts of Türkiye. While some of these caves were studied (Yokes and Galil 2006; Rastorgueff *et al.* 2015; Chevaldonné *et al.* 2015; Filiz and Sevingel 2015; Bilecenoğlu 2019; Çelikok 2019; Çınar *et al.* 2019; Özalp 2019; Öztürk *et al.* 2019; Topaloğlu 2019; Turan *et al.* 2019), many remain unknown about them without any thorough quantitative analysis on their benthic diversity.

In accordance with the guidelines provided by the European Union's (EU) Habitat Directive 92/83/EEC and the "Dark Habitats Action Plan" of the Barcelona Convention (Giakoumi *et al.* 2013; UNEP-MAP 2013; UNEP-MAP-RAC/SPA 2016 a,b; UNEP-SPA/RAC-MAP-OCEANA 2017), the aim of the present study is to quantitatively assess via SfM-p the abundance and spatial distribution of benthic macroinvertebrates in MCs of the Karaburun-Ildır Bay's SEPA (KISEPA, Aegean Sea, Türkiye) and to study the effect of basic environmental factors on the community composition.

Materials and Methods

Region of study and stations

The KISEPA was designated as a SEPA by the Turkish State (decision n°823) via the Turkish Ministry of Environment, Urbanization, Climate Change on the March 15th, 2019 (Türkiye Republic Official Gazette n°30715). Three MCs were sampled in the KISEPA: Eşendere cave (Ec), Ayı Balığı cave (ABc) and Yatak Odası cave (YOc), as depicted in Figures 1-2 and Table 1. ABc is located near Mordoğan and is famous as one of the main breeding caves for *M. monachus* (Kıraç and Veryeri 2009; Sariçam and Erdem 2010). Both Ec and YOc are well-known as touristic spots for local diving clubs, each located respectively near Eşendere and Çeşme.

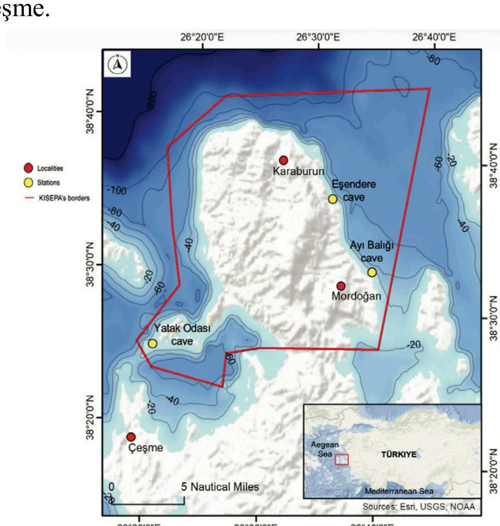

Figure 1. Location of underwater marine caves within Karaburun Ildır Bay Special Environmental Protected Area

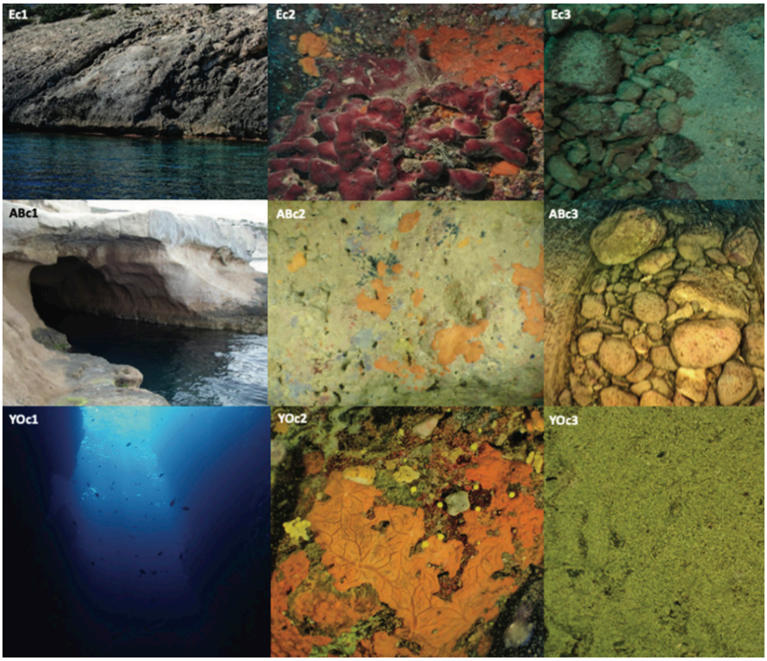

Figure 2. Characteristics of Eşendere cave (Ec), Ayı Balığı cave (ABc) and Yatak Odası cave (YOc) with the number 1 for the cave's entrance, 2 for cave's wall and 3 for cave's floor

Table 1. Descriptive summary of marine caves' geomorphologies in Karaburun Ildır Bay Special Environmental Protected Area

Characteristics of marine caves	Eşendere	Ayı Balığı	Yatak Odası
Proximity to seagrasses meadows	Yes	Yes	No
Presence of monk seals	No	Yes	No
Depth of the main entrance (m)	7.90	3.70	10.00
Height of the main entrance (m)	3.20	8.40	4.30
Width of the main entrance (m)	9.60	5.20	3.90
Number of entrances	3	>2	1+1
Length (m)	13.50	14.70	11.80
Submersion state in the seawater	Partial	Partial	Complete
Geomorphology	Blind-ended	Tunnel	Blind-ended
Bedrock	Rocky	Sedimentary	Rocky
Presence of sandy bottoms	Yes	No	Yes
Averaged internal depth (m)	5.76	2.26	8.52

Sampling strategies

The camera settings used in the present study were configurate to obtain continuous shooting at 20 fps. Although a perpendicular angle between the camera and the substratum is preferable for sharp images, the camera's angle was adjusted up to a maximum of 35° for vertical surfaces through smooth movements (prevention of fast camera wobbles). Pictures with blue water background were removed before digital processing. Pictures taken were used as samples to construct the digital models. In addition, photoquadrats (25x25 cm) were also taken along a 2 m wide transect with roughly the same length as surveyed MCs. Photogrammetric reconstruction was not feasible due to the presence of sandy substrate on the floor of YOc. Instead, 40 photoquadrats (25x25 cm) were used to analyse biotic cover. When possible, the left wall (LW), the right wall (RW) and the floor (F) of each MC was digitally reconstructed. Prior to the SfM-p survey, an assessment of diversity inside MCs made qualitatively through underwater photography and biological samples resulted in finding of 59 taxa inside KISEPA's MCs (Barraud and Öztürk 2025).

Digital workflow

Collected underwater images were processed digitally to reconstruct the scene of KISEPA's MCs benthic communities. The final and scaled products were then annotated, categorized into benthic groups. The workflow was performed with different software tools such as Workspace (v2.4.0) from OM Digital Solutions for managing pictures in RAW format, Metashape Professional (v1.8.5) from Agisoft for SfM-p (Torres-Pulliza *et al.* 2023), GIMP (v2.10.30) for cropping, eCognition Developper (v9) from Trimble for Object-Based Image Analysis (OBIA, Bracchi *et al.* 2022), QGIS (v3.42.3-Münster) for extraction of benthic coverages and finally RStudio (v2025.05.0+496) from Posit Software (PBC) for statistical analyses of communities composition and their ecological indices.

Biocoenoses inside marine caves

When possible, biocoenoses inside MCs were pinpointed by using SfM-p models according to the definition of Pérès and Picard (1964) and additional notes from Gerovasileiou and Bianchi (2021). The coralligenous zone was defined as an area dominated by the phylum Rhodophyta with low faunal cover. The semi-dark zone was characterized by the dominance of sponges/corals over algae ("virtual absence" of rhodophytes) and the presence of specific facies such as those of the species *Agelas oroides*, *Petrosia (Petrosia) ficiformis*, *Spirastrella cunctatrix*, *Chondrosia reniformis*, *Phorbas tenacior*, *Leptopsammia pruvoti*, *Madracis pharensis*, *Hoplangia durotrix* and *Caryophyllia inornata*. The dark zone was delimited by the dominance of sponges/annelids and the disappearance of previously mentioned fascies, except for *C. reniformis* and *P. ficiformis*.

Statistical analyses with RStudio

Once all the data was obtained in CSV format, biotic cover of benthic macroinvertebrates from KISEPA's MCs was statistically analysed using

RStudio software. Packages such as vegan, ggplot2, cluster, factoextra, indicspecies, devtools and pairwiseadonis were used to perform the calculation of ecological indices (Shannon-Wiener, Simpson, Pielou), boxplots, non-parametric test of Kruskal-Wallis, ANOSIM (Analysis of Similarities) and a constrained ordination RDA (Redundancy Analysis).

Results

Abiotic and biotic coverages

Biotic and abiotic coverages are summarized in Table 2. Most of the surface in ABc remained uncolonized by benthos with bare rock covering up to 70.26% of the surveyed surface. Occurrence of shadows (up to 15.25%) resulted from the wall's microtopography. Biotic coverage for each wall did not exceed 15% of the surveyed area. Total faunal benthic cover of ABc reached 7.83 m^2. Not all species reported inside ABc were observed on SfM-p models, with only 15 and 11 taxa out of 25 taxa for the left wall and the right wall, respectively (Figures 3-4).

Unlike ABc, Ec was defined by a large biotic coverage (up to 70.15% per MC's surveyed section). The remaining surface was composed of bare rock (up to 21.24%), shadows (up to 8.79%), sediments (up to 26.78%) and overexposed regions (up to 3.07%). Overall faunal benthic coverage was the highest in Ec with 29.55 m^2 (up to 38.48% per MC's section). According to the prior faunistic inventory, only 18, 13 and 8 taxa out of 51 taxa were visible on the SfM-p models of the left wall, floor and right wall, respectively. The inward slope of the right wall was lower than 45° (angle of slope), so only a fraction of the wall was surveyable by SCUBA divers. As a result, a partial orthomosaic was obtained for the right wall (Figures 5-7).

Overall, 70.76% of the hard substratum inside YOc was covered by benthic species, while the remaining 29.24% consisted of darkness (25.63%), sediments (2.64%) and bare rock (0.96%). Benthic fauna made up 53.37% of the biotic cover. Sixteen taxa out of the 30 reported taxa in YOc were observed via photoquadrats (Figure 8).

Taxa coverages

Faunal benthic coverages were illustrated in Figures 3-8 with all data summarised in Table 2. Among the animal species recorded on ABc's left wall, the dominant phylum in term of biotic coverage was Porifera (78.77% or 2.73 m^2), followed by Mollusca (18.67% or 0.64 m^2), Cnidaria (1.23% or 0.04 m^2, mostly scleractinians), Annelida (0.75% or 0.03 m^2, mostly serpulids) and Echinodermata (0.58% or 0.02 m^2). When assessing phyla respectively on ABc's left wall, different assemblages of dominant species were found with *Phorbas tenacior* (55.73% or 1.52 m^2), *Spirastrella cunctatrix* (18.37% or 0.50 m^2), *Halisarca dujardinii* (9.73% or 0.26 m^2) within sponges, *Lithophaga lithophaga* (0.65 m^2) for molluscs, *Hoplangia durotrix* (0.04 m^2) for corals, *Filograna* sp.

(99.77% or 0.02 m^2), *Metavermilia multicristata* (0.23% or 0.0001 m^2) inside Annelida and *Arbacia lixula* (0.02 m^2) for Echinodermata. Regarding ABc's right wall, Porifera (89.94% or 3.93 m^2) was the most abundant phylum within Animalia in terms of biotic coverage, followed by Mollusca (9.61% or 0.42 m^2) and Echinodermata (0.46% or 0.02 m^2). When taking each phylum separately and considering the most abundant taxa, distinct assemblages of dominant species were identified: *P. tenacior* (54.47% or 2.14 m^2), *S. cunctatrix* (17.33% or 0.68 m^2), *Pseudosuberites* sp. (11.42% or 0.45 m^2) for sponges; *Lithophaga lithophaga* (0.42 m^2) for molluscs and *Arbacia lixula* (0.02 m^2) for Echinodermata (Figures 3-4).

When Ec's left wall was considered, Porifera was the most prevalent animal phylum (99.81% or 10.85 m^2), followed by other small taxa like Echinodermata, Tunicata, and Annelida (less than 0.02 m^2, mostly serpulids). For each phylum, the dominant species were *S. cunctatrix* (5.67 m^2), *P. tenacior* (2.11 m^2), *Mycale (Mycale) lingua* (1.17 m^2) for sponges, *Psammechinus microtuberculatus* and *Arbacia lixula* (both 0.01 m^2) for echinoderms, *Halocynthia papillosa* (0.003 m^2) for Tunicata, and finally *Hermodice carunculata* (0.001 m^2) for Annelida. The most common animal phylum on Ec's floor was Cnidaria (71.04% or 10.62 m^2, mostly scleractinians), followed by Porifera (28.72% or 4.29 m^2) and Echinodermata (0.20% or 0.04 m^2). The prominent species were *Hoplangia durotrix* for corals, *Spirastrella cunctatrix* (1.49 m^2), *Phorbas tenacior* (1.34 m^2), and *Chondrosia reniformis* (0.62 m^2) for sponges, and *Arbacia lixula* and *Psammechinus microtuberculatus* (both smaller than 0.04 m^2) for echinoderms. When just animals were considered for Ec's right wall, Porifera accounted for 73.97% (2.75 m^2) of the fauna, with Cnidaria (mostly scleractinians) coming in second at 26.03% (0.97 m^2). The sponges *Spirastrella cunctatrix* (1.59 m^2), *Agelas oroides* (0.39 m^2) and *Phorbas tenacior* (0.36 m^2) and the coral *Madracis pharensis* (0.97 m^2) were the most common species (Figures 5-7).

Porifera (57.09%) was the most prevalent animal phylum for YOc, followed by Cnidaria (35.31%, mostly scleractinians) and Annelida (7.26%, mostly serpulids). For sponges, the most common species were *Agelas oroides*, *Phorbas plumosus*, and *P. tenacior*, followed by the corals *Madracis pharensis*, *Caryophyllia inornata*, *Leptopsammia pruvoti* and the polychaetes *Serpula vermicularis*, *Metavermilia multicristata*, and *Filograna* sp. (Figure 8).

Biocoenoses inside ABc and Ec

Composition of biocoenoses were shown in Figures 3-6 with all data summarised in Table 2. All biocoenoses were present in ABc with the coralligenous covering 9.50 m^2, semi-dark cave community covering 7.54 m^2, while the dark cave community covered 1.07 m^2. Coralligenous zones were dominated by Rhodophyta. Sponges, corals and molluscs were prevalent in semi-dark zones with up to 65.14% of Porifera's cover, 95.71% of Cnidaria's cover and 53.16% of Mollusca's cover inside ABc. Dark zones were defined by the marginal presence of sponges/molluscs and the highest coverage of annelids (up to 45.37% of the total Annelida coverage in ABc, mostly serpulids). Sea-urchins tended to showcase different distribution between semi-dark and dark zones due to their motility (38.15% of echinoderms from ABc's left wall in the dark zone and 85.20% of echinoderms from ABc's right wall in the semi-dark zone) (Figures 3-4).

In contrast, only the coralligenous (44.70 m^2) and semi-dark (17.15 m^2) zones were available in Ec, while the dark area was composed of inaccessible cavities. Biocoenoses in Ec showed similar trends as in ABc under the dominance of sponges and Rhodophyta, but with small divergences. Up to 65.42% and 53.79% of sponges' and coral coverages within Ec were located inside the coralligenous zones. Moreover, the semi-dark zone of Ec was mainly covered by Cnidaria (mostly scleractinians), especially for Ec's floor. Due to the peculiar topography of the right wall, the MC's zonation could not be clearly defined based on the incomplete model. However, features setting the wall apart from the rest of the cave were observed with the presence of a coralligenous zone in the innermost part of Ec's right wall and the occurrence of a chamber with biostalactites in the middle of the right wall (Figures 5-7).

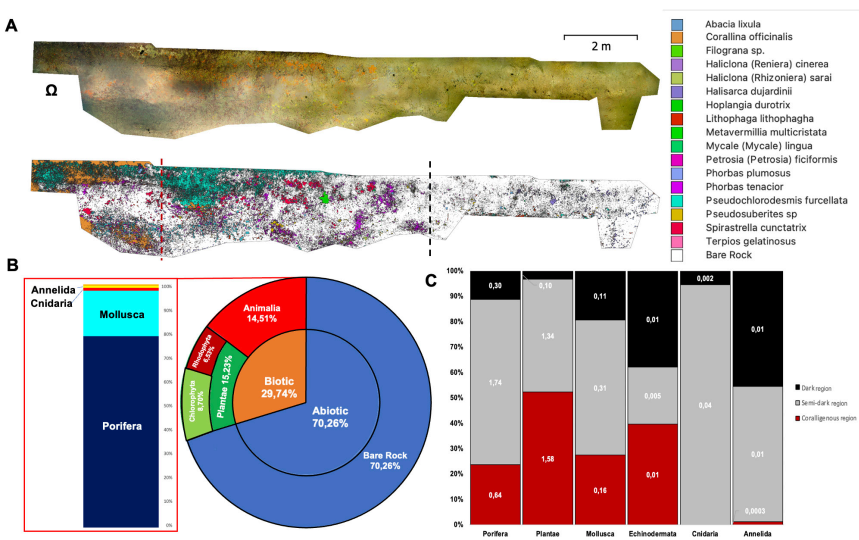

Figure 3. (A) Biotic coverage represented on SfM-p derived orthomosaic of Ayı Balığı cave's left wall (Ω for entrance and dashed lines for biocoenosis borders as defined by Pérès and Picard in 1964), (B) modified pie/ring charts depicting the coverage of benthic groups on ABc's left wall (with faunal phyla in the bar chart on the left side) and (C) stacked-bars chart displaying biotic cover of phyla within their own respective biocoenosis.

Table 2. Synthesis of SfM-p results gathered during the quantitative assessment of benthic macroinvertebrate communities inside the MCs in the KISEPA

Variables	Stations				
	Ayı Balığı cave		**Eşendere cave**		
	Left wall	**Right Wall**	**Left wall**	**Right Wall**	**Floor**
Capture distance (m)	0.34	0.33	1.03	0.89	1.01
Resolution (mm/pixel)	0.10	0.20	0.48	0.38	0.42
Area surveyed (m^2)	23.87	33.42	39.1	7.93	68.6
Faunal cover (%)	14.51	13.07	31.06	38.48	23.01
Faunal surface (m^2)	3.46	4.37	10.87	3.72	14.96
Number of species visible on the model	15	11	18	8	13
Porifera (%)	78.77	89.94	99.81	73.97	28.72
Mollusca (%)	18.67	9.61	0.00	0.00	0.00
Cnidaria (%)	1.23	0.00	0.00	26.03	71.04
Tunicata (%)	0.00	0.00	< 0.19	0.00	0.00
Annelida (%)	0.75	0.00	< 0.19	0.00	0.00
Echinodermata (%)	0.58	0.46	< 0.19	0.00	0.20
The most dominant species	*Phorbas tenacior*	*Phorbas tenacior*	*Spirastrella cunctatrix*	*Spirastrella cunctatrix*	*Hoplangia durotrix*
The second most dominant species	*Lithophaga lithophaga*	*Spirastrella cunctatrix*	*Phorbas tenacior*	*Madracis pharensis*	*Spirastrella cunctatrix*
The third most dominant species	*Spirastrella cunctatrix*	*Pseudosuberites* sp.	*Mycale (Mycale) lingua*	*Agelas oroides*	*Phorbas tenacior*
Coralligenous area surface (m^2)	2.38	7.12	10.37	Not accessible	34.33
Semi-dark area surface (m^2)	3.46	4.08	6.11	Not accessible	11.04
Dark area surface if accessible (m^2)	0.53	0.54	Not accessible	Not accessible	Not accessible

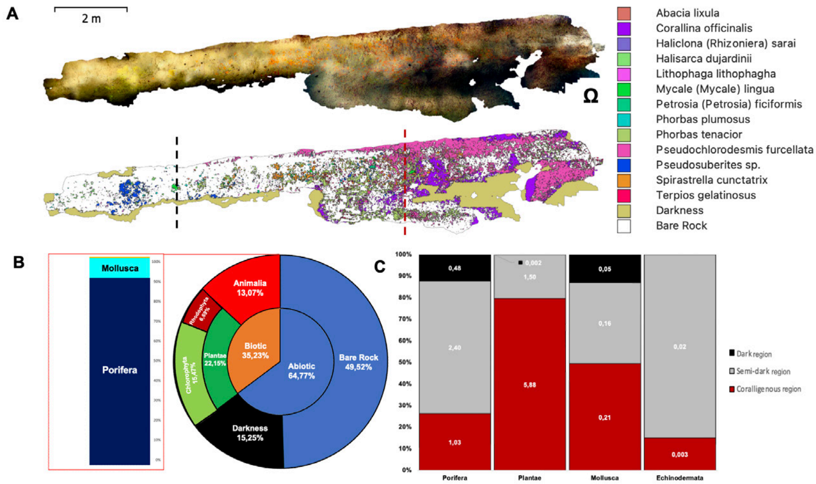

Figure 4. (A) Biotic coverage represented on SfM-p derived orthomosaic of Ayı Balığı cave's right wall (Ω for entrance and dashed lines for biocoenosis borders as defined by Pérès and Picard in 1964), (B) modified pie/ring charts depicting the coverage of benthic groups on ABc's right wall (with faunal phyla in the bar chart on the left side) and (C) stacked-bars chart displaying biotic cover of phyla within their own respective biocoenosis.

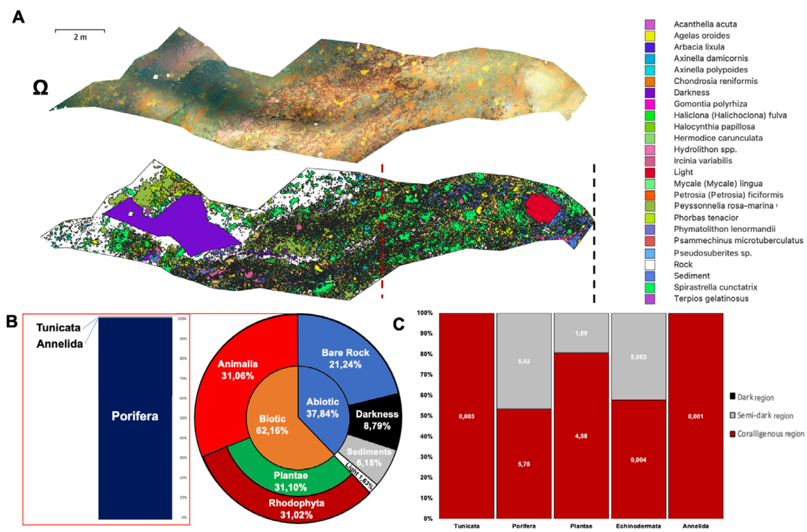

Figure 5. (A) Biotic coverage represented on SfM-p derived orthomosaic of Eşendere cave's left wall (Ω for entrance and dashed lines for biocoenosis borders as defined by Pérès and Picard in 1964), (B) modified pie/ring charts depicting the coverage of benthic groups on Ec's left wall (with faunal phyla in the bar chart on the left side) and (C) stacked-bars chart displaying biotic cover of phyla within their own respective biocoenosis.

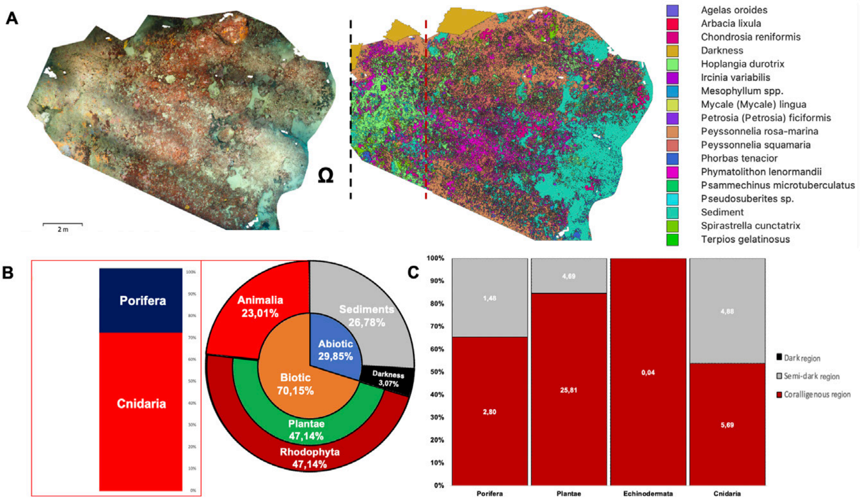

Figure 6. (A) Biotic coverage represented on SfM-p derived orthomosaic of Eşendere cave's floor (Ω for entrance and dashed lines for biocoenosis borders as defined by Pérès and Picard in 1964), (B) modified pie/ring charts depicting the coverage of benthic groups on Ec's floor (with faunal phyla in the bar chart on the left side) and (C) stacked-bars chart displaying biotic cover of phyla within their own respective biocoenosis.

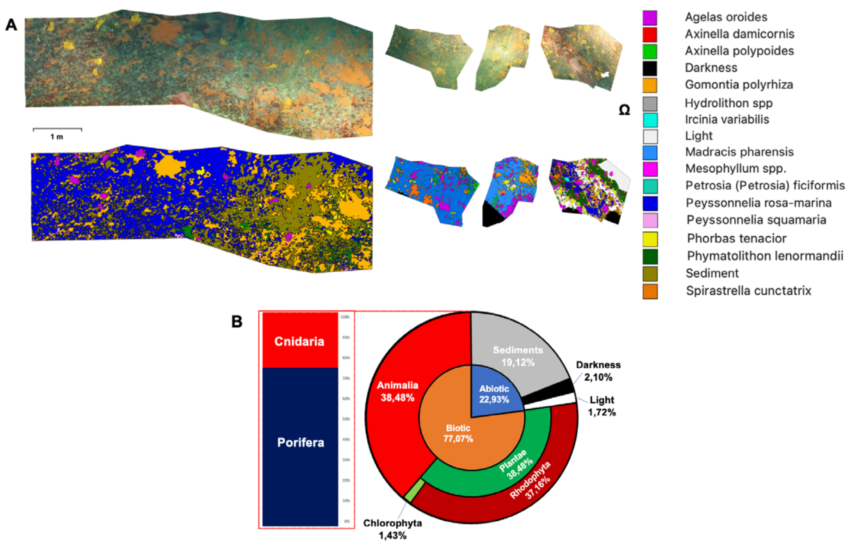

Figure 7. (A) Incomplete biotic coverage represented on SfM-p derived partial orthomosaic of Eşendere cave's right wall (Ω for entrance) and (B) modified pie/ring charts depicting the coverage of benthic groups on Ec's right wall (with faunal phyla in the bar chart on the left side).

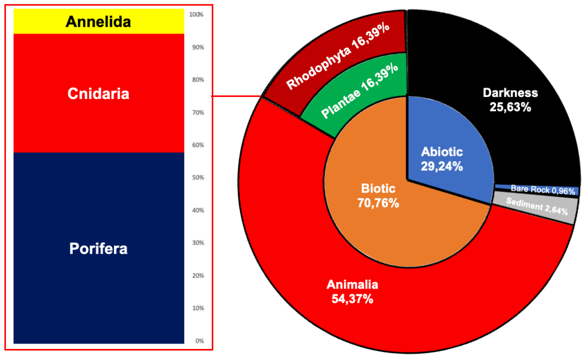

Figure 8. Modified pie/ring charts depicting the coverage of benthic groups in Yatak Odası cave (YOc) with faunal phyla in the bar chart on the left side.

Statistical analysis of macroinvertebrate communities
As previously stated, the photogrammetric methodology was deemed unsuitable for MCs with large sandy bottoms. Therefore, there was a need to establish a new dataset to compare benthic communities of macroinvertebrates between ABc, Ec and YOc. As such, 40 samples were randomly chosen within each MC for a total of 120 photoquadrats. Algae and other abiotic coverages (bare rock, sediment, shadows) were excluded from analyses.

The highest diversity of macroinvertebrates was reported for YOc (Shannon Diversity Index or H' = 1.54 ± 0.18), followed by ABc (H' = 1.02 ± 0.48) and Ec (H' = 0.89 ± 0.43). Macroinvertebrate communities showed high dominance in YOc (Simpson Dominance Index or S = 0.71 ± 0.06), followed by ABc (S = 0.50 ± 0.23) and Ec (S = 0.47 ± 0.20). Assemblages were the most homogenously distributed in Ec (Pielou Evenness Index or J' = 0.63 ± 0.19) followed by YOc (J' = 0.61 ± 0.07) and ABc (J' = 0.51 ± 0.20). Dunn's post-hoc test highlighted that YOc diverged significantly from other stations in terms of both H' and S. The only exception was for J' where ABc was significantly different from Ec. Significant variation was also reported within geomorphologies with high diversity, high dominance and even distribution of macroinvertebrates for blind-ended MCs in comparison to tunnel-shaped MCs (as mentioned in Table 1). Moreover, statistically divergent patterns were observed for MCs submersion levels with lower richness/indices in partially submerged MCs, when compared to entirely submerged MCs. Boxplots were plotted to depict the significant variation among ecological indices along factors (Figure 9). Results from statistical tests are available in Table 3.

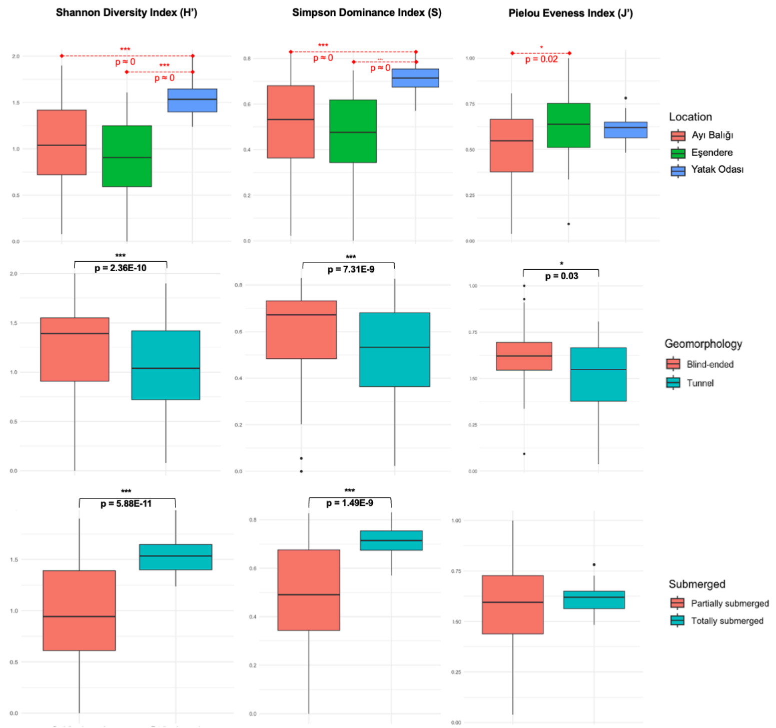

Figure 9. Diversity, dominance and evenness indices of benthic macroinvertebrate communities inside KISEPA's MCs according to stations (ABc, Ec, YOc), MCs' geomorphologies (blind-ended, tunnel) and submersion level (partially, entirely submerged). Statistical tests used were Kruskal-Wallis for geomorphology and submersion factors, Dunn's post hoc test for stations factor (* for $p < 0.05$; ** for $p < 0.01$; *** for $p < 0.001$). All data is based on biotic cover extracted from photoquadrats.

ANOSIM tests highlighted significant differences in the community's composition for macroinvertebrates among stations, geomorphologies and submersion levels ($p = 0.001$ for each factor). The median and interquartile range of "Between" boxplot was higher than medians/interquartile ranges of "Within" boxplots, which underlined a statistically significant and well-defined separation among categories based on biotic coverage (Figure 10).

The result of RDA analysis is shown in Figure 11. Both axes on the RDA biplot (total of RDA1 and RDA2) explained 52.35% of the overall variance in macroinvertebrates abundance, which was deemed satisfactory considering the ecological context. Samples were clearly clustered according to their respective station, although four outliers occurred between ABc and Ec. Different macroinvertebrate communities characterised each station with high abundance of *Lithophaga lithophaga*, co-occurring with *Halisarca dujardinii* within ABc, where the height of the entrance was the greatest, great quantity of *Spirastrella cunctratrix* observed in tandem with *Mycale (Mycale) lingua* and *Axinella polypoides* inside Ec and finally large cover of *Madracis pharensis* concurrently reported with *Phorbas plumosus* and *Agelas oroides* inside YOc, which has the deepest entrance. In addition to station location, the macroinvertebrate community of MCs appeared to be impacted by the submersion level as implied by the importance of the entrance's depth for the distribution of samples within the RDA biplot. Results from statistical tests are presented in Table 3.

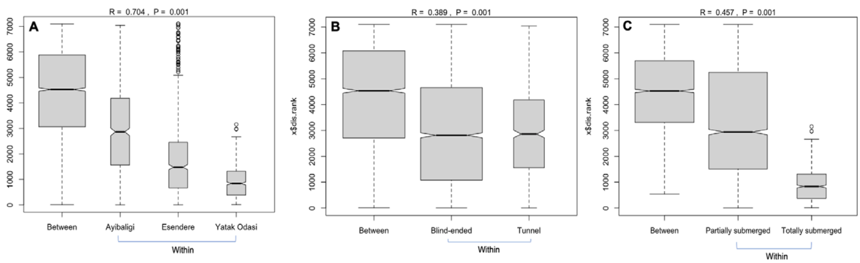

Figure 10. ANOSIM boxplots representing benthic macroinvertebrates' cover (extracted from photoquadrats) in KISEPA's MCs according to (A) stations (ABc, Ec, YOc), (B) MCs' geomorphology (blind-ended, tunnel) and (C) submersion levels (partially, entirely submerged). Difference in All ANOSIM tests were significant different (p<0.05).

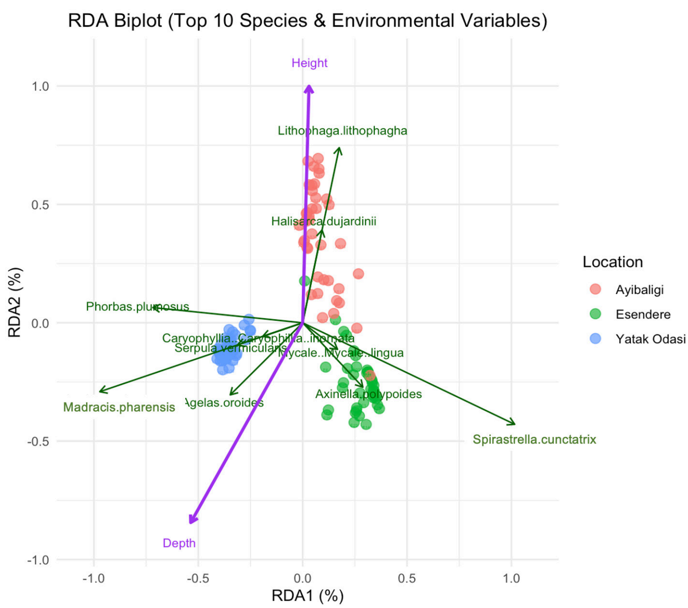

Figure 11. RDA biplot of benthic macroinvertebrates found inside MCs in the KISEPA (biotic cover extracted from photoquadrats). Arrows illustrated the first 10 most abundant species (green colour) and environmental variables contributing the most to the assemblage's variation (purple colour).

Table 3. Results of statistical analyses on the composition of benthic macroinvertebrate communities inside MCs in the KISEPA ($p < 0.05$; ABc: Ayı Balığı cave; Ec: Eşendere cave; Yatak Odası cave)

Methodology	**Variables**	**Stations**			**Factors for Kruskall Wallis test (ecological indexes)**		
		Ayı Balığı cave	**Eşendere cave**	**Yatak Odası cave**	**Station (Dunn's post hoc test)**	**Geomorphology**	**Submersion state**
40 random photoquadrats per station (25 x 25 cm)	Shannon Diversity Index	1.02 ± 0.48	0.89 ± 0.43	1.54 ± 0.18	YOc-Ec and YOc-ABc ($p \approx 0$)	p = 2.36E-10	p = 5.88E-11
	Simpson Diversity Index	0.50 ± 0.23	0.47 ± 0.20	0.71 ± 0.06	YOc-Ec and YOc-ABc ($p \approx 0$)	p = 7.31E-9	p = 1.49E-9
	Pielou Evenness Index	0.51 ± 0.20	0.63 ± 0.19	0.61 ± 0.07	ABc-Ec (p = 0.02)	p = 0.03	No

Methodology	**Variables**	**Stations**			**Factors for ANOSIM (abundance data)**		
		Ayı Balığı cave	**Eşendere cave**	**Yatak Odası cave**	**Station**	**Geomorphology**	**Submersion state**
RDA biplot	Species specific to station	*Lithophaga lithophaga* *Halisarca dujardinii*	*Spirastrella cunctratrix* *Axinella polypoides*	*Madracis pharensis* *Phorbas plumosus*	p = 0.001 but dissimilar samples in Ec	p = 0.001	p = 0.001

Discussion

Due to the complexity of cave topography, some parts of the surveyed area were not exploitable (3.07% - 15.25% of shades). Underwater SfM-p is heavily dependent on seawater properties such as light scattering, hazing, colour distortions, sediments, and turbidity (Calantropio and Chiabrando 2024). The effect of environmental factors in a confined space like MCs was especially well-demonstrated in YOc. The lack of photogrammetric model for YOc was due to the high turbidity inside the MC with a sandy floor. It is usually more difficult to get high quality images above sandy/soft bottoms when compared to other rocky substrata (Skarlatos *et al.* 2019; Adams *et al.* 2024). Particulate matter in the seawater had a negative effect on the image's quality with the increased likelihood of light scattering effect. High concentration of suspended particulate matter tended to reflect light, scattering it back to the camera lens, which resulted in less sharp and less contrasted hazy pictures (Selmo *et al.* 2017). The effect was especially amplified inside dark habitats. It directly impacted the alignment process, preventing an accurate reconstruction of YOc biological coverage via SfM-p.

Considering the previous qualitative inventory (Barraud and Öztürk 2025) with 51 taxa reported in Ec and 25 taxa observed in ABc, counts of taxa spotted on photogrammetric models were lower, with only 44-60% of reported taxa visible on ABc model and only 15.7-35.3% of reported taxa observable on Ec model. Differences in richness between the qualitative inventory and the quantitative survey could be explained by the high motility or cryptic nature of certain taxa such as *Dromia personata*, *Apogon imberbis*, *Blennius ocellaris*, *Chromis chromis*, *Diplodus vulgaris*, *Serranus scriba*, *Symphodus roissali*, *Thalassoma pavo*, *Muraena helena*, *Parablennius gattorugine*, *Parablennius zvonimiri* and *Tripterygion tripteronotum.* They were harder to "stabilise" on the orthomosaic when hidden/moving in small cavities unreachable to the underwater camera (Çınar *et al.* 2019; Brack *et al.* 2025; Yuval *et al.* 2025).

In this study, among animal phyla, Porifera and Cnidaria (mostly scleractinians) were found as the most abundant epifaunal groups. Coverage for sponges varied between 28.72% and 99.81%, followed by corals, which reached a maximum of 71.04%. The remaining phyla had smaller percentages, with molluscs ranging up to 18.67%, up to 0.75% for annelids, less than 0.58% for echinoderms and finally below 0.19% for tunicates. These results are in concordance with trends reported at the scale of Mediterranean Sea with sponges, scleractinians and serpulids being the most abundant inside MCs (Harmelin 1985b; Faulwetter *et al.* 2017; Grenier *et al.* 2018). One major gap in the scientific literature is the lack of multitaxa quantitative studies about marine stygofauna (fauna harboured inside MCs). Until now and at the scale of Türkiye, only Topaloğlu (2019) and the present study provided quantitative data about the abundance of benthic fauna inside Türkiye's MCs. It is worth mentioning that Çınar *et al.* (2019) used a semi-quantitative approach to study the same YOc. According to Topaloğlu (2019), a MC at 10 m depth located in the Northern Aegean Sea at Gökçeada harboured a cover of 76.60% (93.78% of fauna) for Porifera, 4.38% for Polychaeta (5.36% of fauna), 0.60% for Cnidaria (0.73% of fauna), 0.10% for Echinodermata (0.12% of fauna), while another MC named "Güvercin Çatlağı" at 6 m depth in the Marmara Sea at Büyükada sheltered 37.51% of sponges (45.13% of fauna), 33.06% of molluscs (39.63% of fauna), 7.00% of polychaetes (8.39% of fauna), 5.45% of echinoderms (6.53% of fauna) and 0.40% of corals (0.48% of fauna). Results from the Central Aegean, Northern Aegean and Marmara Seas along the Turkish coastline underlined the following abundance patterns among benthic macroinvertebrates in MCs: poriferan/cnidarian covers tended to decrease whereas mollusc/annelid/echinoderm coverages seemed to increase following a south-northern gradient.

The present study offers additional insights when compared to Greek MCs in the Aegean Sea (Gerovasileiou *et al.* 2017; Dimarchopoulou *et al.* 2018; Digenis *et al.* 2022). Both Greek and Turkish coastlines share the common characteristic of Porifera being the most abundant phylum inside Aegean MCs, with benthic coverages varying between 57.09-93.78% for Turkish MCs and 46.31-81.61% for Greek MCs. Within the Aegean Sea, benthic coverages of Porifera increase in the same way for MCs along Greek and Turkish coastlines, following a south-northern gradient. In contrast, the abundance of bryozoan coverages inside MCs along the Greek coastline (from 12.13% to 50.04%) seems to set Greek MCs apart from their Turkish counterparts.

The present study applied the definition of Pérès and Picard (1964) to delimit the ecozones or biocoenoses inside MCs in the KISEPA. Coralligenous zones varied from 2.38 m^2 to 34.33 m^2 near the entrance, from 3.46 m^2 to 11.04 m^2 in the semi-dark zone and only reached 0.54 m^2 within the dark zone. However, not all caves had accessible dark areas. Dark areas were in some cases reduced to small cryptic anfractuosities in the inner parts not explorable for SCUBA divers. A small chamber with biostalactites was found inside Ec but was too narrow to allow exploration. The current study confirmed the high abundance of macrobenthic invertebrates inside the semi-dark zone dominated by sponges and corals, whereas the dark zone's main characteristics were the dominance of serpulid cover and minor presences of other faunal taxa. These findings were in conformity with previous studies (Balduzzi *et al.* 1989; Martí *et al.* 2004 a,b; Bussotti *et al.* 2006; Teixidó *et al.* 2011; Gerovasileiou *et al.* 2017; Dimarchopoulou *et al.* 2018; Digenis *et al.* 2022).

In terms of biological cover inside MCs in KISEPA, the most abundant species were *Phorbas tenacior*, *Spirastrella cunctatrix*, *Lithophaga lithophaga*, *Pseudosuberites* sp., *Mycale (Mycale) lingua*, *Hoplangia durotrix* and *Madracis pharensis*. Additionally, despite not being depicted by SfM-p, facies of *Leptopsammia pruvoti* was also prevalent especially in YOc. Abundance estimations in the present study agreed with the content of previous studies (Çınar *et al.* 2019; Gerovasileiou and Bianchi 2021). Previously mentioned species (except for *Pseudosuberites* sp.) were considered as facies specific to semi-dark and dark zones inside Mediterranean MCs. Other less abundant species reported in the KISEPA were cited in the literature as being the most frequently encountered in Mediterranean MCs within their own respective phylum (*Arbacia lixula* for Echinodermata and *Halocynthia papillosa* for Tunicata) (Gerovasileiou and Bianchi 2021). The present study confirmed the fact that *Leptopsammia pruvoti* and *Madracis pharensis* were widespread in MCs of the Eastern Mediterranean Sea (Gerovasileiou and Bianchi 2021).

Shannon, Simpson, and Pielou indices values between MCs were deemed to be low to moderately high, with ranges of 0.89 to 1.54, 0.47 to 0.71, and 0.51 to 0.63, respectively (Guajardo 2015; Jalil *et al.* 2020). Diversity of benthic macroinvertebrates was, statistically speaking, significantly higher for blind-ended/entirely submerged MCs, especially at YOc. A similar trend was observed for the dominance index. However different patterns were reported for Pielou index with more evenly distributed assemblages at Ec and high evenness for blind-ended MCs. Individual MCs, geomorphologies and submersion levels have been reported to have significant effects on ecological indices (Bianchi and Morri 1994), except for Pielou index where submersion state had no effect at all for MCs in the KISEPA.

MCs are considered as extreme habitats (Harmelin 1985a), so it is usually admitted that communities inhabiting them will have lower diversity dominated by taxa with specialised adaptations and uneven distribution, when compared to other open-water marine habitats (Riedl 1966; Iliffe *et al.* 2009). Environmental gradients tend to increase heterogeneity or patchiness (Bianchi *et al.* 1996). However, Ec had the most evenly distributed and the least dominated assemblage among the three studied MCs. Differences in evenness could be explained by past changes occurring inside Ec with the increased exposure of the internal cavernous structure to outside light via opening/windows located in the cave ceiling. Additional sources of light in the inner parts of Ec were found to affect light penetration as a limiting factor. ANOSIM boxplots not only highlighted individualities of the three MCs, but also underlined the high dissimilarity between photoquadrat samples within Ec.

ANOSIM plots were also used to discriminate peculiar samples within each category. An unusual high number of outliers outside of whiskers were observed within the supposedly homogenous group of Ec. The outliers were samples quite dissimilar from the rest of samples within Ec. Divergent samples might be the result of past disturbances inside Ec which may have altered the composition of benthic macroinvertebrate communities (Clarke 1993), although outliers most likely occurred due to the high small-scaled heterogeneity and patchiness specific to benthic communities inside MCs (Gerovasileiou and Bianchi 2021). Another unusual finding was the low diversity in ABc. Tunnel-shaped MCs are known to show biotic cover reaching 100% even in the darkest area (Harmelin 1985a), owing to the constant hydrodynamic regime. However, it was not the case for ABc with its visibly low biotic cover.

RDA biplot highlighted the presence of cave-specific species and the significant effect of a few environmental factors (depth and height of cave entrance) on the composition of benthic macroinvertebrate communities inside MCs in the KISEPA. Based on the RDA biplot, ABc was defined by a high abundance of *Lithophaga lithophaga* and *Halisarca dujardinii* while Ec harboured high abundance of *Spirastrella cunctatrix* and *Axinella polypoides*. Finally, YOc exhibited high abundances of *Madracis pharensis* and *Phorbas plumosus*. It is also worth mentioning that *Leptopsammia pruvoti* was found in high abundance in YOc, despite its absence from the RDA biplot. Furthermore, our results seemed to be in line with the definition of semi-superficial (0 m - 5 m depth) and deep caves (depth greater than 10 m) by Pouliquen (1972). The difference in community composition inside deep MCs was due to the variation in hydrodynamic regime, as the entirely submerged MC was less exposed to wave action when compared to semi-submerged MCs near the surface (Pouliquen 1972). The importance of MC entrance as a factor, among others, in modulating structure of macro-invertebrate communities is expected, as it determines how far the light penetration and how much nutrient goes inside the inner parts of the enclosed system. Dimensions of the cave's entrance are one of the main limiting factors determining the structure of benthic communities inside MCs (Gerovasileiou *et al.* 2017; Digenis *et al.* 2022).

Conclusion

Biodiversity assessments of marine biota on hard substrate can be performed qualitatively or quantitatively. Each approach has its pros and cons depending on the sampling time, funding availability and requirements for study reliability (Lenat 1988). The photogrammetric methodology in the present study is a prime example of technological innovations applied to marine biodiversity quantitative assessments. Dozens of metre squares of biotic cover was successfully modelled in the digital environment, inside dark habitats difficult to access. SfM-p emerged as an indispensable tool for quantitative marine biodiversity surveys in MCs. Its capacity to generate high-resolution, 3D models and orthomosaics offered a non-invasive and highly repeatable approach to capturing detailed information on benthic assemblages. However, limitations associated to this approach were also observed, especially in MCs whose floor is covered by soft sediment. Nevertheless, it allowed for accurate measurements of species richness and percentage cover which were consistent with the data available in previous studies on Mediterranean MCs. As a result, the use of this method is concordant with the guidelines provided by the EU Habitat Directive 92/83/EEC and the "Dark Habitats Action Plan" of the Barcelona Convention, which emphasize on the employment of non-destructive, repeatable and standardized technics to protect dark habitats.

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Author contributions: T.B. planned the present study. T.B. collected the samples onboard the R/V YUNUS-S. T.B. submitted the samples to taxonomical experts, performed the laboratory work and conducted data analysis. T.B. wrote the initial manuscript draft.

Karaburun-Ildır ÖÇKB deniz mağaralarındaki makro-omurgasızların fotogrametrik değerlendirilmesi

Öz

Karaburun-Ildır Körfezi Özel Çevre Koruma Bölgesi'ndeki (Karaburun–Ildır Körfezi ÖÇKB) bentik makro-omurgasızlar, üç deniz mağarasında (DM) Hareketten Yapı fotogrametrisi (HYF) aracılığıyla incelenmiştir. Bu yaklaşım, 171.92 m²'lik denizel habitatın dijital modellemesini sağlamıştır. Faunal örtü %13.07-38.48 arasında değişirken, epifaunal yüzey DM'nin bölümlerine bağlı olarak 3.37-14.96 m² arasında değişmekteydi. Nicel değerlendirme, Porifera (%28.72-99.81), Cnidaria (≤ %71.04, özelikle skleraktinliler) ve Mollusca (≤ %18.67) filumlarının bolluğunu vurgulamıştır. En fazla bulunan türler *Phorbas tenacior*, *Spirastrella cunctatrix*, *Hoplangia durotrix* ve *Madracis pharensis* iken, diğer türler Ayı Balığı mağarası için *Lithophaga lithophaga*/*Pseudosuberites* sp./*Halisarca dujardinii* ve Eşendere mağarası için *Mycale (Mycale) lingua*/*Agelas oroides*/*Axinella polypoides* gibi istasyona özgüydü. Ne yazık ki, HYF, kumlu tabanlara sahip Yatak Odası mağarası (YOc) gibi DM'ler için uygun değildi. Bunun yerine, Karaburun–Ildır Körfezi ÖÇKB'deki DM'leri karşılaştırmak için 25x25cm'lik fotokuadratlar kullanılmıştır. İstatistiksel analizler, DM'nin bireyselliğinin, jeomorfolojisinin ve batık durumunun çoğu ekolojik indeks üzerinde önemli etkilerini ortaya koymuş, en yüksek değerler kör uçlu/tamamen su altında kalmış DM'ler için gözlenmiştir. DM girişinin yüksekliği ve derinliğinin makro-omurgasız topluluklarındaki ana etkenler olduğu tahmin edilmiştir. Kuzey Ege ve Marmara Denizi'ndeki DM'lerle karşılaştırıldığında, Karaburun–Ildır Körfezi ÖÇKB'deki DM'ler kendilerini daha büyük sünger ve mercan yüzeyleriyle ayırmaktadır.

Anahtar kelimeler: Karaburun-Ildır Körfezi Özel Çevre Koruma Bölgesi, deniz mağaraları, fotogrametri, biyotik örtü, bolluk

References

Abadie, A., Boissery, P., Viala, C. (2018) Georeferenced underwater photogrammetry to map marine habitats and submerged artificial structures. *The Photogrammetric Record* 33(164): 448-469.

Adams, D., Helmholz, P., McMeekin, D., Woods, A. (2024) Improving underwater photogrammetric 3D reconstruction processing of shipwreck sites. *ISPRS Annals of the Photogrammetry, Remote Sensing and Spatial Information Sciences* 10: 7-14.

Aston, E.A., Duce, S., Hoey, A.S., Ferrari, R. (2022) A protocol for extracting structural metrics from 3D reconstructions of corals. *Frontiers in Marine Science* 9. doi: 10.3389/fmars.2022.854395.

Balduzzi, A., Bianchi, C.N., Boero, F., Cattaneo-Vietti, R., Pansini, M., Sarà, M. (1989) The suspension-feeder communities of a Mediterranean Sea cave. *Scientia Marina* 53(2-3): 387-395.

Barraud, T., Öztürk, B. (2025) Stygofaunal inventory of marine caves in Karaburun-Ildır Special Environmental Protected Area (SEPA) (Aegean Sea, Türkiye). *Journal of the Black Sea/Mediterranean Environment* 31(2): 87-124.

Bayley, D.T.I., Mogg, A.O.M. (2020) A protocol for the large-scale analysis of reefs using structure from motion photogrammetry. *Methods in Ecology and Evolution* 11(11): 1410-1420.

Bayley, D.T.I., Mogg, A.O.M., Koldewey, H., Purvis, A. (2019) Capturing complexity: Field-testing the use of 'structure from motion' derived virtual models to replicate standard measures of reef physical structure. *PeerJ* 7. doi: 10.7717/peerj.6540.

Beltrame, C., Costa, E. (2017) 3D survey and modelling of shipwrecks in different underwater environments. *Journal of Cultural Heritage* 25: 3-9.

Benedetti-Cecchi, L., Airoldi, L., Abbiati, M., Cinelli, F. (1996) Estimating the abundance of benthic invertebrates: A comparison of procedures and variability between observers. *Marine Ecology Progress Series* 138: 93-101.

Bennecke, S., Kwasnitschka, T., Metaxas, A., Dullo, W.C. (2016) *In situ* growth rates of deep-water octocorals determined from 3D photogrammetric reconstructions. *Coral Reefs* 35(4): 1227-1239.

Bianchi, C.N., Bedulli, D., Morri, C., Zunino, P. (2004) Hard bottoms. *Biologia Marina Mediterranea* 11(1): 185-215.

Bianchi, C.N., Cattaneo-Vietti, R., Cinelli, F., Morri, C., Pansini, M. (1996) The biological study of underwater caves: Current knowledge and perspectives. *Bollettino dei Musei e degli Istituti Biologici dell'Università di Genova* 60-61: 41-69 (in Italian).

Bianchi, C.N., Morri, C. (1994) Comparative bionomic study of some submerged sea caves; definition of a confinement scale. *Memorie dell'Istituto Italiano di Speleologia Serie II* 6: 107-123 (in Italian).

Bilecenoğlu, M. (2019) Diversity of Cavern Fishes at the Eastern Aegean Sea Coasts (Turkey): Preliminary Observation. In: Öztürk B. (ed.), Marine Caves of the Eastern Mediterranean Sea Biodiversity, Threats and Conservation, Turkish Marine Research Foundation Publication no. 53, Istanbul, Türkiye, pp. 84-90.

Bonin-Font, F., Campos, M.M., Codina, G.O. (2016) Towards visual detection, mapping and quantification of *Posidonia oceanica* using a lightweight AUV. *IFAC-PapersOnLine* 49(25): 500-505.

Bracchi, V.A., Bazzicalupo, P., Fallati, L., Varzi, A.G., Savini, A., Negri, M.P., Calcinai, B., Cerrano, C., Taviani, M., Basso, D. (2022) The main builders of Mediterranean coralligenous: 2D and 3D quantitative approaches for its identification. *Frontiers in Earth Science* 10: 910522.

Brack, I.V., Ferrara, C., Forero-Medina, G., Domic-Rivadeneira, E., Torrico, O., Wanovich, K.T., Dech, H., Rehn, K.M., Fagan, R., Pimm, S.L., Valle, D. (2025) Counting animals in orthomosaics from aerial imagery: Challenges and future directions. *Methods in Ecology and Evolution* 16(6): 1051-1060.

Bridge, T.C.L., Fabricius, K.E., Bongaerts, P., Ferrari, R., Bergmann, L., Miles, J.J., Done, T.J. (2014) Variable responses of benthic communities to anomalously warm sea temperatures on a high-latitude coral reef. *PLoS One* 9(11): e0113079.

Burns, J.H.R., Delparte, D. (2017) Comparison of commercial structure-from-motion photogrammetry software used for underwater three-dimensional modeling of coral reef environments. *The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences* 42(2): 127-134.

Burns, J., Delparte, D., Gates, R., Takabayashi, M. (2015) Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. *PeerJ* 3. doi: 10.7717/peerj.1077.

Bussotti, S., Terlizzi, A., Fraschetti, S., Belmonte, G., Boero, F. (2006) Spatial and temporal variability of sessile benthos in shallow Mediterranean marine caves. *Marine Ecology Progress Series* 325: 109-119.

Bryson, M., Johnson-Roberson, M., Pizarro, O., Williams, S.B. (2013) Automated registration for multi-year robotic surveys of marine benthic habitats. *IEEE/RSJ International Conference on Intelligent Robots and Systems*: 3344-3349).

Bryson, M., Williams, S.B., Pizarro, O., Madin, J.S. (2017) Characterization of measurement errors using structure-from-motion and photogrammetry to measure marine habitat structural complexity. *Ecology and Evolution* 7(14): 5462-5472.

Calantropio, A., Chiabrando, F. (2024) Underwater cultural heritage documentation using photogrammetry. *Journal of Marine Science and Engineering* 12(3): 413.

Cardone, F., D'Alessandro, L., De Pascale, G., Mastropietro, A., Quarto, M., Salvemini, F., Stoppa, F., Tursi, A., D'Onghia, G. (2022) First speleological and biological characterization of a submerged cave of the Tremiti archipelago geomorphosite (Adriatic Sea). *Geosciences* 12(5): 213. doi: 10.3390/geosciences12050213.

Çelikok, M. (2019) Marine Caves alongside Fethiye/Turkey Coasts. In: Marine Caves of the Eastern Mediterranean Sea Biodiversity, Threats and Conservation, (ed., Öztürk, B.), Turkish Marine Research Foundation, Publication no: 53, Istanbul, Türkiye, pp.111-125.

Chemisky, B., Poncet, S., Guillaumont, B., Jouffray, V. (2015) The Marine Funds are Accessible to All with the High-resolution Three-dimensional Return. In: Proceedings of the MerlGéo, de la Côte à l'Océan, l'Information Géographique en Movement, pp. 57-60, (in French).

Chevaldonné, P., Rastorgueff, P.A., Arslan, D., Lejeusne, C. (2015) Molecular and distribution data on the poorly known elusive, cave mysid *Harmelinella mariannae* (Crustacea: Mysida). *Marine Ecology* 36: 305-317.

Çınar, M.E., Evcen, A., Acik, G. (2019) Macrozoobenthic Invertebrates in Three Submarine Caves of the Aegean Sea: Preliminary Results. In: Marine Caves of the Eastern Mediterranean Sea. Biodiversity, Threats and Conservation (ed., Öztürk, B.), Turkish Marine Research Foundation Publication no.53, Türkiye, pp. 69-83.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18(1): 117-143.

Combs, I.R., Studivan, M.S., Eckert, R.J., Voss, J.D. (2021) Quantifying impacts of stony coral tissue loss disease on corals in Southeast Florida through surveys and 3D photogrammetry. *PLoS One* 16(6): e0252593.

D'Urban Jackson, T., Williams, G.J., Walker-Springett, G., Davies, A.J. (2020) Three-dimensional digital mapping of ecosystems: A new era in spatial ecology. *Proceedings of the Royal Society B: Biological Sciences* 287(1920). doi: 10.1098/rspb.2019.2383.

Dede, A., Tonay, A.M. (2019) Mediterranean Monk Seal Caves in the Turkish Aegean Sea and Their Conservation. In: Marine Caves of the Eastern Mediterranean Sea Biodiversity, Threats and Conservation, (ed., Öztürk, B.), Turkish Marine Research Foundation, Publication no: 53, Türkiye, pp. 126-133.

De Oliveira, L.M.C., Lim, A., Conti, L.A., Wheeler, A.J. (2021) 3D classification of cold-water coral reefs: A comparison of classification techniques for 3D reconstructions of cold-water coral reefs and seabed. *Frontiers in Marine Science* 8. doi: 10.3389/fmars.2021.640713.

Derrien, M., Chevaldonné, P., Perez, T. (2024) Patterns of benthic diversity in marine underwater caves of the Marseille Region (France, North-Western Mediterranean Sea). *Mediterranean Marine Science* 25: 666-681.

Díez, S., Goni, R., Mallol, S., Maresca, F., Morató, M., Muñoz, A., Poloni, L., Díaz, D. (2022) Monitoring the complex benthic habitat in semi-dark underwater marine caves using photogrammetry-based 3D reconstructions. 3rd Mediterranean Symposium on the Conservation of the Dark Habitats, p. 113.

Digenis, M., Arvanitidis, C., Dailianis, T., Gerovasileiou, V. (2022) Comparative study of marine cave communities in a protected area of the South-Eastern Aegean Sea, Greece. *Journal of Marine Science and Engineering* 10: 660.

Dimarchopoulou, D., Gerovasileiou, V., Voultsiadou, E. (2018) Spatial variability of sessile benthos in a semi-submerged marine cave of a remote Aegean Island (eastern Mediterranean Sea). *Regional Studies in Marine Science* 17: 102-111.

Faulwetter, S., Simboura, N., Katsiaras, N., Chatzigeorgiou, G., Arvanitidis, C. (2017) Polychaetes of Greece: an updated and annotated checklist. *Biodiversity Data Journal* 5. doi: 10.3897/BDJ.5.e20997.

Ferrari, R., Malcolm, H.A., Byrne, M., Williams, S.B., Figueira, W.F. (2016) Quantifying the response of structural complexity and community composition to environmental change in marine communities. *Global Change Biology* 22(5): 1965-1975.

Filiz, H., Sevingel, N. (2015) A new maximum length for the parrotfish, *Sparisoma cretense* (Linnaeus, 1758) in the Mediterranean Sea. *Journal of Aquaculture Engineering and Fisheries Research* 1(3): 140-143.

Fukunaga, A., Burns, J., Craig, B., Kosaki, R. (2019) Integrating three-dimensional benthic habitat characterization techniques into ecological monitoring of coral reefs. *Journal of Marine Science and Engineering* 7(2): 27.

Garrabou, J., Bavestrello, G., Cattaneo-Vietti, R., Cerrano, C., Garcia, S., Goffredo, S., Linares, C.L., Ocana, O. (2015) *Corallium rubrum* (Mediterranean assessment) (errata version published in 2017). The IUCN Red List of Threatened Species, 50013405, 110609252.

Gerovasileiou, V., Bianchi, C.N. (2021) Mediterranean marine caves: A synthesis of current knowledge. *Oceanography and Marine Biology: An Annual Review* 59: 1-87.

Gerovasileiou, V., Dimitriadis, C., Arvanitidis, C., Voultsiadou, E. (2017) Taxonomic and functional surrogates of sessile benthic diversity in Mediterranean marine caves. *PLoS One* 12(9): e0183707.

Gerovasileiou, V., Voultsiadou, E. (2012) Marine caves of the Mediterranean Sea: a sponge biodiversity reservoir within a biodiversity hotspot. *PLoS One* 7(7): e39873.

Gerovasileiou, V., Trygonis, V., Sini, M., Koutsoubas, D., Voultsiadou, E. (2013) Three-dimensional mapping of marine caves using a handheld echosounder. *Marine Ecology Progress Series* 486: 13-22.

Giakoumi, S., Sini, M., Gerovasileiou, V., Mazor, T., Beher, J., Possingham, H.P., Abdulla, A., Çınar, M.E., Dendrinos, P., Gucu, A.C., Karamanlidis, A.A.

(2013) Ecoregion-based conservation planning in the Mediterranean: dealing with large-scale heterogeneity, *PLoS One* 8(10): e0076449.

Grenier, M., Ruiz, C., Fourt, M., Santonja, M., Dubois, M., Klautau, M., Vacelet, J., Boury-Esnault, N., Pérez, T. (2018) Sponge inventory of the French Mediterranean waters, with an emphasis on cave-dwelling species. *Zootaxa* 4466(3): 205-228.

Guajardo, S. (2015) Measuring Diversity in Police Agencies. *Journal of Ethnicity in Criminal Justice* 13(1): 1-15.

Gunn, J. (2004) Encyclopaedia of Caves and Karst Science. Fitzroy Dearborn, New York. doi: 10.4324/9780203483855.

Gutierrez-Heredia, L., Benzoni, F., Murphy, E., Reynaud, E.G. (2016) End to end digitisation and analysis of three-dimensional coral models, from communities to corallites. *PLoS One* 11(2): e0149641.

Harmelin, J.G. (1985a) Bryozoan dominated assemblages in Mediterranean cryptic environments. In: Bryozoa: Ordovician to Recent (eds., Nielsen, C., Larwood, G.P.), Olsen olsen, pp. 135-143.

Harmelin, J.G. (1985b) Dark underwater caves: an extreme environment and a remarkable biotope refuge. *Téthys* 11: 214-229 (in French).

Iliffe, T.M., Bishop, R.E., Safran, P. (2009) Adaptations to life in marine caves. *Fisheries and Aquaculture, Encyclopedia of Life Support Systems* (5): 183-205.

Iluz, D., Barinova, S., Mayer, D., Golstein, E., Cherniavska, E., Alster, A. Abu-Ghosh, S. (2025) Seasonal dynamics of *Hildenbrandia rubra* in a Mediterranean marine cave: insights into the algal community and biodiversity. *Aquatic Sciences* 87(43). doi: 10.1007/s00027-025-01163-5.

Martí, R., Uriz, M.J., Ballesteros, E., Turon, X. (2004a) Benthic assemblages in two Mediterranean caves: species diversity and coverage as a function of abiotic parameters and geographic distance. *Journal of the Marine Biological Association of the United Kingdom* 84(3): 557-572.

Martí, R., Uriz, M.J., Ballesteros, E., Turon, X. (2004b) Temporal variation of several structure descriptors in animal-dominated benthic communities in two Mediterranean caves. *Journal of the Marine Biological Association of the United Kingdom* 84(3): 573-580.

Irschick, D.J., Christiansen, F., Hammerschlag, N., Martin, J., Madsen, P.T., Wyneken, J., Marshall, G.J., Lauder, G.V. (2022) 3D visualization processes for recreating and studying organismal form. *iScience* 25(9). doi: 10.1016/j.isci.2022.104904.

IUCN (2024) The IUCN Red List of Threatened Species. Available at: https://www.iucnredlist.org (accessed 25 Dec 2024).

Jalil, J., Makkatenni, M., Juhardi, J. (2020) Diversity index, similarity index and dominance index of macrozoobenthos in Pangkajene River Estuary, Pangkep Regency, Indonesia. *International Journal of Scientific Technology Research* 9(2): 5220-5224.

Keith, D.A., Ferrer-Paris, J.R., Nicholson, E., Bishop, M.J., Polidoro, B.A., Ramirez-Llodra, E., Tozer, M.G., Nel, J.L., Mac Nally, R., Gregr, E.J., Watermeyer, K.E. (2022) A function-based typology for Earth's ecosystems. *Nature* 610(7931): 513-518.

Kim, K., Lecours, V., Frederick, P.C. (2018) Using 3D micro-geomorphometry to quantify interstitial spaces of an oyster cluster. *PeerJ Preprints* 7. doi: 10.7287/peerj.preprints.27596v1.

Kıraç, C.O., Veryeri, N.O. (2009) Mediterranean Monk Seal (*Monachus monachus*) in the Karaburun Peninsula, İzmir, Türkiye. Ministry of Environment and Forest - Nature Conservation and National Parks General Directorate 40.

Lenat, D.R. (1988) Water quality assessment of streams using a qualitative collection method for benthic macroinvertebrates. *Journal of the North American Benthological Society* 7(3): 222-233.

Leon, J.X., Roelfsema, C.M., Saunders, M.I., Phinn, S.R. (2015) Measuring coral reef terrain roughness using "Structure-from-Motion" close-range photogrammetry. *Geomorphology* 242: 21-28.

Lochhead, I., Hedley, N. (2020) 3D modelling in temperate waters: Building rigs and data science to support glass sponge monitoring efforts in coastal British Columbia. *The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences* 43: 969-976.

Marlow, J., Halpin, J.E., Wilding, T.A. (2024) 3D photogrammetry and deep-learning deliver accurate estimates of epibenthic biomass. *Methods in Ecology and Evolution* 15(5): 965-977.

McCarthy, J., Benjamin, J. (2014) Multi-image photogrammetry for underwater archaeological site recording: An accessible, diver-based approach. *Journal of Maritime Archaeology* 9(1): 95-114.

Menna, F., Nocerino, E., Malek, S., Remondino, F., Schiaparelli, S. (2022) A combined approach for long-term monitoring of benthos in Antarctica with underwater photogrammetry and image understanding. *The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences* 43: 935-943.

Mizuno, K., Asada, A., Matsumoto, Y., Sugimoto, K., Fujii, T., Yamamuro, M., Fortes, M.D., Sarceda, M., Jimenez, L.A. (2017) A simple and efficient method for making a high-resolution seagrass map and quantification of dugong feeding trail distribution: A field test at Mayo Bay, Philippines. *Ecological Informatics* 38: 89-94.

Mohamed, H., Nadaoka, K., Nakamura, T. (2020) Towards benthic habitat 3D mapping using machine learning algorithms and structures from motion photogrammetry. *Remote Sensing* 12(1): 127.

Morais, J., Morais, R., Tebbett, S.B., Bellwood, D.R. (2022) On the fate of dead coral colonies. *Functional Ecology* 36(12): 3148-3160.

Morsy, S., Yánez Suárez, A.B., Robert, K. (2023) 3D Mapping of Benthic Habitat Using XGBoost and Structure from Motion Photogrammetry. *ISPRS Annals of the Photogrammetry, Remote Sensing and Spatial Information Sciences* 10: 1131-1136.

Napolitano, R., Chiariotti, P., Tomasini, E.P. (2019) Preliminary Assessment of Photogrammetric Approach for Detailed Dimensional and Colorimetric Reconstruction of Corals in Underwater Environment. In: IEEE International Workshop on Metrology for the Sea; Learning to Measure Sea Health Parameters (MetroSea) pp. 39-45.

Özalp, H.B. (2019) Biodiversity of Marine Caves and Cave-like Formations around the Northern Aegean Islands of Turkey (Gökçeada and Bozcaada), In: Marine Caves of the Eastern Mediterranean Sea Biodiversity, Threats and Conservation, (ed., Öztürk, B.), Turkish Marine Research Foundation Publication no.53, Istanbul, Türkiye, pp.166-185.

Öztürk, B., Güngör, A., Barraud, T. (2019) Marine Caves Biodiversity and Conservation in the Turkish part of the Mediterranean Sea: Preliminary Results of East Med Cave Project. In: Marine Caves of the Eastern Mediterranean Sea Biodiversity, Threats and Conservation, (ed., Öztürk, B.), Turkish Marine Research Foundation Publication no.53, Türkiye, pp. 147-158.

Ouerghi, A., Gerovasileiou, V., Bianchi, C.N. (2019) Mediterranean Marine Caves: A Synthesis of Current Knowledge and the Mediterranean Action Plan for the Conservation of “Dark Habitats”. In: Marine Caves of the Eastern

Mediterranean Sea. Biodiversity, Threats and Conservation, (ed., Öztürk, B.), Turkish Marine Research Foundation, Publication no. 53, Türkiye, pp. 1-13.

Palma, M., Casado, M., Pantaleo, U., Pavoni, G., Pica, D., Cerrano, C. (2018) SfM-based method to assess gorgonian forests (*Paramuricea clavata* (Cnidaria, Octocorallia)). *Remote Sensing* 10(7): 1154.

Pavoni, G., Corsini, M., Ponchio, F., Muntoni, A., Edwards, C., Pedersen, N., Sandin, S., Cignoni, P. (2021) TagLab: AI-assisted annotation for the fast and accurate semantic segmentation of coral reef orthoimages. *Journal of Field Robotics* 38(6): 903-918.

Pérès, J.M. (1967) Mediterranean benthos. *Oceanography and Marine Biology: An Annual Review* 5: 449-533.

Pérès, J.M., Picard, J. (1964) New manual of benthic bionomy of the Mediterranean Sea. *Recueil des Travaux de la Station Marine d'Endoume* 47: 3-137 (in French).

Piazza, P., Cummings, V., Guzzi, A., Hawes, I., Lohrer, D., Marini, S., Marriott, P., Menna, F., Nocerino, E., Peirano, A., Kim, S., Schiaparelli, S. (2019) Underwater photogrammetry in Antarctica: Long-term observations in benthic ecosystems and legacy data rescue. *Polar Biology* 42(6): 1061-1079.

Piazza, P., Cummings, V.J., Lohrer, D.M., Marini, S., Marriott, P., Menna, F., Nocerino, E., Peirano, A., Schiaparelli, S. (2018) Divers-operated underwater photogrammetry: Applications in the study of Antarctic benthos. *The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences* 42(2): 885-892.

Pizarro, O., Friedman, A., Bryson, M., Williams, S.B., Madin, J. (2017) A simple, fast, and repeatable survey method for underwater visual 3D benthic mapping and monitoring. *Ecology and Evolution* 7(6): 1770-1782.

Pouliquen, L. (1972) Sponges of the underwater caves of the Marseille region: ecology and systematics. Ecology and systematic. *Téthys* 3(4): 717-758 (in French).

Prado, E., Cristobo, J., Rodríguez-Basalo, A., Ríos, P., Rodríguez-Cabello, C., Sánchez, F. (2021) *In situ* growth rate assessment of the hexactinellid sponge *Asconema setubalense* using 3D photogrammetric reconstruction. *Frontiers in Marine Science* 8. doi: 10.3389/fmars.2021.612613.

Prado, E., Rodríguez-Basalo, A., Cobo, A., Ríos, P., Sánchez, F. (2020) 3D fine-scale terrain variables from underwater photogrammetry: A new approach to benthic microhabitat modeling in a circalittoral rocky shelf. *Remote Sensing* 12(15): 2466.

Price, D.M., Robert, K., Callaway, A., Lo Iacono, C., Hall, R.A., Huvenne, V.A. I. (2019) Using 3D photogrammetry from ROV video to quantify cold-water coral reef structural complexity and investigate its influence on biodiversity and community assemblage. *Coral Reefs* 38(5): 1007-1021.

Pulido Mantas, T. (2022) 3D Mapping of a Marine Cave, the Importance of Establishing a Baseline. In: 3rd Mediterranean Symposium on the Conservation of the Dark Habitats, 21-22 September 2022, Genoa, Italy.

Pulido Mantas, T. (2023) Innovative methodologies to assess multiscale structural complexity of marine benthic habitats. Doctoral Dissertation submitted to Università Politecnica delle Marche.

Pulido Mantas, T., Roveta, C., Calcinai, B., Coppari, M., Di Camillo, C.G., Marchesi, V., Montagna, M., Musco, L., Palma, M., Pica, D., Ponti, M., Cerrano, C. (2023) Photogrammetry as a promising tool to unveil marine caves' benthic assemblages. *Scientific Reports* 13(1): 7587.

Quiles-Pons, M., Díez, S., Goñi, R., Mallol, S., Maresca, F., Morató, M., Muñoz, A., Poloni, L., Díaz, D. (2022) Monitoring the Complex Benthic Habitat on Semi-dark Underwater Marine Caves Using Photogrammetry-based 3D Reconstructions. In: 3rd Mediterranean Symposium on the Conservation of the Dark Habitats, 21-22 September 2022, Genoa, Italy.

Raoult, V., David, P.A., Dupont, S.F., Mathewson, C.P., O'Neill, S.J., Powell, N. N., Williamson, J.E. (2016) GoPros™ as an underwater photogrammetry tool for citizen science. *PeerJ* 4. doi: 10.7717/peerj.1960.

Rastorgueff, P.A., Bellan-Santini, D., Bianchi, C.V., Bussotti, S., Chevaldonne, P., Guidetti, P., Harmeline, J.G., Montefalcone, M., Morri, C., Perez, T., Ruitton, S., Vacelet, J., Personnic, S. (2015) An ecosystem-based approach to evaluate the ecological quality of Mediterranean undersea caves. *Ecological Indicators* 54: 137-152.

Remondino, F., Del Pizzo, S., Kersten, T.P., Troisi, S. (2012) Low-cost and Open-source Solutions for Automated Image Orientation - A Critical Overview. In: Progress in Cultural Heritage Preservation 4th International Conference (eds., Ioannides, M., Fritsch, D., Leissner, J., Davies, R., Remondino, F., Caffo, R.) EuroMed, Springer, pp. 40-54.

Riedl, R.J. (1966) Biology of Sea Caves. Paul Parey, Hamburg, 636 p (in German).

Ríos, P., Prado, E., Carvalho, F.C., Sánchez, F., Rodríguez-Basalo, A., Xavier, J.R., Ibarrola, T.P., Cristobo, J. (2020) Community composition and habitat characterization of a rock sponge aggregation (Porifera, Corallistidae) in the Cantabrian Sea. *Frontiers in Marine Science* 7(578). doi: 10.3389/fmars.2020.00578.

Roach, T.N., Yadav, S., Caruso, C., Dilworth, J., Foley, C.M., Hancock, J.R., Harris, T., Holmes, D., LaScaleia, M., Leichter, J.J., Leon, J.X., Limer, B., Lohmann, B., MacRae, R., O'Brien, T.M., O'Connell, S., Smith, J., Williams, G. J., Madin, J.S. (2021) A field primer for monitoring benthic ecosystems using structure-from-motion photogrammetry. *Journal of Visualized Experiments* 170.

Robert, K., Huvenne, V.A.I., Georgiopoulou, A., Jones, D.O.B., Marsh, L., Carter, G.D.O., Chaumillon, L. (2017) New approaches to high-resolution mapping of marine vertical structures. *Scientific Reports* 7(1): 9005.

Romero, A. (2009) Cave Biology: Life in Darkness. New York: Cambridge University Press. doi: 10.1017/cbo9780511596841.

Russo, F., Del Pizzo, S., Di Ciaccio, F., Troisi, S. (2023) An enhanced photogrammetric approach for the underwater surveying of the *Posidonia* meadow structure in the Spiaggia Nera area of Maratea. *Journal of Imaging* 9(6): 113. doi: 10.3390/jimaging9060113.

Sariçam, S.Y., Erdem, U. (2010) Planning the Izmir-Karaburun Peninsula as a Biosphere Reserve Area. *Ekoloji* 19(77): 42-50 (in Turkish).

Selmo, D., Sturt, F., Miles, J., Basford, P., Malzbender, T., Martinez, K., Earl, G., Bevan, G. (2017) Underwater reflectance transformation imaging: A technology for *in situ* underwater cultural heritage object-level recording. *Journal of Electronic Imaging* 26(1): 011029-011029.

Skarlatos, D., Demestiha, S., Kiparissi, S. (2012) An 'Open' method for 3D modelling and mapping in underwater archaeological sites. *International Journal of Heritage in the Digital Era* 1(1): 1-24.

Skarlatos, D., Menna, F., Nocerino, E., Agrafiotis, P. (2019) Precision potential of underwater networks for archaeological excavation through trilateration and photogrammetry. *The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences* 42(2/W10): 175-180.

Snavely, N., Seitz, S.M., Szeliski, R. (2008) Modeling the world from Internet photo collections. *International Journal of Computer Vision* 80(2): 189-210.

Spaccavento, M., Tassetti, A., D'Errico, G., D'Annunzio, F., Palma, M., Pantaleo, U., Pica, D., Roccaforte, V., Spano, N., Valente, T., Cerrano, C. (2022) A Non-invasive Monitoring Method to Assess the Composition of Megabenthic Communities in Semi-submerged Marine Caves. IEEE International Workshop on Metrology for the Sea; Learning to Measure Sea Health Parameterspp. 257-261. doi: 10.1109/MetroSea55331.2022.9950848.

Spyksma, A.J.P., Miller, K.I., Shears, N.T. (2022) Diver-generated photomosaics as a tool for monitoring temperate rocky reef ecosystems. *Frontiers in Marine Science* 9. doi: 10.3389/fmars.2022.953191.

Teixidó, N., Garrabou, J., Harmelin, J.G. (2011) Low dynamics, high longevity and persistence of sessile structural species dwelling on Mediterranean coralligenous outcrops. *PLoS One* 6(8): e0023744.

Topaloğlu, B. (2019) Comparison of Two Small Marine Caves Located on Gökçeada Island (Northern Aegean Sea) and Büyükada Island (Marmara Sea) in Terms of Macrobenthic Cover. In: Marine Caves of the Eastern Mediterranean Sea Biodiversity, Threats and Conservation, (ed., Öztürk, B.), Turkish Marine Research Foundation Publication no. 53, Istanbul, Türkiye, pp. 186-194.

Torres-Pulliza, D., Charendoff, J., Couch, C.S., Suka, R., Gray, A., Lichowski, F., Amir, C., Lamirand, M., Asbury, M., Winston, M., Basden, I., Oliver, T.A. (2023) Processing Coral Reef Imagery Using Structure-from-Motion Photogrammetry: Standard Operating Procedures (2023 update) (NOAA Technical Memorandum NMFS-PIFSC-159). U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Pacific Islands Fisheries Science Center. doi: 10.25923/cydj-z260.

Turan, C., Uygur, N., Igde, M., Dogdu, S.A. (2019) Habitat Mapping of Underwater Bilge Tas Cave (Wisdom Stone Cave) in the Northeastern Mediterranean Sea: Structure and Biodiversity. In: Marine Caves of the Eastern Mediterranean Sea Biodiversity, Threats and Conservation, (ed., Öztürk, B.), Turkish Marine Research Foundation Publication no.53, Istanbul, Türkiye, pp. 195-206.

UNEP-MAP (2013) Eighteenth Ordinary Meeting of the Contracting Parties to the Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean and its Protocols. UNEP MAP, Istanbul, Türkiye.

UNEP-MAP-RAC/SPA (2016a) Montenegro: Platamuni and Ratac Areas. Mapping of Marine Key Habitats and Initiation of Monitoring Network. MedKeyHabitats Project.

UNEP-MAP-RAC/SPA (2016b) Montenegro: Platamuni and Ratac Areas. Summary Report of the Available Knowledge and Gap Analysis. MedKeyHabitats Project.

UNEP-MAP-RAC/SPA-OCEANA (2017) Guidelines for Inventorying and Monitoring of Dark Habitats in the Mediterranean Sea. SPA/RAC -Deep Sea Lebanon Project.

Vallicrosa, G., Fumas, M. J., Huber, F., Ridao, P. (2020) Sparus II AUV as a Sensor Suite for Underwater Archaeology: Falconera Cave Experiments. In: IEEE/OES Autonomous Underwater Vehicles Symposium, pp.1-5. doi: 10.1109/AUV50043.2020.9267935.

Westoby, M.J., Brasington, J., Glasser, N.F., Hambrey, M.J., Reynolds, J.M. (2012) 'Structure-from-Motion' photogrammetry: A low-cost, effective tool for geoscience applications. *Geomorphology* 179: 300-314.

Yokeş, B., Galil, B.S. (2006) New records of alien decapods (Crustacea) from the Mediterranean coast of Turkey, with a description of a new palaemonid species. *Zoosystema* 28(3): 747-755.

Yuval, M., Terán, F., Iñiguez, W., Bensted-Smith, W., Keith, I. (2025) Spatial variation in coral diversity and reef complexity in the Galápagos: Insights from underwater photogrammetry and new data extraction methods. *Remote Sensing* 17(11): 1831.