

First record of a remarkable *Cladocora caespitosa* bank in Aristotle's Lagoon (N Aegean Sea): Structure and health status

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Abstract

Cladocora caespitosa is a Mediterranean scleractinian that can form large bioconstructions. Once widespread, the IUCN classified this coral as Endangered (EN) as a consequence of severe population declines over the past two decades. This study provides the first quantitative description of a coral bank in the Gulf of Kalloni, Lesvos Island, Greece. Colony abundance, size, coral cover, attachment mode (i.e., fixed or unattached), percentage of necrosis, and species richness were recorded. Overall, 1505 colonies were assessed within a total area of 1080 m² and a depth range of 0.5-5.8 m. Approximately 20% of the colonies sampled were unattached. The most typical size range was 10-20 cm, but aggregated colonies (up to 203 cm in diameter) were frequently found. Coral density (5.2 ± 5.2 colonies m⁻², mean \pm SD; max = 34 colonies m⁻²) and coral cover ($22.0 \pm 34.4\%$) were negatively correlated with depth. Necrosis levels ($33.6 \pm 38.1\%$) were high, 46.5% of the colonies showing $\geq 10\%$ necrotic surface, 8.7% dead, while most necrosis was old. A total of 10 macrophyte and 63 animal taxa were identified in the wider bank area, including biotic aggregations of dead or live coral colonies. With an estimated core bank area of approximately 560 m², this population is one of the largest *Cladocora* banks in the Mediterranean, out of the fewer than 20 documented ones. Its proximity to smaller, isolated *C. caespitosa* bioconstructions suggests that the area is a hotspot for these coral formations and highlights the need for further monitoring and conservation actions.

Keywords: Scleractinia; coral bank; benthic community; marine biodiversity; necrosis; mapping; Mediterranean Sea; climate change.

Introduction

Cladocora caespitosa (Linnaeus, 1767) (Cladocoridae, Scleractinia), commonly known as cushion coral, is a zooxanthellate coral endemic to the Mediterranean that is considered as the only remnant of the ancient Mediterranean coral reef communities (Chefaoui *et al.*, 2017). It forms massive hemispherical colonies of branching tubular skeletons (Campbell, 1982), consisting of fragile, transparent, greenish-brown polyps within a frequently compact corallite of up to 10 cm high. It is a long-lived species, with low rates of growth and natural mortality, a high rate of juvenile mortality, and an estimated generation time of 30 years (Kružić & Požar-Domac, 2002; Kersting & Linares, 2012; Kersting *et al.*, 2014; Casado-Amezúa *et al.*, 2015).

Cladocora caespitosa plays an essential ecological

role as a bioconstructor, since it can generate stable carbonate frameworks that help consolidate the substrate and increase habitat complexity (Ingrosso *et al.*, 2018; Zunino *et al.*, 2018). In sheltered areas, aragonite building may be boosted by higher sedimentation rates, as fine sediments fill interstices among corallites, enhancing the build-up (Morri *et al.*, 2001). Additionally, the basal and apical parts of *C. caespitosa* can act as a habitat for many animals such as polychaetes, crustaceans and echinoderms, which either attach themselves to the coral, bore into its skeleton, find shelter or are enclosed in its ramifications (Chintiroglou, 1996; Pitacco *et al.*, 2017, 2021). When corals die, their calcareous remains, i.e., coral rubble, provide additional substrate for the settlement of other organisms (Ingrosso *et al.*, 2018). *Cladocora caespitosa* is primarily found as solitary scattered colonies, but, depending on hydrodynamic conditions (wave and cur-

rent exposure), type of substrata and seafloor morphology, this species may generate three distinct types of formations, namely (a) beds – dense populations of several small-sized colonies (10-30 cm in diameter); (b) banks – constituted by several large, interconnected colonies that cover several square meters and rise up to several decimetres in height; and (c) free-living (unattached) coral nodules or coralloliths, usually smaller than 10 cm in diameter (Peirano *et al.*, 1998; Morri *et al.*, 2000; Kersting *et al.*, 2017a, 2017b). Banks originate from beds under conditions of undisturbed accretion through three mechanisms: fusion of adjacent colonies, gravitational “pouring” of the mass and the inclusion of satellite colonies (Peirano *et al.*, 1998).

Cladocora caespitosa inhabits shallow, euphotic areas (0-40 m), across rocky or sandy substrates (Özalp & Alparslan, 2011). This species thrives in diverse environmental conditions, from well-lit shallow waters to areas of reduced light, due to its mixotrophic metabolism (Schiller, 1993). In low-light conditions (e.g., turbid or deep waters rich in organic content), *C. caespitosa* shifts from autotrophy to heterotrophic feeding, a strategy that significantly enhances skeletal growth (Anthony & Fabricius, 2000; Ferrier-Pagès *et al.*, 2013). However, exposure to excessive irradiance levels or elevated temperatures may lead to coral tissue atrophy and mass mortalities (Rodolfo-Metalpa *et al.*, 2005).

The distribution and abundance of *C. caespitosa* has substantially diminished across the Mediterranean Sea, as evidenced by its extensive fossil record (Fornós *et al.*, 1996; Kühlman, 1996; Aguirre & Jiménez, 1998; Bernas-

coni *et al.*, 1997; Dornbos & Wilson, 1999), and it has been suggested that this is due to climatic or ecological changes, or a combination of both (Laborel, 1987). Furthermore, large bioconstructions are becoming scarce as increasing anthropogenic pressure (e.g., coastal development and net or dynamite fishing) (Casado-Amezúa *et al.*, 2015) is having cumulative impacts on long-lived species over time. Currently, less than 30 living beds and less than 20 living banks of *C. caespitosa* have been documented in the Mediterranean Sea (Chefaoui *et al.*, 2017; Mačić *et al.*, 2019; Monnier *et al.*, 2021; Antoniadou *et al.*, 2023; Kersting *et al.*, 2023). The easternmost documented populations have been reported in Potamos Liopeetriou and Krio Nero, Cyprus (Jiménez *et al.*, 2016). In the northern Aegean Sea (NE Mediterranean), few *C. caespitosa* populations are known to form beds in the Gulfs of Siggitikos (Koukouras *et al.*, 1998), Thermaikos (Ganias *et al.*, 2023), Toroneos (Antoniadou *et al.*, 2023), and banks in Evoikos Gulf (Laborel, 1961), or discrete but abundant colonies around Gökçeada Island, Turkey (Guresen *et al.*, 2015) (Fig. 1). A dead *C. caespitosa* population has also been found in the Gulf of Pagasitikos (M.S., personal observation). In the rest of the Greek seas, records of *C. caespitosa* colonies are common but refer mainly to sightings of individual colonies and non-dense aggregations (Sini *et al.*, 2017).

The most apparent cause of the population decline of *C. caespitosa* is a rise in seawater temperature, especially the recurrent marine heat waves (MHWs) that are triggering mass mortality events or MMEs (Rodolfo-Metalpa *et al.*, 2005; Kersting *et al.*, 2013a; Kružić *et al.*, 2014; Gar-

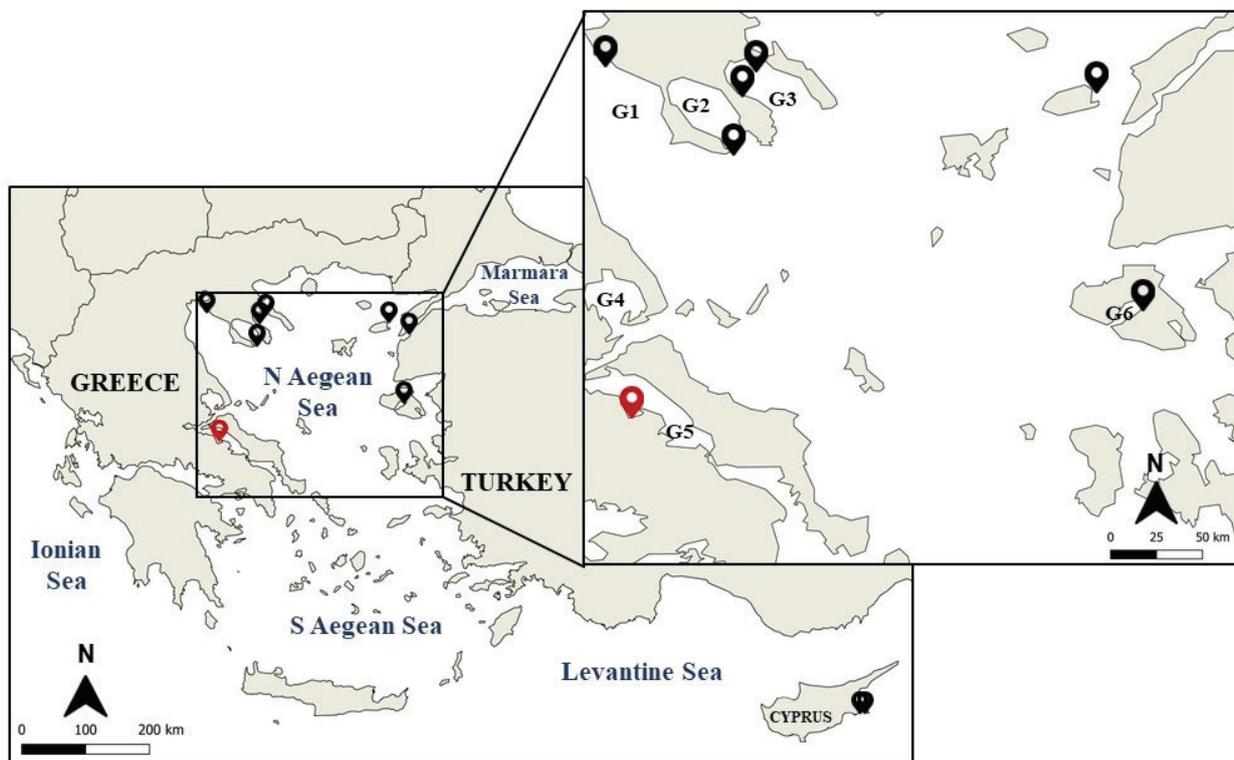


Fig. 1: Locations of *Cladocora caespitosa* aggregations studied in the eastern Mediterranean Sea. Red location markers represent populations of an indeterminate current status or dead. Inset: *C. caespitosa* populations exclusively in the north Aegean Sea. The following gulfs are indicated: G1 = Thermaikos, G2 = Toroneos, G3 = Siggitikos, G4 = Pagasitikos, G5 = North Evoikos, G6 = Kalloni.

rabou *et al.*, 2019, 2022). Other reported threats that have been associated with *C. caespitosa* declines include pollution and eutrophication (Kružić & Požar-Domac, 2007; El Kateb *et al.*, 2016), habitat degradation due to coastal development (Kersting *et al.*, 2023) and direct mechanical damage primarily caused by destructive fishing practices (Casado-Amezúa *et al.*, 2015; Ganiás *et al.*, 2023), anchoring (Mačić *et al.*, 2019) and several biotic stressors such as outbreaks of corallivorous organisms (Kružić *et al.*, 2013), the spread of invasive algae (Kersting *et al.*, 2015) and blooms of mucilaginous algal aggregates (De Biasi *et al.*, 2021). Colonies under thermal stress typically display partial or full necrosis (i.e., progressive tissue loss with no apparent zooxanthellae loss - Rodolfo-Metalpa *et al.*, 2005; Kersting *et al.*, 2013a) and, in some cases in the eastern Mediterranean, bleaching (i.e., loss of colour due to the expulsion of symbiotic dinoflagellates, which produce the photosynthetic pigments; Kružić *et al.*, 2014).

Individual colonies may recover relatively fast from partial bleaching (Kružić *et al.*, 2014). In certain cases, isolated polyps found within necrosed colonies may also recover after a transitory resistance phase through a process known as rejuvenescence (Kersting & Linares, 2019). Nevertheless, reports of this mechanism are limited and its exact trigger remains unclear. As a result, recovery at population level principally relies on the overgrowth of healthy polyps via asexual reproduction (López-Márquez *et al.*, 2021), or the settlement of new recruits and the establishment of new colonies through sexual reproduction (Kersting *et al.*, 2013a). Given the low recruitment and juvenile survival rates, low dispersal capacity of planulae over long distances and, hence, high dependence of distinct populations on self-recruitment (Casado-Amezúa *et al.*, 2014; López-Márquez *et al.*,

2021), the recovery potential of this species is not sufficient to compensate the fast rate of population decline, which may persist or intensify in view of future climate change-driven conditions (Kersting *et al.*, 2013a; Garra-bou *et al.*, 2019, 2022).

A decade ago, in 2015, the IUCN classified *C. caespitosa* as Endangered (EN) on the Red List of Threatened Species and highlighted the need to advance scientific knowledge of its ecology and distribution. This designation also stressed the importance of expanding the assessment and monitoring of key subpopulations to support its conservation and long-term survival (Casado-Amezúa *et al.*, 2015). Within this framework, the current study describes a previously unknown *C. caespitosa* community in the Gulf of Kalloni, Lesvos Island (N Aegean Sea), in order to provide essential baseline data for its future monitoring and conservation.

Materials and Methods

Study site

The Gulf of Kalloni (39.171°N, 26.290°E), located in Lesvos Island (NE Aegean Sea) (Fig. 2), is a large, semi-enclosed bay that is connected to the sea through a narrow 4 km-long channel. It has a surface area of 110 km², a maximum length of 22 km and a width of 10 km. It has an average and maximum depth of 10 m and 25 m, respectively. Seawater is replenished by strong currents that are particularly intense at the strait of the gulf, with various factors modulating their intensity and direction, e.g., tidal forces and prevailing winds (Kolovoyiannis *et al.*, 2018; Mamoutos *et al.*, 2018; Petalas *et al.*, 2020). Seawater temperature displays a wide seasonal range,

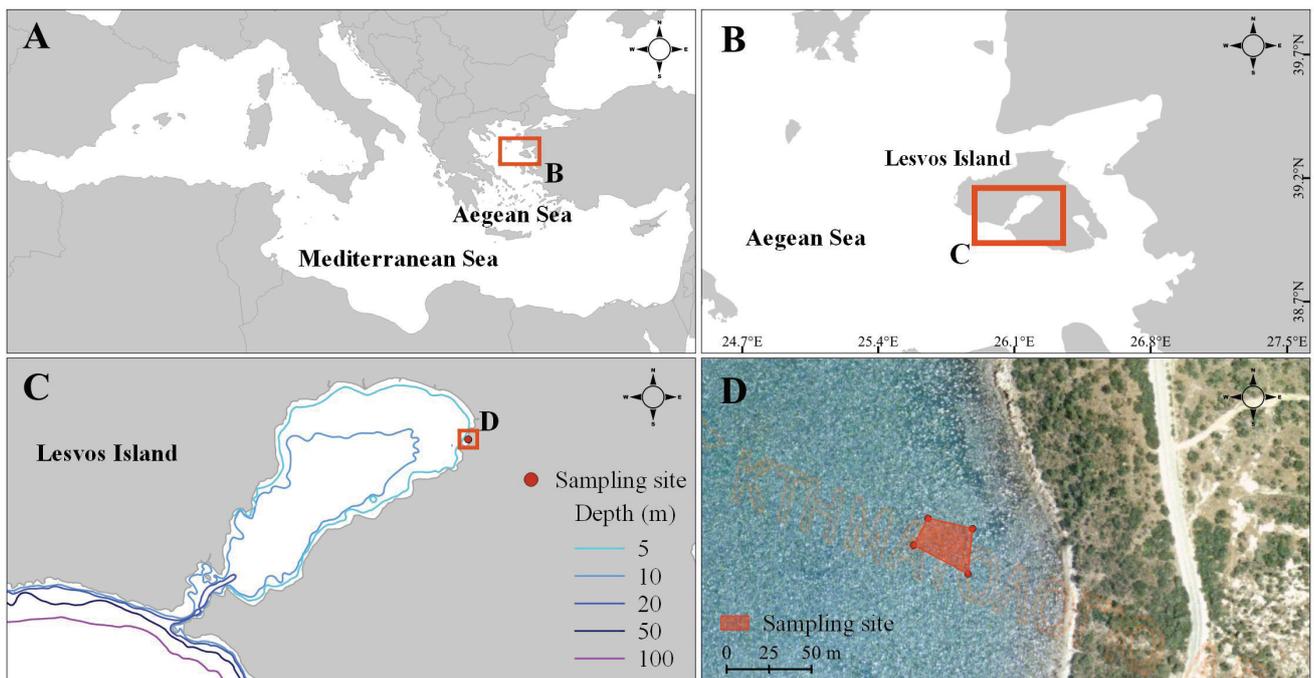


Fig. 2: Location of the study area. A) Map of the Mediterranean Sea. B) Lesvos Island, north-eastern Aegean Sea. C) Kalloni Gulf and its bathymetry. D) Delimitation of the *Cladocora caespitosa* sampling site, north-eastern Kalloni Gulf.

from 6.5°C in January to 30.5°C in August (2020–2021, unpublished data), and an equally broad salinity range, which may vary from 34 psu in winter to 41 psu during the summer (Spatharis *et al.*, 2007; Papantoniou *et al.*, 2015; Kolovoyiannis *et al.*, 2018). The Gulf of Kalloni is a highly productive ecosystem, hosting rich biodiversity and numerous valuable habitats (Evangelopoulos & Koutsoubas, 2008; Kefalas *et al.*, 2016; Topouzelis *et al.*, 2016; Sini *et al.*, 2019; Zotou *et al.*, 2020), and is included in the Natura 2000 European network of protected areas (Site Code: SCI GR4110004). The site's rich biodiversity is also reflected in its informal name, "Aristotle's Lagoon" (Williams, 2010), since Aristotle's biological work, *Historia Animalium*, was largely based on his observations of the living organisms in the area (Voultsiadou *et al.*, 2017). Nevertheless, the area is highly impacted by human activities primarily related to overfishing, illegal fishing, poaching of molluscs, and pollution caused by agricultural run-off (e.g., Koutsoubas *et al.*, 2007; Spatharis *et al.*, 2007; Nikolaou *et al.*, 2024).

Satellite imagery

Following the first sighting of the *C. caespitosa* assemblage during a SCUBA diving survey in 2019, a World View -2 (WV-2) satellite image (acquisition of 7 Oct 2012) was analysed in order to locate other similar structures in the Gulf of Kalloni. The WV-2 has 8 spectral bands from 400 nm to 1050 nm and a panchromatic band covering 450-800 nm. The WV-2 image was pansharp-ened to 1 m spatial resolution using the panchromatic band and then land-masked using the infrared band.

Underwater sampling

Sampling took place during May-June 2022 through SCUBA surveys. An underwater grid was set up using ropes to delimit the area of the *C. caespitosa* assemblage. Transect lines were fixed every 2 m to subdivide the grid into 4-m² grid cells. Within each 4-m² grid cell, an area of 1 m² was sampled using a quadrat frame that was placed at the lower right corner of the grid cell. The number of colonies, attachment mode (i.e., fixed or unattached), major colony axis (D1, i.e., maximum diameter; cm) and minor colony axis (D2, i.e., the maximum distance perpendicular to D1; cm), percentage of necrosis (i.e., the proportion of colony surface area – SA – that underwent tissue loss relative to its total SA; %), the type of injuries (necrotic tissue, burial, breakage) and the epibiotic organisms were recorded *in situ* in each grid cell. Fused colonies were treated as a single colony. If a colony was intersected by the transect lines/ropes, it was counted only if its centre fell within the quadrat. Unattached colonies were counted solely for calculating colony abundance and were assessed only if their D1 was ≥9 cm. This size threshold was applied to reduce the time needed to search, handle and assess all small unattached colonies. Necrosis was visually estimated according to the follow-

ing classes: 0-10%, 10-25%, 25-50%, 50-75%, 75-99% and 100%. Colonies with necrosis covering <10% of their total SA were classified as healthy, according to Kersting *et al.* (2013a), whereas colonies with ≥10% necrosis were classified as affected, and considered dead if necrosis was 100%. Colony sections covered by sludge were noted but not classified as necrosed if the underlying colony tissue and polyps remained alive. If epibiotic organisms (e.g., macroalgae, sponges, bivalves) were attached to a colony, the underlying SA was classified as affected only if the coral tissue appeared necrosed. The number of colonies with partial loss due to breakage was also recorded, with separate fragments that appeared to belong to a single large colony being counted as one. All macrobenthic species observed within the sampling area during the surveys were recorded for quantitative biodiversity assessment, and underwater photographs of selected organisms were taken to facilitate species identification. Depth (for each grid cell) and temperature were recorded using dive computers. Signs of human pressure were reported when detected.

Data handling and statistical analyses

The values recorded within each quadrat frame (1 m²) were used to make inferences at grid cell level (4 m²). The number of colonies recorded per quadrat frame was used to assess coral density (colonies m⁻²), and the ratio of fixed versus unattached colonies was also calculated.

Colony surface area (SA; cm²) was estimated by approximating the geometry of the colonies to that of a circle (D1 = D2) or an ellipse (D1 ≠ D2) (Kersting & Linares, 2012), using the following equation:

$$SA = \pi \cdot \left(\frac{D1}{2}\right) \cdot \left(\frac{D2}{2}\right)$$

Mean live coral cover (CC; %) per quadrat frame was calculated based on the SA data of colonies presenting <10% necrosis, divided by the total surface of the quadrat.

All colonies recorded (both dead and live) were segregated into seven size classes, based on D1 (cm): D1 ≤10, 10 < D1 ≤20, 20 < D1 ≤30, 30 < D1 ≤40, 40 < D1 ≤50, 50 < D1 ≤100 and >100. Mean necrosed SA was then depicted in relation to size class.

Collected data was statistically processed using MATLAB R2020b (The MathWorks Inc., 2020). Descriptive statistics were used to estimate the size-frequency distribution of the population, based on the D1 values of the colonies displaying <100% necrosed SA (Kersting & Linares, 2012). A Kolmogorov-Smirnov (K-S) test was applied to ascertain whether the data were normally distributed, and the skewness (g₁) and kurtosis (g₂) coefficients were calculated. Their respective confidence intervals and standard errors (SE) were computed based on a bootstrap method (Gardner-O'Kearny, 2021). g₁ and g₂ were considered significant if the ratio to their SE was >2 (Wright & Herrington, 2011). A significant value for skewness means that the size structure presents an asym-

metric distribution, with *positive skewness* values indicating a prevalence of the smaller size classes, and *negative skewness* signifying a prevalence of the larger size classes. On the other hand, *positive kurtosis* expresses a more peaked distribution (i.e., leptokurtic), while *negative kurtosis* is indicative of a flatter distribution (i.e., platykurtic) (DeCarlo, 1997).

Correlation analyses were performed between the following parameters: depth and coral density (based on total density m⁻² per grid cell), depth and colony diameter, depth and live coral cover (based on total cover per grid cell), depth and necrosed SA, colony SA and necrosed SA, and coral density and necrosed SA (both based on mean values per grid cell). A 95% significance level ($p < 0.05$) was established for all statistical analyses carried out. Distribution maps of coral abundance, CC and mean necrosed SA were generated from the aforementioned data, and a list of all organisms associated with or close to the colonies was compiled.

Results

Satellite imagery

From the processed satellite images (Fig. 3), four visually similar biogenic structures were identified apart from the biogenic structure under study (Fig. 3B, D).

Ground truth sampling revealed two smaller *C.*

caespitosa-dominated assemblages: one located approximately 100 m away from the assemblage under study (Fig. 3B, E), and one located approximately 1 km away in a nearby embayment (Fig. 3B, C), as well as a rocky reef with dense molluscan agglomerations (approximately 5-10 cm long per individual mollusc; Fig. 3B, F).

General description of the area

The study area covers 1080 m² over both hard and soft substrates at 0.7-5.8 m depth (Fig. 4), while the core bank (which comprises a large, continuous, *C. caespitosa*-dominated assemblage) was estimated to cover around 560 m². The coral community exhibits a clear spatial pattern. The central parts of the community (i.e., the core *C. caespitosa* bank), host a high density of colonies, sometimes growing in multiple layers (i.e., one colony growing on top of another) over hard substrates, such as rock, old coral skeletons or other biogenic substrate of unknown origin. In this central zone, *C. caespitosa* colonies alternate with patches of molluscan agglomerations, which are especially prominent in the shallower sections (Fig. 5A). In the peripheral zone, *C. caespitosa* colonies are sparsely distributed, and are found either rooted or / embedded in the thick muddy substrate by means of their own weight, or lying unattached from the muddy bottom, while some small colonies are attached to the remains of other animals (such as molluscan shells, e.g., dead *Pinna*

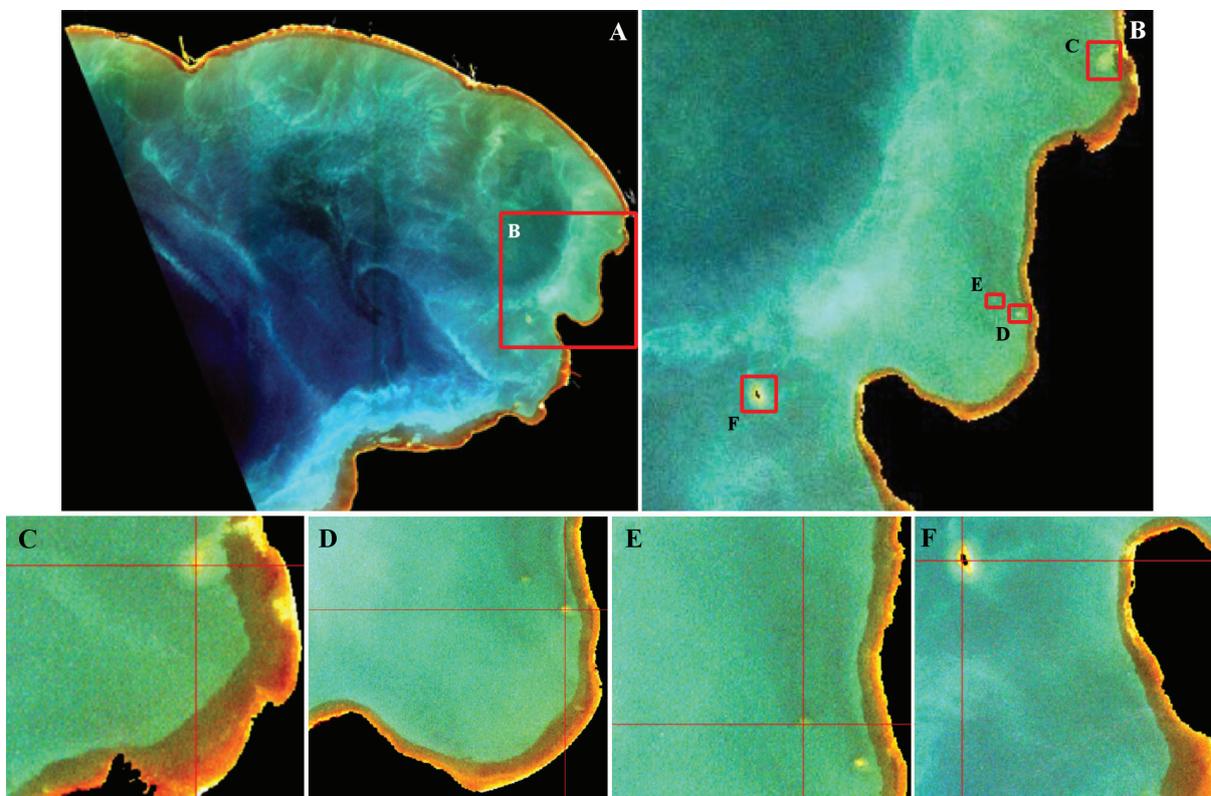


Fig. 3: Satellite images (7 October 2012) showing the N-NE part of the Kalloni Gulf, Lesvos Island, Greece (A), and the location of biogenic structures (B-F). Red rectangles and associated letters show the position of the respective images. Red crossed lines in images C-F indicate the exact position of the different structures. Images C-E correspond to *C. caespitosa*-dominated assemblages. Image D corresponds to the *C. caespitosa*-dominated assemblages of this study. Image F refers to a mollusc-dominated assemblage.

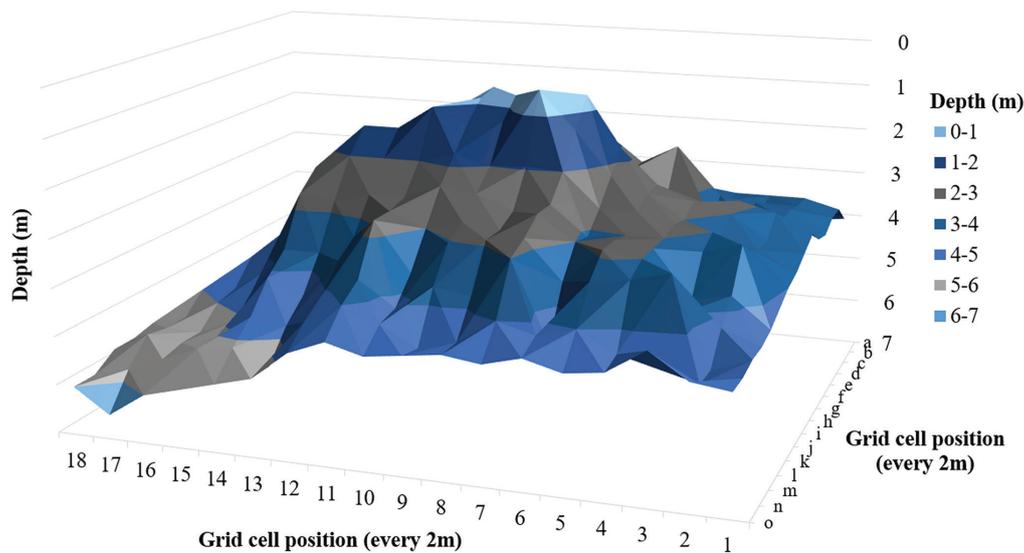


Fig. 4: Bathymetric profile of the *Cladocora caespitosa* bank in Kalloni Gulf, Lesvos Island, Greece. Colours denote different depth zones in meters (y axis). The numbers (1-18) and letters (a-o) of the grid cells are indicated in the x and z axes, respectively.

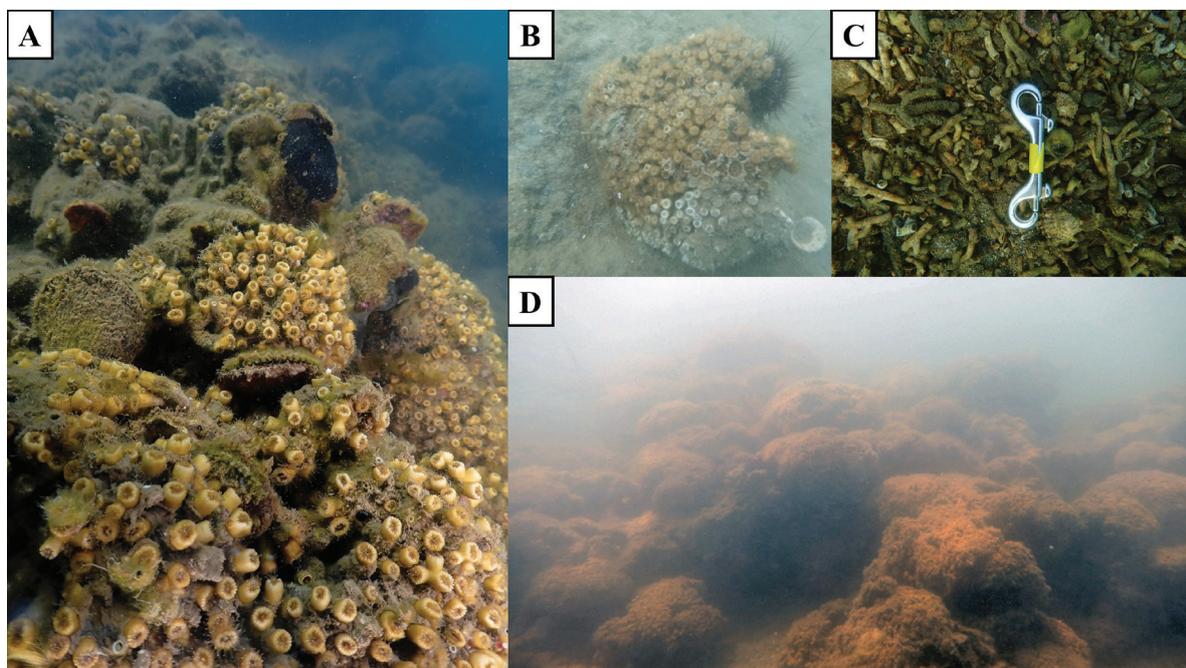


Fig. 5: *Cladocora caespitosa* coral bank in Kalloni Gulf, Lesvos Island, Greece. A) Healthy *C. caespitosa* colonies in association with bivalves (photograph provided by G. Pitarra). B) Free-living *C. caespitosa* colony showing partial necrosis due to sediment burial (photograph provided by N. Quintano). C) Area with a high prevalence of *C. caespitosa* coral rubble (double-ended bolt snap size: 10 cm; photograph provided by E. Kytinou). D) General overview of a section of the coral bank (photograph provided by K. Tsirintanis).

nobilis shells). In the surrounding area, the seabed is flat and uniform, composed of muddy sediments, with abundant dead fragments and buried colonies of *C. caespitosa*, and few scattered patches of the seagrass *Cymodocea nodosa* (Ucria) Ascherson, 1870. Due to the substrate composition, the visibility in the area was generally around 2 m (but often less than 1 m), while light intensity was particularly low, giving an overall impression of being in much deeper waters. During fieldwork, water temperature ranged between 23 and 24°C.

Several human activities that may exert pressure on

the *C. caespitosa* bank were observed. Evidence of boat collision was found at the shallowest tip of the structure, where a small section of thin rock at 0.5 m depth appeared broken and stained blue – likely due to contact with a boat hull. Set trammel nets were documented once, approximately 5 m away from the *C. caespitosa* colonies, while a few lost fishing lines were also found around the colonies. Molluscan poaching was once observed directly within the coral community, where numerous molluscan species inhabit the assemblage. Furthermore, trolling is a common fishing practice in the surrounding area.

Population assessment

Overall, a total of 1505 *C. caespitosa* colonies were assessed, out of which 78.9% were fixed to the substrate and represent the core of the coral bank (Fig. 5A, D), and 21.1% were unattached and primarily found on the adjacent muddy substrates (Fig. 5B; Fig. 6A). Certain parts of the study area were densely covered by coral rubble (Fig. 5C), while 39 small, free-living colonies (i.e., D1 < 9 cm) and >700 coral fragments were counted but excluded from further analysis.

As regards the study area as a whole (including the core bank and the surrounding mudflat), mean coral density was estimated to be 5.2 ± 5.2 colonies m^{-2} (\pm SD), with grid cell 13i (named following the x and y axes in Fig. 6) displaying maximum coral density (34 colonies m^{-2}), followed by 3h (29 colonies m^{-2}) and 3i (27 colonies m^{-2}) (Fig. 6A). On the contrary, areas with no coral presence became less frequent from the deeper surroundings of the coral bank – where muddy substrates prevail – to the central, shallower parts of the bank (e.g., in grid cells 9g, 5i, 15f, 15k) – where limited sediment-covered parts of rocky substrate and biogenic concretions were found. A significant, moderate negative correlation ($r = -0.541$, $p < 0.005$) was found between coral density and depth (Fig. 7A).

Colony size, based on D1 values, ranged from 1 cm (in 10c) to 203 cm (in 4m) for fixed colonies, while the largest unattached live colony (but showing 50% necrosis) reached 47 cm (in 16h). The largest unattached, dead (old necrosis) colony had a D1 of 92 cm (in 14n). Considering live colonies as a whole (i.e., <100% necrosis, $N = 1373$), mean colony size was 22.8 ± 19.3 cm, while the size-frequency distribution revealed a non-normal distribution (K-S), with significant, highly positive skewness ($g_1 = 3.305$; SE = 0.414; Sig. (> 2) = 7.977) and kurtosis ($g_2 = 18.310$; SE = 4.360; Sig. (> 2) = 4.200). These results indicate the prevalence of small-sized colonies in the population (Fig. 8). The 10-20 cm size class predominated (37.6%), followed by ≤ 10 cm (21.8%) and 20-30 cm (20.6%) size classes, while 15 colonies (corresponding to 1%) were particularly large, with D1 > 100 cm. No significant correlation was found between depth and colony diameter ($r = 0.032$, $p = 0.215$).

Coral cover greatly varied between grid cells across the entire study area, with a mean value of $22.0 \pm 34.4\%$ (Fig. 6B). Live coral cover values exceeding 100% were obtained in areas where very large colonies (D1 > 100 cm) were recorded with several overlapping layers of coral surface (Fig. 5D), e.g., 258.4% in 4m, where the largest colony was found (D1 = 203 cm, D2 = 144 cm), at 3.2 m depth; 250.5% in 4c, where 18 colonies were recorded, 5 of them with D1 > 50 cm (the largest colony being D1 = 100 cm, D2 = 65 cm) and 180.6% in S6d (with a colony D1 = 202 cm, D2 = 97 cm). As for coral density, the number of grid cells with no coral cover decreased from the deeper mud-dominated surroundings of the bank to the shallower, central parts (with an increased presence of rocky and biogenic substrate patches). A significant, low negative correlation ($r = -0.462$, $p < 0.005$) was found between live coral cover and depth (Fig. 7B).

Health status assessment

Among the surveyed colonies, 43.6% were healthy, with minimal or no necrosis (<10% of colony SA; e.g., Fig. 5A), 46.5% were affected by necrosis (i.e., $10\% \leq$ necrosis <100%; e.g., Fig. 5B); and 8.7% were dead (i.e., 100% of their SA necrosed) (Fig. 6C; Fig. 9). Overall, the mean percentage of necrosis was found to be $33.6 \pm 38.1\%$ of the SA, increasing to $52.6 \pm 29.0\%$ when considering only those colonies affected by necrosis (i.e., excluding dead and healthy colonies; $N = 706$). Among the necrosed colonies, 53.5% exhibited signs of old necrosis (i.e., presence of epibionts and black encrusted skeletons, presumed to be >6 months old), 22.5% showed signs of recent necrosis (i.e., denuded corallites, necrosis presumed to be <6 months old), and 23.9% displayed both old and recent necrosis. Moreover, 18.8% of all the live colonies (<100% of necrosed SA; $N = 1367$) were found to be at least partly covered by mud (Fig. 5B), and 6.3% had broken parts.

With regards to size, D1 values of 40-50 cm, 50-100 cm and >100 cm were associated with a higher percentage of necrosed colonies (i.e., 7.7%, 7.6%, and 6.7%, respectively) than the intermediate size classes (30-40 cm: 6.4%, 20-30 cm: 6.1%, 10-20 cm: 5.7%), while the smallest size class (≤ 10 cm) had the lowest number of necrosed colonies (Fig. 8). Overall, affected colonies showed a significant, negative correlation between colony SA and percentage of necrosis (i.e., the larger the colony SA the smaller the percentage of necrosis; $r = -0.148$, $p < 0.005$). However, no significant correlation was found between necrosed SA ($r = -0.027$, $p = 0.312$) or coral density ($r = 0.013$, $p = 0.087$) and depth.

Biodiversity assessment

A total of 73 taxa / morphotaxonomic groups were recorded around the bank, on the colonies and within the crevices created by the *C. caespitosa* colonies. These taxa belong to 12 phyla, namely Chlorophyta (3 taxa/morphotaxa), Ochrophyta (3), Rhodophyta (3), Tracheophyta (1), Porifera (9), Bryozoa (3), Cnidaria (6), Mollusca (14), Annelida (4), Arthropoda (4), Echinodermata (8) and Chordata (15) (Table S1). The most common epibiotic taxa/morphotaxonomic groups were turf algae, found in 21.2% of the total number of colonies ($N = 1505$), followed by Porifera (11.7%), Bivalvia (2.0%), Bryozoa (1.5%), encrusting calcareous algae (1.4%) and Cnidaria (1.2%), while Annelida - Polychaeta and Chordata - Ascidiacea were found as epibionts in less than 1% of the colonies.

Some parts of the bank were covered by agglomerations of molluscs (Fig. 4A), such as clams and oysters, including the non-indigenous species *Dendostrea folium* (Linnaeus, 1758), while some patches of the seagrass *Cymodocea nodosa* were also found in the surroundings of the coral bank.

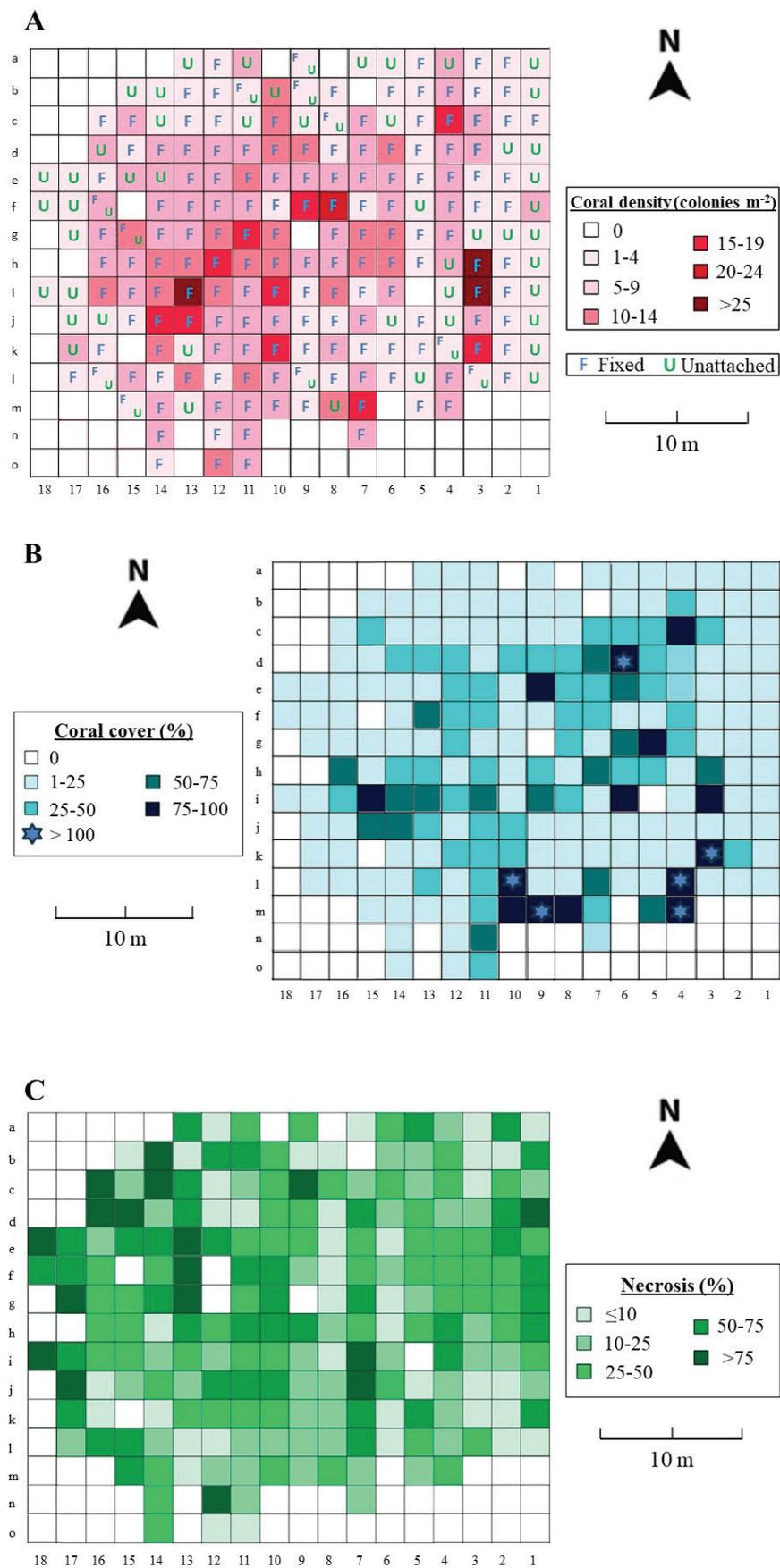


Fig. 6: Distribution maps divided into 4 m² grid cells overlaid on the *Cladocora caespitosa* community under study in the Kalloni Gulf, Lesvos Island, Greece, showing (A) colony abundance and the most prevalent (>50% colonies in the grid cell) association of coral colonies with the substrate (i.e., fixed or unattached), (B) live coral cover, and (C) mean percentage of necrosed colony surface area. The position of the different grid cells is identified by a specific number (1-18) and letter (a-o) on the x and y axes, respectively. The values displayed in each grid cell were obtained per m² (i.e., using the quadrat frame).

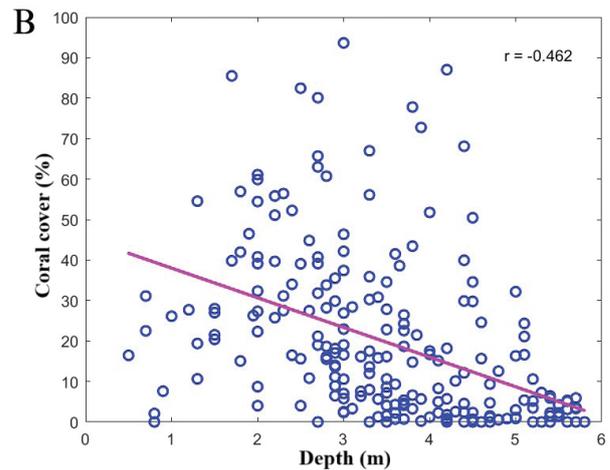
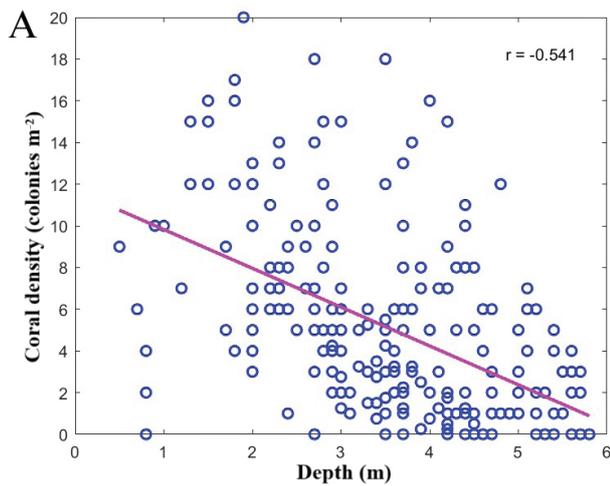


Fig. 7: Correlation plots between (A) coral density and depth (based on total density per grid cell), and (B) live coral cover and depth (based on total cover per grid cell) of the *Cladocora caespitosa* bank in Kalloni Gulf, Lesvos Island, Greece (N = 1505); r indicates the correlation coefficient.

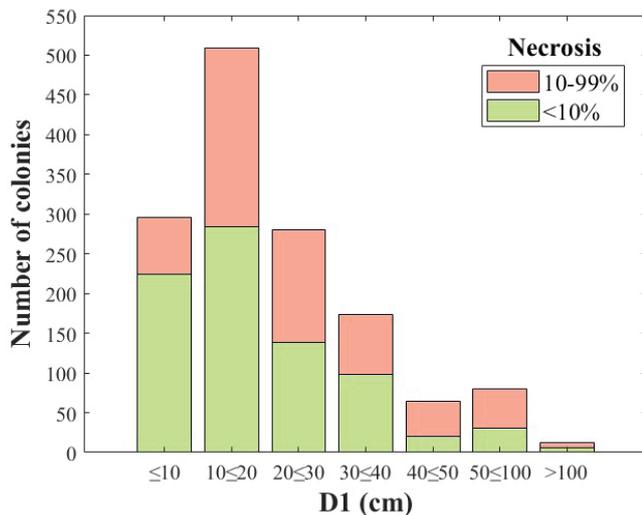


Fig. 8: Size-frequency distribution based on the maximum diameter (D1) of *Cladocora caespitosa* colonies sampled (N = 1505) in the coral community of Kalloni Gulf, Lesvos Island, Greece. The percentage of necrosis is displayed within each size class.

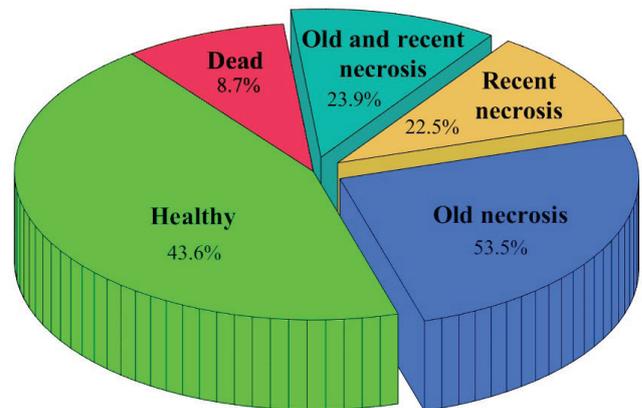


Fig. 9: Healthy (<10% necrosed surface area), affected by necrosis (≥10%-99%, subdivided into categories based on age) and dead (100%) *Cladocora caespitosa* colonies assessed (N = 1505).

Discussion

Our findings suggest that the studied coral bioconstruction in Kalloni Gulf can indeed be classified as a *C. caespitosa* bank, since it is mainly composed of various interconnected colonies, sometimes reaching over 1 m in height (*sensu* Monnier *et al.*, 2021). In sheltered areas such as gulfs, reduced hydrodynamic forces encourage the growth of large coral colonies, which often merge into extensive coral banks as adjacent colonies come into contact (Kružić *et al.*, 2008; Kersting & Linares, 2012; Kersting *et al.*, 2023). With an estimated surface area of 560 m², this *C. caespitosa* bank ranks among the largest in the Mediterranean Sea, comparable to those in the Marine Reserve of the Columbretes Islands, Spain (cumulative cover area of 2,900 m²; Kersting *et al.*, 2013a) and Veliko Jezero in the Mljet National Park, Croatia (650 m² bank; Kružić *et al.*, 2014). Although the majority

of colonies on the bank under study are fixed onto hard substrate (including rock, old dead colonies, molluscan shells and secondary biogenic substrate of unknown origin), a high percentage is unattached or loosely rooted in the surrounding muddy substrate, including colonies that are larger than the average unattached colonies (D1 = 38 cm) and do not present signs of injury. Similarly, Kersting *et al.* (2017a) described a *C. caespitosa* bed in the waters of the islet of Espardelló, Spain, characterised by a large number of unattached colonies. Coral rubble, which is generally considered to be more abundant in areas with increased coral mortality (Sánchez-Quinto & Falcon, 2021), was quite abundant in certain sections of the study area.

Focusing on the spatial distribution of the corals on the studied bank, the highest coral density values are located in the central part of the bank, whereas the lowest was found along the boundaries of the area, where muddy substrates prevail. Likewise, the proportion of colonies

attached to the substrate tends to diminish from the centre to the edges of the bank. Remarkably, coral density on Kalloni bank ($\bar{x} = 5.2 \pm 5.2$ colonies m^{-2} ; $\max = 34$ colonies m^{-2}), is among the highest reported, comparable to the Meloria Shoals ($\bar{x} = 3.4$ colonies m^{-2} ; De Biasi *et al.*, 2021), and Bocca di Magra, Punta Bianca and Fiascherino, Italy ($\bar{x} = 2.9, 4.0,$ and 1.9 colonies m^{-2} , respectively), with a notable maximum density of 8 colonies per m^{-2} at Punta Bianca, Italy (Peirano *et al.*, 2001), and Illa Grossa Bay, Columbretes Islands (maximum density of 5.5 colonies per m^{-2} ; Kersting & Linares, 2012).

Regarding the size of the colonies, mean colony size ($D1 = 22.8 \pm 19.3$ cm) is greater than that of the colonies recorded in the Gulf of Trieste, northern Adriatic (11.6 ± 7.5 cm; Zunino *et al.*, 2018), Boka Kotorska Bay in the eastern Adriatic (common $D1$ range of 5-10 cm, with few colonies larger than 15 cm; Mačić *et al.*, 2019) and Tremiti Islands in the southern Adriatic (70-95% of the colonies smaller than 10 cm $D1$; Chimienti *et al.*, 2025), and lower than Illa Grossa Bay, Columbretes (31.5 ± 21.0 cm; Kersting & Linares, 2012). As also observed in the Kalloni Gulf, smaller and medium-sized colony classes usually dominate in the majority of the reported *C. caespitosa* bioconstructions, e.g., in the Gulf of Trieste, Piran, Slovenia, (Zunino *et al.*, 2018), Bocca di Magra, Punta Bianca and Fiascherino (Peirano *et al.*, 2001); and Cape Madonna, Piran, Slovenia (Kružić *et al.*, 2014). On the contrary, large colonies (i.e., above 1 m in diameter) are usually rare on *C. caespitosa* banks, with the maximum diameter being recorded in Kalloni Gulf (203 cm; present study), followed by the Veliko Jezero bank (up to 100 cm; Kružić & Požar-Domac, 2003) and the Columbretes Islands (150 cm; Kersting & Linares, 2012). Whereas the existence of several fused, large colonies enhances the structural complexity of a bank, a high abundance of small colonies (21.8% had a $D1 \leq 10$ cm in the population studied in Kalloni Gulf) is indicative of a high level of recruitment (Peirano *et al.*, 2001), which is vital for the persistence of the population. Future studies should focus on the survival and growth rates of the *C. caespitosa* colonies of this population in order to elucidate its dynamics and long-term survival.

As regards the importance of depth as a structuring factor of the *C. caespitosa* bioconstructions, our results, along with data available in the literature, suggest that depth alone does not exert a primary influence. Instead, its effect is often obscured by other environmental factors, such as light, type of substrate, sedimentation, bottom currents and wave exposure, which appear to have a more intricate influence on population structure and type of formation. In Kalloni Gulf, we found a negative correlation between both coral density and depth, and coral cover and depth, while no correlation was found between colony diameter and depth. These results are in agreement with the study of Zunino *et al.* (2018), who reported a decrease in coral abundance over the first few metres of the water column (3-5.5 m), but contrast with the findings of Kersting *et al.* (2017b), who found a positive relationship between depth and coral cover attributed to higher wave exposure at shallower depths. As

Kalloni is a semi-enclosed bay, wave action is expected to have a lower impact on corals found in the inner parts of the gulf, thus allowing them to grow at shallower depths rather than in more exposed areas. Moreover, the observed decrease in coral density with depth is probably related to the gradual reduction of hard substrate and its substitution by muddy sediments, resulting in a dramatic reduction of light availability due to increased turbidity caused by resuspension of muddy sediments. On the other hand, with regards to colony size, Zunino *et al.* (2018) showed that colonies had a tendency to be larger with depth, whereas several studies report on coral colonies reaching larger sizes (Bak & Meesters, 1999) and higher energy reserves (Anthony, 2006) under conditions of increased sedimentation and turbidity. Regardless of the high turbidity and sedimentation levels observed in Kalloni, colony diameter was not correlated with depth, as also observed by Kersting & Linares (2012). Our study also found a negative correlation between colony size and necrosis, which contrasts with the results of Rodolfo-Metalpa *et al.* (2005) and Azzola *et al.* (2022) obtained in the eastern Ligurian Sea, and Quintano *et al.* (2025) in the north-western Mediterranean.

Another remarkable feature of the *C. caespitosa* bank in Kalloni Gulf is the abundance of corals thriving on the surrounding muddy sediments. Typically, *C. caespitosa* colonies establish on hard substrates, ranging from large rocky surfaces and small boulders to mollusc shells, or exist as free-living nodules on sand (Özalp & Alparslan, 2011; Zunino *et al.*, 2018). They are rarely found on muddy sediments unless a secondary hard substrate – such as old coral skeletons, shells or other naturally occurring or artificial structures – is present in the mud, which facilitates larval settlement (Zunino *et al.*, 2018; Mačić *et al.*, 2019). However, in the Gulf of Kalloni, a substantial number of colonies are observed directly anchored on the muddy substrate surrounding the core bank. These colonies include both large coral fragments ($D1 > 20$ cm), which may be former parts of some parent colonies that have been fragmented either through natural processes (e.g., increased weight) or through mechanical damage, and remain stabilised in the mud by means of their own weight, as well as smaller colonies that have settled on the skeletal remains of other organisms, e.g., bivalves. Furthermore, several colonies were also found among small patches of the phanerogam *C. nodosa*, similar to other *C. caespitosa* beds and banks, which have been found to thrive among *Cystoseira* forests and *Posidonia oceanica* meadows (Özalp & Alparslan, 2011; Kersting *et al.*, 2017b; Pons-Fita *et al.*, 2020; Monnier *et al.*, 2021).

Coral communities are known to be among the most diverse ecosystems harbouring high levels of biotic associations and interactions. Whereas the host provides food and complex three-dimensional biostructures that enhance the availability of refuges and micro-habitats for other species (Stella *et al.*, 2011; González-Rivero *et al.*, 2017), the associated organisms (e.g., fan worms, hydrozoans and sponges) can protect corals against warming or predators (DeVantier *et al.*, 1986; Montano *et al.*, 2017); in some cases through the synthesis of benefi-

cial chemical and metabolic products for the coral host (Hentschel *et al.*, 2001; Thoms *et al.*, 2006) and zooxanthellae (Pawlik *et al.*, 2007). Moreover, the abundance of certain sessile invertebrates that rely on hard substrates (e.g., mollusc) is known to be directly affected by coral density (e.g., Mohammed & Yassien, 2008). Studies on the biodiversity of *C. caespitosa* communities and bioconstructions in the Mediterranean Sea remain scarce, but the few available studies report on a high biodiversity of benthic macrofauna. For example, Antoniadou & Chintiroglou (2010) identified 31 megabenthic and 54 macrobenthic animal species at a *C. caespitosa* bank in the north Aegean Sea, with polychaetes, gastropods and peracarids being the most speciose groups, while Schiller (1993) reported that the vagile cryptofauna of *C. caespitosa* banks in the northern Adriatic is dominated by polychaetes, brittle stars and crustaceans. Similarly, our study of the Kalloni coral bank, though qualitative and focusing only on conspicuous and easily distinguishable species, revealed a highly speciose community characterised by a high frequency of multispecies agglomerations, typically consisting of coral colonies, molluscs, sponges and algae. Mutualistic relationships between scleractinian corals and other animals have been observed, which can provide protection against corallivory (Samsuri *et al.*, 2018), algal epibiosis (Stachowicz & Hay, 1999) and sediment deposition (Stewart *et al.*, 2006), amongst other pressures. The majority of colonies assessed in Kalloni exhibited turf algae in the interstitial spaces around their polyps, with no apparent negative consequences on the colonies. The coexistence of *C. caespitosa* with structurally dominant species, such as canopy-forming algae, has been documented in various regions of both the western and eastern Mediterranean (e.g., Pons-Fita *et al.*, 2020 and references therein). Notably, *C. caespitosa* has also been observed to inhibit algal overgrowth, likely through the synthesis of toxic secondary metabolites, which may act as a chemical defence (Kersting *et al.*, 2013b). Such trait may therefore confer a competitive advantage as regards space and light. On the other hand, in the cases of old necrosis, damaged parts of corals were commonly overgrown by several benthic epibiotic species, e.g., macroalgae, sponges and bryozoans, which may have a negative effect on the settlement of new coral recruits (Sin *et al.*, 2012; Chui & Ang Jr., 2017) and exacerbate the effects of MMEs (Chimienti *et al.*, 2021), leading to a dramatic loss of corals in the long term. A quantitative analysis would be very useful to provide further insights on the biodiversity status of the area, and the biotic interactions between the different species assemblages.

With regards to the health status of the bank, necrosis levels were high, with approximately half of the population displaying >10% of necrosed SA and a considerable number of colonies being completely dead. Moreover, the average necrosed SA of affected colonies was also relatively high. However, as the greatest part of necrosis was characterised as “old necrosis”, indicating past mortality events, it is important to note that the aforementioned values reflect accumulated necrosis, i.e., the effects of old and more recent mortality events. Understanding the

exact causes and timing of the observed necrosis is not possible, as the specific population appears to be exposed to a variety of pressures, while no monitoring has been conducted to date. The high levels of necrosis reported could be due to MMEs caused by MHWs (Garrabou *et al.*, 2022; Estanque *et al.*, 2023), which are known to have greatly affected numerous *C. caespitosa* populations (Rodolfo-Metalpa *et al.*, 2005; Kersting *et al.*, 2013a; Kružić *et al.*, 2014; Jiménez *et al.*, 2016), as well as several other benthic organisms throughout the Mediterranean (Garrabou *et al.*, 2009, 2019, 2022). These temperature-induced mortalities, usually occurring during late summer-mid autumn, are characterised by partial loss of coral tissue that accumulates over recurrent mortality events, and remain evident for several years thereafter (Kersting *et al.*, 2023). Given the shallow depth range of the *C. caespitosa* population in the Gulf of Kalloni, old necrosis values may partly reflect past mortality events due to prolonged times of exceptionally high sea water temperatures in the area. Based on the extreme annual minimum and maximum temperature values in the Gulf of Kalloni (Spatharis *et al.*, 2007; Papantoniou *et al.*, 2015; Mamoutos *et al.*, 2018; Petalas *et al.*, 2020; Nikolaou *et al.*, 2024), its shallow depth range, the ever-increasing frequency and duration of MHWs in the Aegean Sea (Androulidakis & Krestenitis, 2022) and the expected further exacerbation of such extremes under a future climate change scenario, *C. caespitosa* populations may undergo more severe mortality events (Kružić *et al.*, 2014, Garrabou *et al.*, 2022). Other known mass mortality events (MMEs) in Kalloni Gulf have previously impacted a large *P. nobilis* (Linnaeus, 1758) population (Zotou *et al.*, 2020; Nikolaou *et al.*, 2024), and the populations of two gorgonian species (Sini *et al.*, 2015; Sini *et al.*, 2019). The MME affecting the *P. nobilis* population has been attributed to an outbreak of a *haplosporidian* parasite, with infections likely exacerbated by elevated seawater temperatures (Lattos *et al.*, 2023). The causes of the gorgonian MME remain unclear, primarily due to the absence of long-term monitoring data (Sini *et al.*, 2015; 2019). Concerning recent necrosis (i.e., less than six months old), its presence was unexpected, as the survey was conducted in early spring rather than in late summer or early autumn, when a cumulative effect of increased summer temperatures is more likely to be observed. Once again, the lack of systematic long-term monitoring limits our ability to draw robust conclusions. However, tissue loss has been reported in colonies affected by outbreaks of corallivorous species (Kružić *et al.*, 2013) and blooms of mucilaginous algal aggregates (De Biasi *et al.*, 2021), which are sometimes triggered by eutrophication (Kružić & Požar-Domac, 2007). These or similar factors might also be triggering the observed recent necrosis, but further monitoring is needed to validate this hypothesis.

Sediment burial and breakage of corals were also identified as additional injuries affecting the *C. caespitosa* colonies assessed in Kalloni Gulf. While partially or fully buried colonies are probably a result of the increased natural resuspension of the surrounding muddy sediments, broken colonies are partly a result of natural

processes, such as wave action and coral fragmentation (Roff, 2008), and partly a consequence of other anthropogenic activities. Specific anthropogenic pressures that were observed during sampling include anchoring, poaching of molluscs, fishing with set nets, and a boat collision that destroyed some of the shallowest parts of the bank. Moreover, nutrient-rich environments might lower the skeletal density of *C. caespitosa*, thus increasing their vulnerability to breakage, as hypothesised by Vergotti *et al.* (2025), which may also be promoted by high bioerosion. The causes and the rate of coral necrosis and breakage deserve further investigation and quantification in order to evaluate the health status of the bank and identify the pressures that need to be managed.

Overall, considering that two smaller *C. caespitosa* formations have also been located at nearby sites, the area appears to be a hotspot for *C. caespitosa* communities that deserves specific monitoring and conservation actions. Apart from the regular systematic monitoring of the health status of this *C. caespitosa* bank and its associated communities, a sclerochronological analysis is needed to determine the age and growth rate of the colonies (see c; Kersting & Linares, 2012; Monnier *et al.*, 2021; Vergotti *et al.*, 2025), while genetic characterisation of the bank is required to investigate the connectivity of this particular bank to other *C. caespitosa* populations located within the Kalloni Gulf and beyond, and assess the recruitment potential of the species. This would enable an investigation of the adaptive potential of the species with regards to metabolic processes and critical thermal limits in response to sea surface temperature rise. Such studies will provide important information required to evaluate future population trends of the species, and identify key traits that make corals (including tropical reef-building species) more resistant to thermal stress.

Compared to the open waters of the Aegean Sea, the nutrient-rich waters of Kalloni Gulf (Pavlidou *et al.*, 2005; Spatharis *et al.*, 2007; Tsirtsis *et al.*, 2008; Papantoniou *et al.*, 2015) may be influencing the skeletal growth (see Vergotti *et al.*, 2025) of the *C. caespitosa* colonies and their vulnerability to thermal stress, as noted by Quintano *et al.* (2025) in the western Mediterranean. This subject also warrants further exploration. The ability of this species to switch between autotrophic and heterotrophic feeding pathways (Ferrier-Pagés *et al.*, 2011) may allow it to offset energy limitations driven by thermal stress and low light availability. Future research focusing on the seasonal physiological assessment of *C. caespitosa* colonies, and a more detailed analysis of the hydrodynamic regime of the area, would provide valuable insights into nutrient circulation and its influence on coral growth.

Given the uniqueness of the *C. caespitosa* bank of Kalloni Gulf, the area should be declared as strictly protected following the example of other *C. caespitosa* bioconstructions such as the Mljet Island (Kružić & Benković, 2008), Meloria Shoals (De Biasi *et al.*, 2021) and the Columbretes Islands (Pons-Fita *et al.*, 2020), and systematic monitoring of the health status of the bank should be conducted regularly in order to apply adaptive conservation measures. Lastly, population assessment of

C. caespitosa throughout the Kalloni Gulf is needed to identify other potential hotspots in need of management and protection.

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Appendix

Table S1. Marine organisms recorded during the sampling period on the *Cladocora caespitosa* bank area in the Gulf of Kalloni, Lesvos Island, Greece, classified according to their phyla. The corresponding species and/or genus (or morphotype, when neither of these could be identified), family and class of each taxon is specified. Organisms found on the soft sediments around the bank (*) and alien species (♦) are indicated.

PHYLUM	Species / Genus / Morphotype	Family	Class
	- <i>Dictyota</i> spp.	Dictyotaceae	Phaeophyceae
OCHROPHYTA	- <i>Padina pavonica</i> (Linnaeus) Thivy	Dictyotaceae	Phaeophyceae
	-Unidentified turf algae	-	Phaeophyceae
TRACHEOPHYTA	- <i>Cymodocea nodosa</i> (Ucria) Ascherson	Cymodoceae	Magnoliopsida
CHLOROPHYTA	- <i>Blidingia minima</i> (Nägeli ex Kützing) Kylin	Kommaniaceae	Ulvophyceae
	- <i>Valonia utricularis</i> (Roth) C. Agardh	Valoniaceae	Ulvophyceae
	-Unidentified long, thin, filamentous green algae	-	Bryopsidales
RHODOPHYTA	- <i>Lithophyllum</i> sp.	Lithophyllaceae	Florideophyceae
	-Unidentified red filamentous algae	-	Florideophyceae
	-Unidentified red foliaceous algae	-	Florideophyceae
PORIFERA	- <i>Aplysina aerophoba</i> (Nardo, 1833)	Aplysinidae	Demospongiae
	- <i>Cliona</i> sp.	Clionidae	Demospongiae
	- <i>Crambe crambe</i> (Schmidt, 1862)	Crambeidae	Demospongiae
	- <i>Geodia cydonium</i> (Linnaeus, 1767)	Geodiidae	Demospongiae
	- <i>Haliclona</i> (Reniera) <i>mediterranea</i> Griessinger, 1971	Chalinidae	Demospongiae
	- <i>Ircinia</i> sp.	Irciniidae	Demospongiae
	- <i>Phorbas tenacior</i> (Topsent, 1925)	Hymedesmiidae	Demospongiae
	-Unidentified black and pink sponge	-	Demospongiae
	-Unidentified white and purple sponge	-	Demospongiae
BRYOZOA	- <i>Schizobrachiella sanguinea</i> (Norman, 1868)	Schizoporellidae	Gymnolaemata
	- <i>Schizomavella</i> (<i>Schizomavella</i>) <i>mamillata</i> (Hincks, 1880)	Bitectiporidae	Gymnolaemata
	-Unidentified white bryozoon	-	Gymnolaemata
CNIDARIA	- <i>Aiptasia mutabilis</i> (Gravenhorst, 1831)	Aiptasiidae	Anthozoa
	- <i>Anemonia viridis</i> (Forsskål, 1775)	Actiniidae	Anthozoa
	- <i>Cereus pedunculatus</i> (Pennant, 1777)	Sagartiidae	Anthozoa
	- <i>Pachycerianthus solitarius</i> (Rapp, 1829) *	Cerianthidae	Anthozoa
	- <i>Veretillum cynomorium</i> (Pallas, 1766) *	Veretillidae	Anthozoa
	-Unidentified: leaf-like filamentous body of <100 mm long, with blue and orange segments on its main axis, and short, white branches to the sides	-	Hydrozoa
MOLLUSCA	- <i>Arca noae</i> Linnaeus, 1758	Arcidae	Bivalvia
	- <i>Mimachlamys varia</i> (Linnaeus, 1758)	Pectinidae	Bivalvia
	- <i>Mytilus galloprovincialis</i> Lamarek, 1819	Mytilidae	Bivalvia
	- <i>Dendostrea folium</i> (Linnaeus, 1758) ♦	Ostreidae	Bivalvia
	- <i>Ostrea edulis</i> Linnaeus, 1758	Ostreidae	Bivalvia
	- <i>Bursatella leachii</i> Blainville, 1817 * ♦	Aplysiidae	Gastropoda
	- <i>Cerithium vulgatum</i> Bruguière, 1792	Cerithiidae	Gastropoda

Continued

Table S1 continued

PHYLUM	Species / Genus / Morphotype	Family	Class
	- <i>Aporrhais pespelecani</i> (Linnaeus, 1758)	Aporrhaidae	Gastropoda
	- <i>Bolinus brandaris</i> (Linnaeus, 1758)	Muricidae	Gastropoda
	- <i>Hexaplex trunculus</i> (Linnaeus, 1758)	Muricidae	Gastropoda
	- <i>Muricopsis cristata</i> (Brocchi, 1814)	Muricidae	Gastropoda
	- <i>Felimare villafranca</i> (Risso, 1818)	Chromodorididae	Gastropoda
	- <i>Thuridilla hopei</i> (Vérany, 1853)	Plakobranchidae	Gastropoda
	- <i>Lepidopleurus cajetanus</i> (Poli, 1791)	Leptochitonidae	Polyplacophora
ANNELIDA	- <i>Myxicola infundibulum</i> (Montagu, 1808)	Sabellidae	Polychaeta
	- <i>Protula</i> sp.	Sabellidae	Polychaeta
	- <i>Sabella spallanzanii</i> (Gmelin, 1791)	Sabellidae	Polychaeta
	- <i>Serpula</i> sp.	Sabellidae	Polychaeta
ARTHROPODA	- <i>Herbstia condyliata</i> (Fabricius, 1787)	Epialtidae	Malacostraca
	- <i>Inachus phalangium</i> (Fabricius, 1775)	Inachidae	Malacostraca
	- <i>Macropodia</i> sp.	Inachidae	Malacostraca
	- <i>Stenopus spinosus</i> Risso, 1827	Stenopodidae	Malacostraca
	- <i>Arbacia lixula</i> (Linnaeus, 1758)	Arbaciidae	Echinoidea
	- <i>Paracentrotus lividus</i> (Lamarck, 1816)	Parechinidae	Echinoidea
ECHINODERMATA	- <i>Holothuria (Holothuria) tubulosa</i> Gmelin, 1791	Holothuriidae	Holothuroidea
	- <i>Holothuria (Panningothuria) forskali</i> Delle Chiaje, 1823	Holothuriidae	Holothuroidea
	- <i>Asterina gibbosa</i> (Pennant, 1777)	Asterinidae	Asteroidea
	- <i>Astropecten</i> sp.	Astropectinidae	Asteroidea
	- <i>Ophioderma longicauda</i> (Bruzelius, 1805)	Ophiodermatidae	Ophiuroidea
	- <i>Ophiothrix fragilis</i> (Abildgaard in O.F. Müller, 1789)	Ophiotrichidae	Ophiuroidea
	- <i>Phallusia nigra</i> Savigny, 1816 ♦	Asciidiidae	Ascidacea
CHORDATA	- <i>Styela plicata</i> (Lesueur, 1823)	Styelidae	Ascidacea
	- <i>Boops boops</i> (Linnaeus, 1758)	Sparidae	Actinopteri
	- <i>Diplodus vulgaris</i> (Geoffroy Saint-Hilaire, 1817)	Sparidae	Actinopteri
	- <i>Symphodus cinereus</i> (Bonnaterre, 1788)	Labridae	Actinopteri
	- <i>Gobius bucchichi</i> Steindachner, 1870	Gobiidae	Actinopteri
	- <i>Gobius cruentatus</i> Gmelin, 1789	Gobiidae	Actinopteri
	- <i>Gobius incognitus</i> Kovačić & Šanda, 2016	Gobiidae	Actinopteri
	- <i>Gobius niger</i> Linnaeus, 1758	Gobiidae	Actinopteri
	- <i>Microlipophrys canevae</i> (Vinciguerra, 1880)	Blenniidae	Actinopteri
	- <i>Microlipophrys dalmatinus</i> (Steindachner & Kolombatovic, 1883)	Blenniidae	Actinopteri
	- <i>Parablennius incognitus</i> (Bath, 1968)	Blenniidae	Actinopteri
	- <i>Parablennius tentacularis</i> (Brünnich, 1768)	Blenniidae	Actinopteri
	- <i>Sarpa salpa</i> (Linnaeus, 1758)	Sparidae	Actinopteri
	- <i>Syngnathus typhle</i> Linnaeus, 1758*	Syngnathidae	Actinopteri