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Submarine caves as potential climate microrefugia for symbiotic octocorals

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Climatic refugia are receiving increasing attention in the context of global warming and the rising frequency and intensity of marine heatwaves (MHWs). Long-lived and slow-growing organisms, such as many octocorals, are highly threatened by the increase in seawater temperatures and the associated mass mortality events. Here, we evaluated the potential role of a submarine cave as climatic microrefugium for the symbiotic Mediterranean white gorgonian, *Eunicella singularis*. Environmental conditions (light and temperature) and biological responses (population structure, reproductive output, and physiological traits) were compared between colonies located inside and outside a submarine cave. Colonies outside the cave are exposed to high light and slightly increased temperatures compared to the inside of the cave, exhibiting high mortality (61% of dead colonies) and reduced reproductive output (65% of non-reproducing colonies and absence of mature oocytes). In contrast, colonies inside the cave showed lower signs of MHWs related stress (17 times lower mortality rate), higher reproductive output, and different photoadaptations to low-light conditions (chlorophyll content and pigment ratio). Although the observed differences are likely driven by lower light and temperature inside the cave, other environmental factors not considered in this study, such as hydrodynamic conditions and food availability, could also contribute. Our findings highlight the potential role of some submarine caves as climatic microrefugia, capable of buffering symbiotic octocorals from the combined effects of light and thermal stress.

KEYWORDS

anthozoa, caves, global change, mass mortalities, Mediterranean Sea, refugia, reproduction, symbiosis

1 Introduction

Global change is causing rapid increases in ocean warming worldwide, leading to higher mean annual sea surface temperatures and more frequent extreme thermal events (IPCC, 2019). The Mediterranean Sea is one of the fastest-warming regions on the planet, with a sea surface temperature increase of $0.38^{\circ}\text{C} \cdot \text{decade}^{-1}$ from 1982 to 2019 (Pisano et al., 2020; Garrabou et al., 2022), more than three times higher than the global mean of $0.11^{\circ}\text{C} \cdot$

decade⁻¹ from the 1970s to 2019 (IPCC, 2019). This warming trend has been accompanied by an increase in the frequency and intensity of marine heatwaves (MHWs), affecting different benthic communities, particularly coralligenous habitats (Garrahou et al., 2009; Rivetti et al., 2014). Elevated temperatures during MHWs often exceed the thermotolerance limits of key habitat-forming species such as gorgonians, causing both lethal and sublethal effects (Linares et al., 2005; Gómez-Gras et al., 2022; Viladrich et al., 2022; Sarda et al., 2025). In addition to direct thermal stress, prolonged summer conditions and enhanced stratification reduce food availability, further increasing the vulnerability of benthic organisms and driving shifts in species distribution, community structure, and the regression of habitat-forming species in the Mediterranean (Coma et al., 2009; Garrahou et al., 2013; Ponti et al., 2019; Viladrich et al., 2026). These trajectories call for a better understanding of the habitats and mechanisms that may buffer vulnerable species from ongoing thermal stress.

In this context, climatic refugia are gaining attention as potential buffers against climate change impacts (Keppel et al., 2012; Sanz-Martín et al., 2026). Originally used to describe areas where species survived the last glacial period (Bennett and Provan, 2008; Ashcroft, 2010), the term ‘climatic refugia’ is now also used to describe habitats where species may retreat to, persist in, and expand from under changing and unfavourable environmental conditions, helping species to limit the impacts of rising temperatures in the 21st century (Keppel et al., 2012; Keppel and Wardell-Johnson, 2012; Ashcroft, 2010; Ban et al., 2016). At large spatial scales, these habitats are defined as macrorefugia or classical refugia (Ashcroft, 2010). Conversely, at small geographical scales they are known as microrefugia or cryptic refugia, referring to locations where environmental conditions remain relatively more stable or less extreme than in surrounding areas (Rull, 2009; Ashcroft, 2010; Sanz-Martín et al., 2026). In marine ecosystems, these microrefugia may include habitats characterized by low temperatures, reduced light, higher turbidity, or hydrodynamics, among others (Lesser et al., 2009; Keppel et al., 2012; Cacciapaglia and Van Woesik, 2016; Kavousi and Keppel, 2018; Bramanti et al., 2023).

Among the marine microrefugia identified in the Mediterranean Sea, submarine caves stand out as well documented examples, recognised as biodiversity reservoirs and as habitats capable of buffering species from temperature fluctuations (Harmelin et al., 1985; Gerovasileiou and Voultsiadou, 2012; Rastorgueff et al., 2015; Gerovasileiou and Bianchi, 2021; Lanza-Arroyo et al., 2024). The geological and geomorphological characteristics of Mediterranean rocky coastlines have enabled the formation of many submarine caves, which present strong environmental gradients over short spatial scales, including pronounced reductions in light, water movement, and trophic input (Pérès and Picard, 1949; Harmelin et al., 1985; Gili et al., 1986; Fichez, 1991; Resaikos et al., 2026). Despite their ecological value, marine caves are not immune to disturbance and are threatened by increasing seawater temperatures, over-frequentation by recreational diving, and habitat degradation (Parravicini et al., 2010; Giakoumi et al., 2013; Rastorgueff et al., 2015; Derrien et al., 2024). Nevertheless, some studies suggest that these habitats may mitigate temperature impacts on certain species by reducing light, highlighting their

potential role as climatic microrefugia (Garrahou et al., 2001; Chevaldonné and Lejeune, 2003; Gerovasileiou and Bianchi, 2021).

Gorgonians are among the species that could benefit the most from such microrefugia in the Mediterranean Sea, as some of the most affected by MHWs, with important declines in population densities reported across multiple species (Cerrano et al., 2000; Perez et al., 2000; Zentner et al., 2023; Sarda et al., 2025). The white gorgonian, *Eunicella singularis* (Esper, 1794), is one of the most abundant species in the NW Mediterranean Sea (Linares et al., 2008), with a broad depth distribution from 0 to 80 m depth (Gori et al., 2011; Grinyó et al., 2016). It was considered to be one of the most resilient Mediterranean gorgonians due to its mixotrophic strategy (Fava et al., 2009), being the only known gorgonian species in the Mediterranean with a symbiosis with photosynthetic algae (Carpine and Grasshoff, 1975). However, recent mass mortality events have also deeply impacted *E. singularis* populations, particularly at shallow depths, highlighting its vulnerability under the ongoing warming regime (Coma et al., 2006; Linares et al., 2008; Rubio-Portillo et al., 2016; de la Linde-Rubio et al., 2018; Sarda et al., 2025). Given its mixotrophic strategy (Coma et al., 2015; Ferrier-Pagès et al., 2015) and vulnerability to MHWs (Coma et al., 2006; Sarda et al., 2025), *E. singularis* constitutes a suitable model species to test whether the semi-dark environment of a submarine cave can act as a climate microrefugium for symbiotic octocorals.

Light availability plays a crucial role in the physiology and stress responses of symbiotic corals (Cacciapaglia and Van Woesik, 2016; Bellworthy and Fine, 2017; Cerrano et al., 2019). The interaction between thermal stress and light has been shown to be additive, with high light increasing the effects of elevated temperatures (Bhagooli and Hidaka, 2004; Lesser and Farrell, 2004; Courtial et al., 2017). Indeed, corals living in unshaded environments are more likely to bleach and experience thermal stress than corals living in shaded microhabitats such as mangrove canopies or other naturally or artificially shaded habitats (Baker et al., 2008; Muir et al., 2017; Stewart et al., 2021; Tagliafico et al., 2022; Bassett et al., 2026). Corals inhabiting low-light environments, such as mangrove canopies, marine caves or mesophotic zones, can often display changes in colony morphology, symbiont density, and photosynthetic traits that enhance performance under reduced light (Chalker et al., 1983; Dinesen, 1983; Anthony and Hoegh-Guldberg, 2003; Hoogenboom et al., 2009; Stewart et al., 2021). However, it remains poorly understood how light limitation, while helping colonies resist thermal stress, may also influence the energetic balance of mixotrophic corals, with consequences for demographic traits such as reproductive output, a key trait linking colony condition to long-term population persistence.

Despite growing evidence for the role of marine caves as thermal microrefugia, empirical assessments of their buffering capacity for symbiotic gorgonians remain scarce. In this study, we aim to assess whether a submarine cave can act as a climatic microrefugium for the mixotrophic gorgonian *E. singularis*, providing novel insights into the integration of population structure, reproductive status, physiological responses and photosymbiosis of the species in this specific microhabitat. We compared colonies located inside and outside the cave to evaluate differences in size, mortality, reproductive output, and symbiotic traits, including

symbiont density, chlorophyll content, and symbiont taxonomic identification to determine whether observed differences were associated with photoacclimation or shifts in symbiont identity. We hypothesized that colonies inhabiting the cave under low-light conditions would experience reduced stress and therefore exhibit lower signs of thermal damage under MHW exposure. Furthermore, we expected that reduced light could be associated with adjustments in the symbiotic relationship and trophic strategy of the gorgonians.

2 Materials and methods

2.1 Sampling and environmental conditions monitoring

The study was conducted in Cova de la Vaca (42°02'51.0"N, 003°13'33.3"E), a submerged, semi-dark, tunnel-like marine cave located in the Medes Islands, within the Montgri, Medes Islands and Baix Ter Natural Park (Catalan coast, NW Mediterranean Sea). Sampling was carried out at 19–21 m depth both inside and outside the cave by scuba diving in May 2024, coinciding with the period when *E. singularis* sexual products are developed but have not yet been released (Ribes et al., 2007; Gori et al., 2007). A fragment of a primary branch (5–7 cm length) was collected from each of 40 colonies inside and 40 colonies outside the cave. Each fragment was divided into two pieces: one was fixed in >95% ethanol for reproductive and genetic analyses, and the second was frozen at -20°C for subsequent determination of symbiont density, chlorophyll and organic matter content.

To characterise the thermal and light environment experienced by the colonies during the warming season, temperature and light were continuously recorded every 30 s using HOBO MX2202 data loggers. The data loggers were deployed at 21 m depth adjacent to colonies located inside and outside the cave from June to October during both 2024 and 2025. For each location the number of days on which temperature exceeded 23, 24 and 25°C was calculated, as well as the duration of each event. Mean light was calculated considering only daylight hours, defined as the period between sunrise and sunset. Hydrodynamic conditions and food availability were not directly quantified in this study and are discussed based on previous studies of Mediterranean submarine caves.

2.2 Population structure

A demographic census of the previously sampled colonies was conducted in July 2025 both inside and outside the cave. Data were obtained using 50 x 50 cm quadrats (surface = 0.25 m²) haphazardly placed along the suitable rocky substrate to capture the natural spatial variability of the population. A total of 28 and 25 quadrats were surveyed inside and outside the cave, respectively. This sampling effort is consistent with the minimum sampling effort previously identified for characterizing *E. singularis* populations (Coma et al., 2006; Linares et al., 2008). From each quadrat we recorded the number of colonies, their maximum height, and the percentage of colony surface with necrosis (recent mortality;

denuded axis) and epibiosis (old mortality; overgrowth by other organisms) (Linares et al., 2008). From these data, we calculated: the mean population density, mean, minimum and maximum colony height, population size-frequency distribution, percentage of colony surface affected by mortality, and proportion of colonies affected by mortality (more than 10% of affected surface, considered to be natural for the species before the occurrence of MHWs; Linares et al., 2008).

2.3 Reproduction

Colonies were classified as male, female, or undetermined (when no sexual products were observed after inspecting 10 polyps), based on sexual products colour and morphology (Ribes et al., 2007). To quantify reproductive effort, 10 male and 10 female colonies were haphazardly selected from colonies inside and outside the cave. Ten polyps per colony were dissected under a stereomicroscope, and all sexual products were photographed. Image analyses were performed using ImageJ software (Image J 1.54p 2025, National Institute of Health, US) to measure the area (A) of each sexual product to then calculate their diameter (d) according to the equation: $d = 2(A/\pi)^{1/2}$. Volume (V) was calculated assuming a spherical shape, using the equation: $V = 4/3 \cdot \pi \cdot (d/2)^3$. Fertility (expressed as the percentage of fertile polyps), fecundity (number of sexual products per polyp), and the mean total volume of sexual products per polyp (mm³·polyp⁻¹) were subsequently calculated.

2.4 Symbiont density, chlorophyll and organic matter content

Gorgonian fragments were lyophilised for 24h at -50°C and 0.05 mbar using a Telstar LyoQuest lyophilizer. After lyophilisation, the gorgonian axis of each sample was carefully removed and the dry coenenchyma and polyps were powdered. For each sample, approximately 0.005 g (± 0.001) of the obtained homogenized powder were used for symbiont density quantification, 0.025 g (± 0.001) for chlorophyll analysis, and the remaining for organic matter analysis.

For symbiont density determination, 200 µl of miliQ water, 100 µl of 37% HCl and 50 µl of Lugol's solution was added to each sample, sonicated for 30 min, and symbiont cells were counted using a Neubauer haemocytometer under a microscope. Chlorophyll pigments were extracted twice in >99% acetone at 4°C for 24h each (7 ml in total). Extracts were centrifuged at 1000 rpm and 15°C for 10 min, and chlorophyll *a* and *c2* concentrations were determined spectrophotometrically following the equations of Jeffrey and Humphrey (1975). Finally, organic matter content was determined by ashing the powdered dry coenenchyma and polyps for 5h at 500°C in a muffle furnace. Organic matter was calculated as the difference between dry weight and ash weight. All results are expressed as micrograms per milligram of gorgonian organic matter.

2.5 Symbiont taxonomic identification

To identify the symbiont species in each colony, DNA was extracted from gorgonian samples using the cetyltrimethylammonium bromide (CTAB) protocol (Winnepeenninckx et al., 1994). The non-coding region of the *psbA^{ncr}* gene from the chloroplast photosystem II

was amplified by polymerase chain reaction (PCR). This region was amplified using primers Philozoon-psbAF (5'-ATTTGGTT CACAGCGCTTGG-3') and Philozoon-psbAR (5'-CCATTTGACTC CCACACTGGA-3'). PCR products were sequenced by Sanger sequencing at Macrogen Europe. Few sequences were obtained due to low amplification success of this region, probably resulting from the low symbiont densities. Chromatograms were inspected, and sequences were edited and aligned using ClustalW in BioEdit and MEGA11 (Molecular Evolutionary Genetics Analysis). Phylogenetic analyses were conducted using the Maximum Likelihood method in RStudio (packages *ape*, Paradis and Schliep, 2019; and *phangorn*, Schliep, 2011), including reference sequences from other Symbiodiniaceae species (GenBank PopSet accession number: 2292923562; LaJeunesse et al., 2022). *Cladocopium latusorum* was used as the outgroup (GenBank accession numbers: OP279755.1, OP279756.1, OP279774.1; Brown et al., 2022). Node support was assessed using 100 bootstrap replicates. Sequences obtained in this study have been deposited in GenBank (accession numbers: PZ464134, PZ464135).

2.6 Statistical analysis

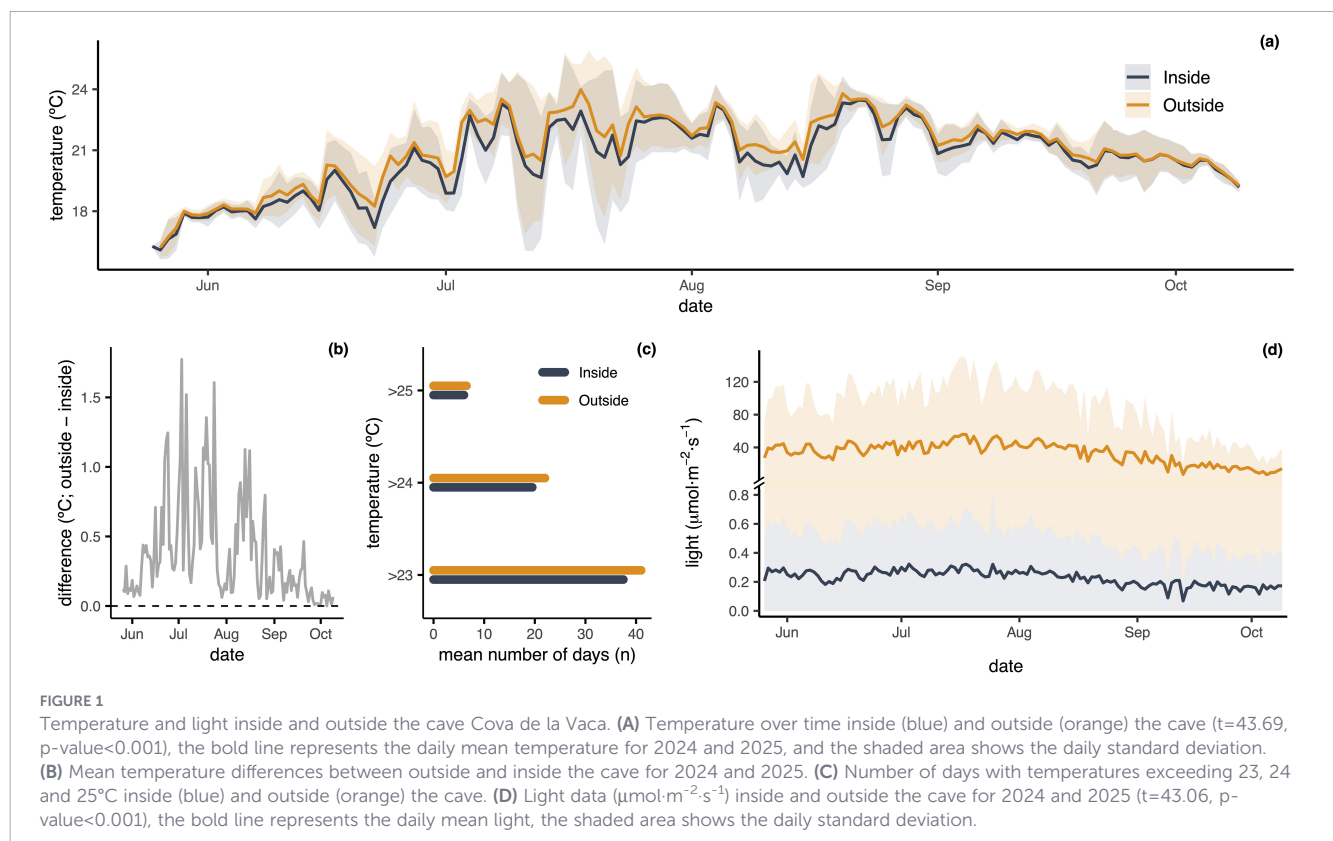
All statistical analyses were performed using the software R (v4.2.2; R Core Team 2022) and RStudio. Differences in environmental variables (temperature and light) and biological traits between colonies inside and outside the cave were assessed using Student's t-tests. The variables analysed include populations density, colony height, percentages of mortality, diameter of sexual products, fertility, fecundity, gonadal volume, symbiont density, chlorophyll concentrations, and organic matter content. When assumptions of normality (Shapiro-Wilk test) and homoscedasticity

(Levene's test) were not met (p -value < 0.05), non-parametric Wilcoxon tests were applied. Differences in size-frequency distributions of the studied colonies were assessed using skewness and kurtosis descriptors and tested with the Kolmogorov-Smirnov test for two-distributions comparisons. Sex ratios in each population were evaluated using chi-square tests to determine whether they deviated from a 1:1 male to female ratio. The significance level used during the study was p -value < 0.05.

3 Results

3.1 Environmental conditions

Differences in seawater temperature and light availability were found between the two studied locations. Seawater temperature followed a similar temporal pattern inside and outside the cave, with warming from early to late summer followed by a gradual decrease in autumn (Figure 1A). Seawater mean temperature and standard deviation, inside and outside the cave, respectively, was $18.8 \pm 1.6^\circ\text{C}$ and $19.3 \pm 1.6^\circ\text{C}$ in June, $21.5 \pm 2.6^\circ\text{C}$ and $22.2 \pm 2.3^\circ\text{C}$ in July, $21.8 \pm 1.7^\circ\text{C}$ and $22.2 \pm 1.4^\circ\text{C}$ in August, and $21.1 \pm 1.0^\circ\text{C}$ and $21.2 \pm 1.0^\circ\text{C}$ in September. Overall, mean temperature was significantly higher outside than inside the cave ($t=43.69$, p -value<0.001), with an average difference of $0.39 \pm 0.4^\circ\text{C}$ (Figure 1B). Furthermore, the number of days in which temperature exceeded 23, 24 and 25°C was also consistently higher outside than inside the cave (Figure 1C; see Supplementary Table 1 for details on events frequency and duration).



In terms of light conditions, colonies outside the cave were exposed to $59.3 \pm 72.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in June, $72.4 \pm 87.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in July, $64.2 \pm 75.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in August, and $35.2 \pm 42.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in September as mean light and standard deviation between sunrise and sunset. Whereas light levels inside the cave remained consistently lower throughout the study period ($t=-43.06$, $p\text{-value}<0.001$), with an average of $0.4 \pm 0.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Figure 1D).

3.2 Population structure

Significant differences in demographic parameters were observed with higher colony density ($W = 538.5$, $p\text{-value}<0.001$; Figure 2A), higher mean colony height ($W = 3449.5$, $p\text{-value}<0.001$; Figure 2B), as well as lower mean percentage of surface affected by mortality ($W = 231$, $p\text{-value}<0.001$; Figure 2C) inside than outside the cave.

Colonies affected by mortality were predominantly observed outside the cave, where 61% of the colonies were classified as dead and only 4% as non-affected (Figure 3A). In contrast, colonies inside the cave were mostly characterized by low levels of affected surface, with 85% of the surveyed colonies classified as non-affected (Figure 3A).

Population size structure also differed significantly between locations ($D = 0.53$, $p\text{-value}<0.001$). Colonies inside the cave were generally larger, mostly ranging between 10 and 40 cm in height (maximum 42 cm), whereas colonies outside the cave were predominantly smaller, mostly between 10 and 20 cm in height (maximum 27 cm) (Figure 3B).

3.3 Reproduction

Reproductive traits differed between colonies inside and outside the cave, with colonies inside showing higher reproductive output than colonies outside. The frequency of indetermined (non-reproductive) colonies was lower among colonies inside than outside the cave, with a 1:1 male to female sex ratio ($X^2 = 1$, $p\text{-value}=0.317$)

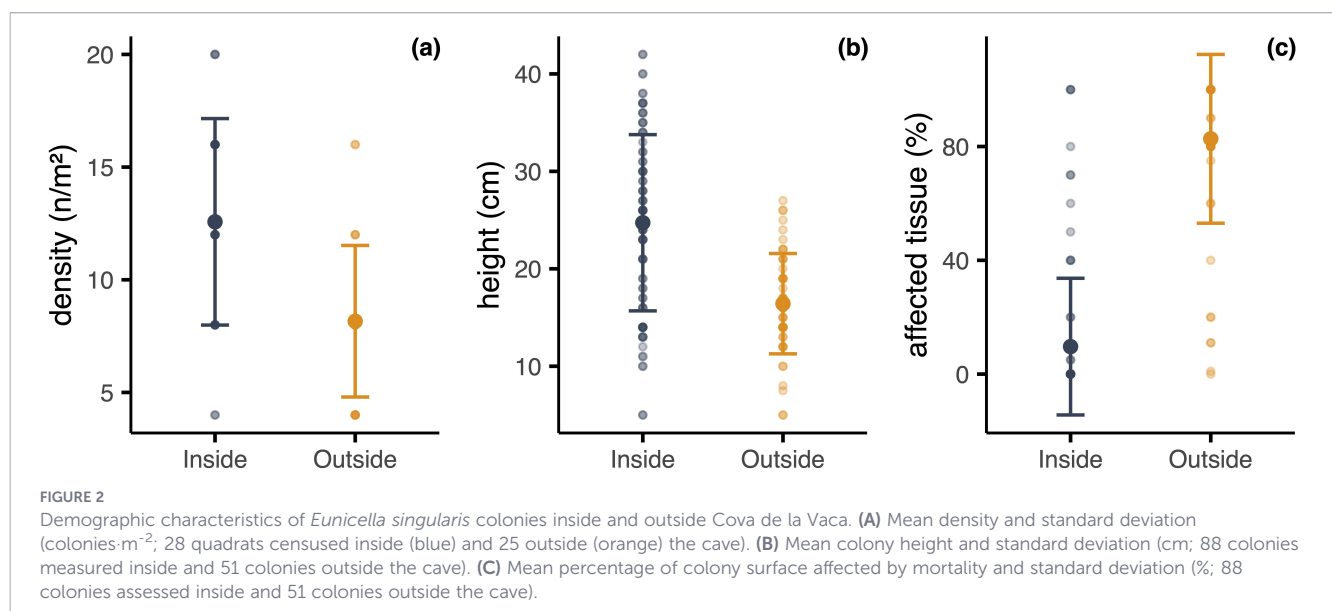
inside, contrasting with a significantly deviated 2.5:1 sex ratio outside the cave ($X^2 = 17.64$, $p\text{-value}<0.001$) (Figure 4A).

In female colonies, both fertility and fecundity were significantly higher in colonies inside than in those outside the cave for the first cohort of oocytes ($<450 \mu\text{m}$ diameter) ($W = 37.5$, $p\text{-value}=0.014$; $t=4.195$, $p\text{-value}=0.001$; Table 1). The second female cohort ($>450 \mu\text{m}$ diameter) were only found in colonies inside the cave. In contrast, in male colonies, neither fertility nor fecundity differed significantly between colonies from inside and outside the cave ($W = 60$, $p\text{-value}=0.375$; $t=0.582$, $p\text{-value}=0.568$; Table 1).

Similarly, oocyte diameters were significantly larger inside than outside the cave ($W = 21624$, $p\text{-value}<0.001$; Figures 4B, C), although no significant differences were detected in males' sexual products ($W = 264200$, $p\text{-value}=0.091$; Figures 4B, C).

3.4 Symbiont density, chlorophyll and organic matter content

Physiological traits associated with symbiont density and chlorophyll content differed between colonies inside and outside the cave. Symbiont density was significantly higher in colonies located outside the cave compared to those living inside ($t=-4.11$, $p\text{-value}=0.002$; Figure 5A). In contrast, chlorophyll *a* content per symbiont cell did not differ between inside and outside the cave ($t=1.35$, $p\text{-value}=0.206$; Figure 5B). Colonies inside the cave showed significantly higher content of chlorophyll *c2* per cell than colonies outside the cave ($t=4.91$, $p\text{-value}<0.001$; Figure 5C). When expressed per mg of organic matter, colonies outside the cave showed significantly higher values of chlorophyll *a* and significantly lower values of chlorophyll *c2* than those inside ($W = 55$, $p\text{-value}=0.016$; $W = 162$, $p\text{-value}=0.041$; Figure 5D). Consequently, the ratio between chlorophyll *a* and chlorophyll *c2* was higher in colonies outside than inside the cave ($W = 15$, $p\text{-value}<0.001$; Figure 5E). Finally, organic matter content (expressed as percentage) was significantly higher in colonies living inside than those living outside the cave ($t=4.89$, $p\text{-value}<0.001$; Figure 5F).



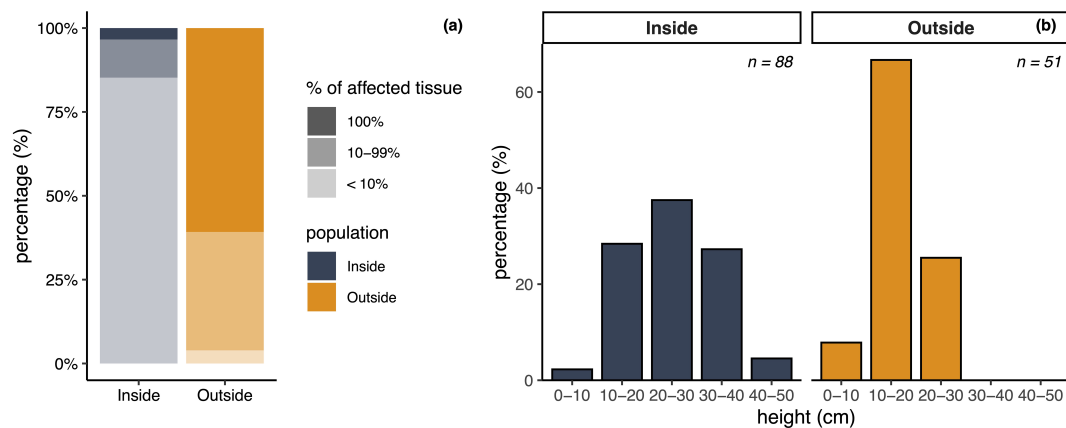


FIGURE 3

Population structure of *Eunicella singularis* inside and outside Cova de la Vaca. (A) Percentages of colonies with different levels of mortality inside (blue) and outside (orange) the cave; proportion of non-affected colonies (with less than 10% of affected surface) in light colour, affected colonies (with between 10 and 99% of affected tissue) in medium colour, and dead colonies (with 100% of injured surface) in dark colour. (B) Size-frequency distribution of colonies in each location, the number on the top right corner of each plot indicates the number of measured colonies ($D = 0.53$, p -value < 0.001).

3.5 Symbiont taxonomic identification

Phylogenetic analyses based on the *psbA^{ncr}* gene revealed that the photosymbionts associated with *E. singularis* colonies from both inside and outside the cave are closely related to *Philozoon* species, as previously observed in colonies from the same geographic areas (Medes Islands and Cap de Creus, Figure 6; Sarda et al., 2025). PCR amplifications of this gene marker from cave colonies were challenging, likely due to the low symbiont densities. Nevertheless, successful amplification and sequencing were ultimately achieved for one individual from inside the cave. Sequences obtained from *E. singularis* colonies inside and outside the cave clustered together with other *Philozoon* sequences from the same host species. In addition, these sequences were clearly differentiated with strong bootstrap support from *Philozoon* species associated with other anthozoan hosts.

4 Discussion

Marine caves are characterized by environmental conditions that differ from adjacent open areas (Rastorgueff et al., 2015; Gerovasileiou and Bianchi, 2021). In our study, light inside the cave was, as expected, substantially lower than outside, and despite the short distance separating the two locations (~ 15 m), slight but consistent differences in temperature were also detected. Although the mean thermal difference was relatively small ($\sim 0.4^\circ\text{C}$), even such minor increases during MHWs may prolong and intensify exposure to temperatures exceeding species-specific thermotolerance thresholds. The small but consistent higher thermal stress and longer exposure to temperatures above 23, 24 and 25°C observed outside the cave, may increase the vulnerability of long-lived, slow-growing octocorals, potentially explaining the results observed in this study.

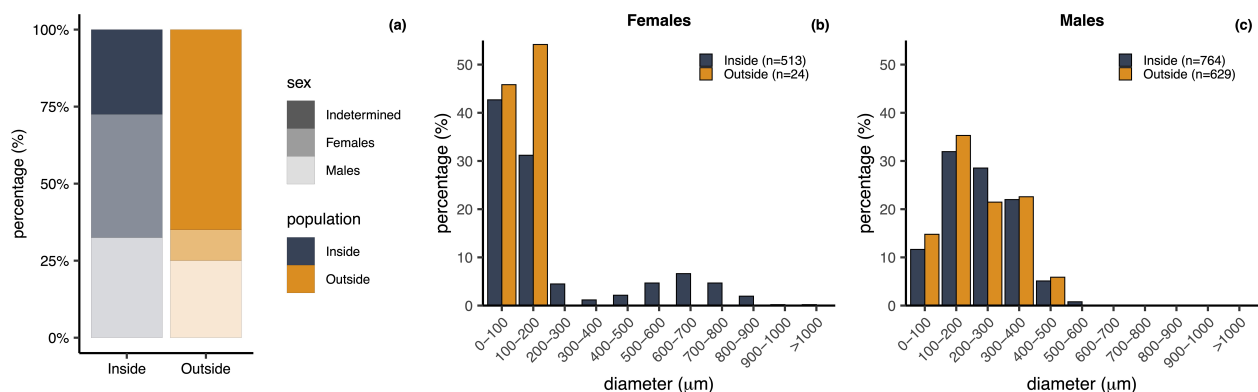


FIGURE 4

Reproduction characteristics of *Eunicella singularis* colonies inside and outside Cova de la Vaca. (A) Sex ratio of the studied colonies inside (blue) and outside (orange) the cave; male colonies are indicated in light colours, female colonies in medium colours, and indeterminate (non-reproductive) colonies in dark colours. (B) Size frequency distribution of the sexual products of female colonies inside and outside the cave ($D = 0.51$, p -value < 0.001). (C) Size frequency distribution of the sexual products of male colonies inside and outside the cave ($D = 0.08$, p -value $= 0.03$).

TABLE 1 Reproductive output of *Eunicella singularis* colonies inside and outside Cova de la Vaca; mean fertility (Fert., percentage of fertile polyps), mean diameter of the sexual products (Diam., μm), mean fecundity (Fec., number of sexual products per polyp) and mean total gonadal volume per polyp (GV, $\text{mm}^3 \cdot \text{polyp}^{-1}$).

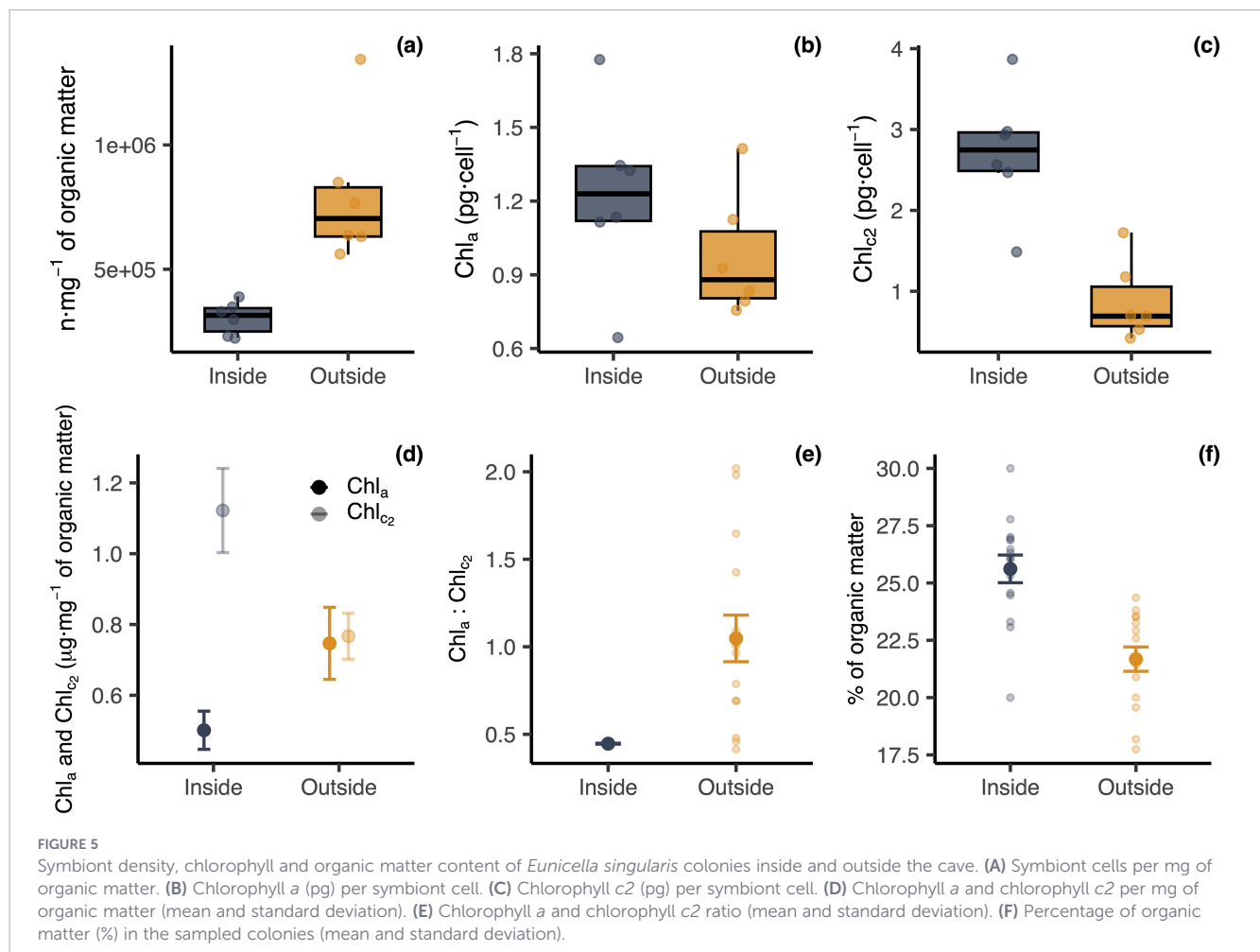
Location		Male colonies				Female colonies (1 st cohort)				Female colonies (2 nd cohort)			
		Fert.	Diam.	Fec.	GV	Fert.*	Diam.	Fec.**	GV*	Fert.	Diam.	Fec.	GV
INSIDE	mean	90	227	7.6	0.081	81	103	4.0	0.0045	56	633	1.1	0.171
	sd	25	110	5.7	0.080	25	53	2.3	0.0040	41	143	1.1	0.160
OUTSIDE	mean	80	220	6.3	0.065	30	103	0.6	0.0004	0	-	-	-
	sd	35	114	4.7	0.080	34	34	0.7	0.0004	-	-	-	-

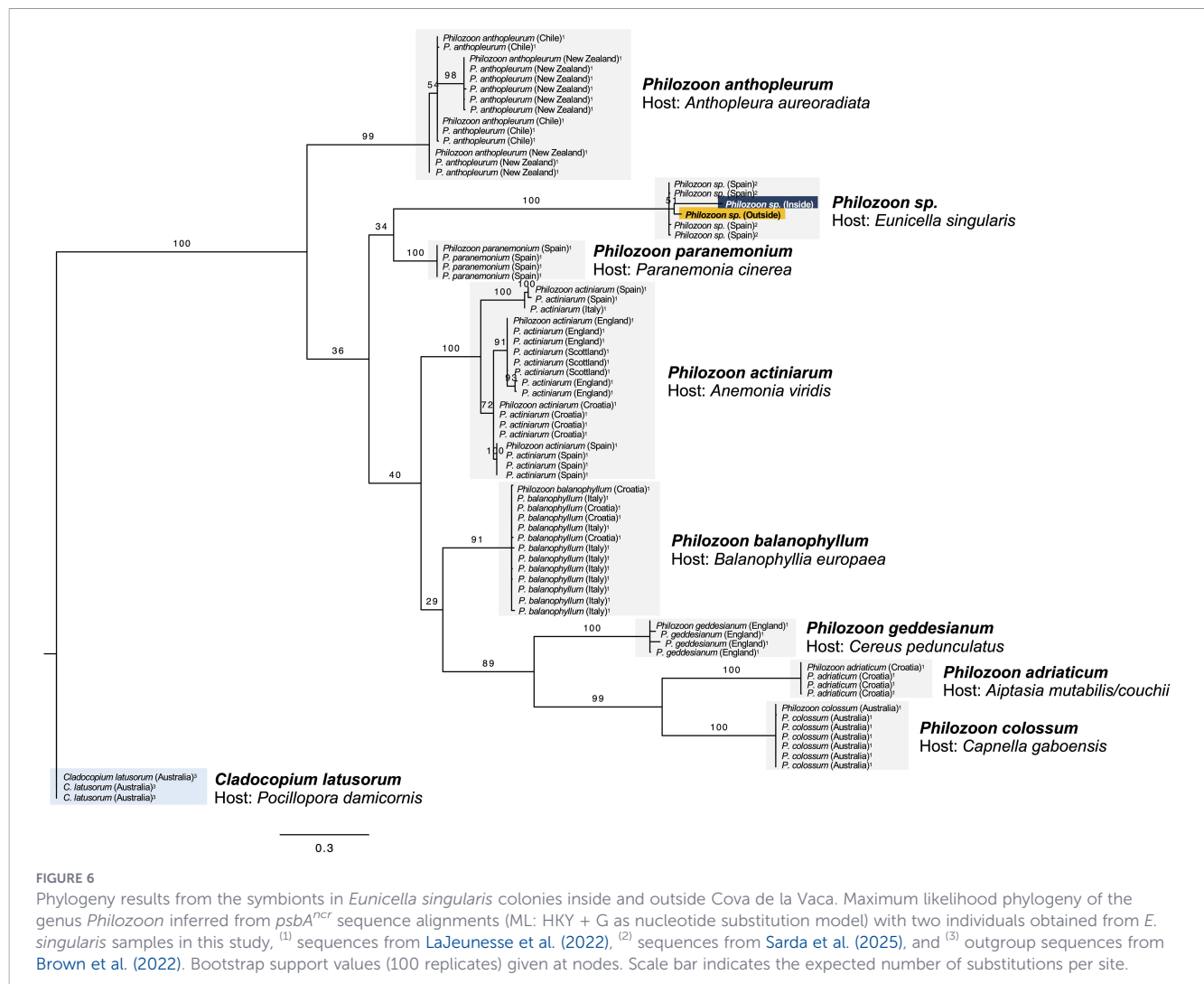
Asterisks indicate statistically significant differences between colonies inside and outside the cave (*p-value < 0.05; **p-value < 0.01).

Overall, this study supports the hypothesis that gorgonian colonies in caves exhibit lower signs of thermal damage from MHWs. Recurrent MHWs over the last 27 years in the NW Mediterranean Sea (Garrabou et al., 2022), have caused severe and widespread impacts on invertebrate populations, including *E. singularis* (Cerrano et al., 2000; Perez et al., 2000; Linares et al., 2008; Orenes-Salazar et al., 2023; Sarda et al., 2025). Before 2017, our study location was considered a climatic refugia for octocorals, however MHWs have become too frequent and severe for these species to withstand the impacts (Rovira et al., 2025). Nevertheless, colonies of *E. singularis* living inside the cave showed significantly higher population density, lower percentages of affected tissue and more than seventeen times lower mortality compared to those

outside the cave. These findings reinforce the role of marine caves as potential climate microrefugia.

Previous studies have demonstrated that natural shading reduced bleaching incidence and mortality in tropical corals under thermal stress (Hoogenboom et al., 2017; Muir et al., 2017; Tagliafico et al., 2022), as high light increases temperature-induced oxidative damage and promotes host-symbiont dissociation (Warner et al., 1999; Muir et al., 2017; Courtial et al., 2017; McCauley et al., 2018; Bongaerts and Smith, 2019). High mortality of *E. singularis* outside the cave may therefore result from an interaction between light and thermal stress, leading to increased oxidative damage in this symbiotic species. In contrast, colonies inside the cave may present reduced photooxidative pressure during thermal events. This may be further reinforced by the





lower symbiont densities observed in colonies inside the cave, which could limit the accumulation of photosynthetically derived reactive oxygen species. However, lower symbiont densities were accompanied by adjustments in the photosynthetic pigments, including higher chlorophyll concentrations per symbiont cell and a shift towards chlorophyll c2 as the dominant pigment. Similar patterns have been reported in corals inhabiting shaded environments and deeper habitats, where increased chlorophyll c2 enhances light absorption under reduced light (Fitt and Cook, 2001; Dove et al., 2006; Asner et al., 2024). These pigment-level differences suggest that colonies inside the cave have undergone substantial photoacclimation to their low light environment, potentially reducing photooxidative damage and contributing to lower tissue damage and greater thermal stress resilience.

These photoadaptations or photoacclimatory responses allow corals to compensate for reduced light availability by increasing photosynthetic capacity (Ferreira et al., 2015). Adaptations have been described in corals from mesophotic and shaded habitats, including variations in symbiont density and pigment concentrations, lower respiration rates, and increased photosynthetic efficiency (Anthony and Hoegh-Guldberg, 2003; Mass et al., 2007; Frade et al., 2008; Bongaerts et al., 2010; Lesser et al., 2010; Forcioli et al., 2011; Ziegler et al., 2015; Stewart et al., 2021). However, unlike tropical corals, which may shift symbiont species in response to the environment (Baker et al., 2003; Iglesias-Prieto et al., 2004; Cooper

et al., 2011; Bongaerts et al., 2013; Fiesinger et al., 2025), our genetic analyses and previous studies in the same region (Sarda et al., 2025) suggest that *E. singularis* colonies host the same symbiont both inside and outside the cave. Therefore, the observed differences could most likely be driven by physiological plasticity rather than symbiont turnover in *E. singularis*. Symbionts belong to the genus *Philozoon* and show clear genetic differentiation from other species within the genus (LaJeunesse et al., 2018), supporting a high degree of host-symbiont specificity (LaJeunesse et al., 2022) and the fact that *E. singularis* likely harbours an own *Philozoon* species (Sarda et al., 2025). However, the low amplification success in this study indicates that these results should be interpreted with caution, as we may not be detecting alternative symbiont species. Future studies should optimize molecular protocol for low-symbiont densities, for example by enriching symbiont cells prior to DNA extraction or using more sensitive molecular markers and amplification protocols.

Similarly to this study, the non-symbiotic red coral (*Corallium rubrum*) also showed reduced affectation by MHWs in colonies living inside compared to those at the entrance of a cave (Garrabou et al., 2001). This suggests that additional environmental factors beyond light reduction may sustain gorgonian colonies inside caves under the current climatic conditions (Martí et al., 2004; Rastorgueff et al., 2015; Gerovasileiou and Bianchi, 2021). Water circulation and food availability are key drivers of benthic community structure in

some submarine caves (Fichez, 1991; Gerovasileiou and Bianchi, 2021) and may strongly influence energetic balance of suspension feeders, such as gorgonians (Wildish and Kristmanson, 1997). Cova de la Vaca is a relatively small semi-dark and tunnel-like marine cave, in which hydrodynamic characteristics may potentially improve oxygen supply, facilitate waste removal and increase food and nutrients availability, thereby supporting metabolic demands under stress conditions. Although hydrodynamic conditions and food availability were not directly quantified in this study, previous studies in Mediterranean caves suggest that water circulation and the retention of suspended particulate matter can contribute to more favourable trophic conditions in tunnel-like caves (Morri et al., 1994; Gerovasileiou and Bianchi, 2021). Such conditions may allow heterotrophic food supply inside the cave to compensate for reduced photosynthetic carbon acquisition. In fact, the higher organic matter content observed in cave colonies likely reflects a combination of environmental and physiological processes, such as food supply or variations in metabolic demand, supporting differences in energy allocation between colonies. Overall, the refuge effect of this type of cave likely results from multiple interacting factors, including slightly lower temperatures, reduced light that may limit photooxidative stress during thermal events, and potential differences in hydrodynamic and trophic conditions, rather than light reduction alone.

It is important to note that this study has some limitations, as it was conducted in a single submarine cave. Therefore, the findings should be interpreted with caution and should not be generalized beyond semi-dark and tunnel-like caves with similar environmental characteristics. Submarine caves exhibit a wide range of morphologies and environmental gradients, including fully dark caves, semi-dark caves, tunnels, blind-ended caves, pits, among others (Gerovasileiou and Bianchi, 2021), which are likely to differ in the extent and the taxa to which they provide refuge from stressors. Further studies across a broader range of submarine cave types and environmental gradients, from cave entrances to inner sectors, are needed to assess the extent to which these refuge effects are consistent across Mediterranean submarine caves.

Despite the better conditions of *E. singularis* colonies inside the cave, they are not free from stress. 14.8% of colonies displayed a partial mortality higher than 10% of their tissue surface (considered to be natural for the species before the occurrence of MHWs; Linares et al., 2008). Additionally, a substantial proportion of non-reproductive colonies (28%) was still observed inside the cave, whereas in a study performed prior to the impacts of MHWs, non-reproductive colonies only accounted for 4% in the same Medes Islands (Ribes et al., 2007). Mortality patterns likely reflect the cumulative mortality of recent and past thermal stress, whereas reduced reproductive output may indicate delayed effects of previous temperature anomalies during 2023–2024.

Colonies outside the cave exhibited a male-deviated sex ratio, and both fertility and gonadal volume in female and male colonies were much lower than values reported in 2002, 2003, 2009, 2010 and 2021 for nearby populations (Gori et al., 2007, 2012; Sarda et al., 2025). Moreover, the 65% of non-reproducing colonies found outside the cave represents the highest value reported in the literature for shallow colonies of the species during May–June

(Ribes et al., 2007; Gori et al., 2012; Sarda et al., 2025). Female fertility is negatively correlated with the percentage of affected tissue (Sarda et al., 2025), indicating that the most impacted colonies also experience reduced reproductive output. Furthermore, the absence of large mature oocytes in the colonies outside the cave indicates their failure in reproducing during the study year.

The reproductive failure and elevated mortality observed outside the cave are consistent with an energetic trade-off framework driven by the combined effects of thermal and light stress. Elevated temperatures together with high light availability increase photo-oxidative stress in symbiotic corals, requiring greater energetic investment in cellular repair, antioxidant defences and maintenance of tissue integrity (Lesser and Farrell, 2004; Courtial et al., 2017). Because energy reserves are finite, increased allocation towards stress mitigation necessarily reduces the resources available for other essential biological processes such as growth and reproduction (Richmond, 1987; Ward, 1995). Reproduction is particularly energy-demanding and closely linked to the nutritional condition of colonies (Stimson, 1987; Ben-David-Zaslow and Benayahu, 1999; Gori et al., 2012, 2013; Viladrich et al., 2016). The lower organic matter content observed in colonies outside the cave likely reflects reduced energetic reserves, limiting investment in gametogenesis, particularly in females, which allocate substantially more energy to gamete production than males (Viladrich et al., 2017). Such energetic limitation is consistent with the reduced reproductive output, the absence of large mature oocytes and higher mortality observed outside the cave. As gorgonians rely on stored reserves to sustain metabolic demands and tissue repair under stress, depleted energy reserves may compromise both reproductive success and colony survival (Viladrich et al., 2017; Tignat-Perrier et al., 2022).

The presence of two cohorts of developing oocytes in cave colonies further highlights the potential importance of the refuge effect. This suggests that colonies inside the cave may retain sufficient energetic reserves to sustain gametogenesis, thereby preserving reproductive potential and future recruitment capacity under thermal and light stress. Consequently, submarine caves may function not only as climatic microrefugia for adult colonies but also as reproductive refugia. However, whether these populations can contribute to long-term persistence remains uncertain and will likely depend on their demographic and genetic connectivity with surrounding populations, which was not assessed in this study. Given the limited larval dispersal capacity of *E. singularis* (Theodor, 1967; Costantini et al., 2016), particularly at elevated temperatures (Viladrich et al., 2022), future studies should investigate connectivity between cave and open-habitat populations to determine the extent to which cave populations are demographically and genetically connected. Such studies will be essential for evaluating the long-term persistence of these potential refugia, assessing whether limited connectivity may increase their vulnerability to local population decline or other extinction processes (Gilpin and Soulé, 1986), and defining the broader applicability and temporal limits of the buffering capacity observed here.

The results of our study are particularly concerning, as in locations where the species has been most affected by MHWs, it also exhibits constrained population recovery capacity due to diminished reproductive investment and reproductive failure,

thereby suggesting an extinction debt for its shallow populations under recurrent MHWs (Hughes et al., 2013). In contrast, reproductive colonies inside the cave invested in reproduction as much as reported for colonies outside the cave before the impacts of MHWs (Gori et al., 2007, 2012). Our findings thus highlight the potential role of some submarine caves as climatic microrefugia for this gorgonian species, as well as the importance of identifying, monitoring, and protecting these habitats. Submarine caves are unevenly distributed across the Mediterranean Sea, and although 69% of known caves are located within marine protected areas (Gerovasileiou et al., 2026), many still lack specific conservation measures. Marine conservation strategies should explicitly incorporate these habitats into long-term monitoring programs to assess regional climate impacts, including the monitoring of mortality, population dynamics and distribution of cave communities and their associated habitat-forming species. Additionally, effective management measures to minimize local disturbances, such as regulating diving restrictions and limiting visitor access when appropriate are essential in these habitats particularly sensitive to physical damage. Based on our results, semi-dark and tunnel-like caves, such as the one studied here, should be considered priority sites for conservation. Finally, given the limited size and connectivity of cave populations, management strategies should also consider prioritizing the evaluation of demographic and genetic connectivity among cave and open-habitat populations to determine the long-term conservation value of these potential refugia. As MHWs recurrence intensifies across the Mediterranean Sea, understanding which microrefugia will remain effective, for how long and for which species, is a pressing conservation need.

Data availability statement

The DNA sequences presented in this study can be found online in GenBank. The address to the repository and accession numbers can be found below: <https://www.ncbi.nlm.nih.gov/genbank/>, accession numbers: PZ464134, PZ464135. Further data supporting the findings in this study is available under request.

Ethics statement

Ethical approval was not required for the studied species in accordance with the local legislation and institutional requirements. Sampling permits and official authorization from the Natural Park were given for the study.

Author contributions

JS: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. NV: Conceptualization, Investigation, Methodology, Resources, Supervision, Writing – review & editing. CL: Conceptualization, Funding acquisition,

Investigation, Project administration, Resources, Supervision, Writing – review & editing. FC: Methodology, Resources, Supervision, Writing – review & editing. YZ: Investigation, Writing – review & editing. PC: Investigation, Writing – review & editing. LF-F: Investigation, Writing – review & editing. AG: Conceptualization, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2026.1914797/full#supplementary-material>

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