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Research Article

Benthic foraminifera and brachiopods from a marine cave in Spain: environmental significance

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Abstract

Sediment samples from a marine cave in the Murcia region (eastern Spain) were analysed for grain size, total benthic foraminifera and dead brachiopoda to obtain environmental information through physical and ecological data in order to understand the benthic communities of cave environments and their ecological significance. A total of 100 foraminiferal and 7 brachiopod species were classified, highlighting the first occurrence in the western Mediterranean of *Gwynia capsula* (Jeffreys, 1859). Statistical analysis applied to foraminiferal data allowed the identification of three assemblages characterised by decreasing species diversity along the cave. This corresponded to a similar separation recognisable through changes in brachiopod species abundance and well-correlated with cave morphology. The relative abundance of epifaunal clinging-attached foraminifera as well as the rate of cave and sciaphilic/coralligenous Brachiopoda, thought to be representative of the degree of separation from marine conditions, were found to be highly correlated, increasing towards the inner cave. Our hypothesis was that despite the different lifestyles of these two groups, the strict correlation of environmental factors (i.e. light, nutrients, sediment texture, water parameters) changing along the length of the cave determines a comprehensive environmental gradient, causing an increase in environmental stress that has similar effects on the different taxonomic groups.

Keywords: Marine caves; grain size; benthic Foraminifera; Brachiopoda; ecological indicators; Murcia region.

Introduction

As a result of the overlap of several anthropogenic factors with natural variability, marine systems have undergone certain major changes in the last century. Global warming, sea-level rise and ocean acidification are among the main issues being studied and monitored because of their significant social consequences on a global scale. As a result, the development of innovative studies to highlight the temporal variability of these phenomena and their effects on marine ecosystems is of great importance. In this context, marine caves located at the boundary between continental and marine realms are unique environments where wide seasonal and annual environmental changes form a critical zone due to the interplay of different contributions. These caves may be considered as subterranean estuaries where the upper meteoric water mass of varying salinity buoys on a saline groundwater mass (van Hengstum *et al.*, 2019). Thus, marine caves represent an excellent opportunity - with the support of scientific divers - to investigate different topics in geo- and biosciences, such as macrofaunal biodiversity, food web structure, effects of sea-level change on habitat development, hydrogeological aspects, etc. (Brankovits *et al.*, 2018 and references therein). In these habitats, the living organisms develop highly adaptive strategies to face extreme spatial and temporal environmental variability and, for this reason, understanding how they respond to this stress provides basic knowledge on these effects on a larger scale.

In the Mediterranean basin, the marine caves are renowned for their biodiversity and ecological value,

although they remain poorly understood due to the difficulty of exploration and monitoring (Gerovasileiou & Voultsiadou, 2012; Ouerghi *et al.*, 2019). The position of these habitats makes them particularly sensitive to short- (seasonal) and long-term environmental variability, which determines changes in the distribution of species (Chevaldonné & Lejeusne, 2003; Montefalcone *et al.*, 2018; Sempere-Valverde *et al.*, 2019). They are generally characterised by a decreasing pattern of biodiversity and biomass proceeding from the marine entrance to the inside, which singles out successive ecozones, each inhabited by homogeneous benthic fauna as a response to the gradient of abiotic parameters such as light, nutrients and salinity (Bussotti *et al.*, 2006). Nevertheless, available environmental information on marine caves is mainly based on hard bottom assemblages such as sponges, which are the dominant group, as well as coralline algae, serpulids, brachiopods and bryozoans (Taddei Ruggiero, 1994; Taddei Ruggiero *et al.*, 1996; Rosso *et al.*, 2013; Gerovasileiou *et al.*, 2015; Gerovasileiou & Voultsiadou, 2016; Guido *et al.*, 2019). On the other hand, sediments have rarely been studied from either a biological or a sedimentological viewpoint, although they are of scientific interest both because their texture is proxy for hydrodynamic conditions and water flow patterns and because they host rich benthic communities (Fornós *et al.*, 2009; Navarro-Barranco *et al.*, 2012).

Benthic Foraminifera (BF), unicellular organisms living in soft sediments (with epiphytic, epifaunal and infaunal microhabitats) from transitional and coastal to deep-sea zones, have been increasingly recognised as reliable ecological indicators for the characterisation and monitoring of marine habitats (Dimiza *et al.*, 2015; Jorissen *et al.*, 2018). The advantage of studying BF in marine caves, where sampling is particularly difficult, is linked to the small sediment volume required for a quantitative study because of their small size and high abundance. Moreover, their mineralised shells, called 'tests', are preserved in the sedimentary record and provide a record of long-term environmental and sea-level change (e.g. van Hengstum *et al.*, 2009a; van Hengstum *et al.*, 2009b). Studies of recent BF in marine caves began in the last decade in tropical karst systems of the Yucatan peninsula (van Hengstum *et al.*, 2008) and Bermuda (van Hengstum & Scott, 2011). More recently, similar studies have been applied in the Mediterranean Sea, which is the only temperate region in which this research has been developed (Romano *et al.*, 2018a; Bergamin *et al.*, 2018). This research in the Mediterranean area began in 2013 in some marine caves of the Gulf of Orosei (Sardinia, Italy) with the intent to apply BF as environmental proxies, and it continues in other Mediterranean sites to advance our knowledge of the ecology of these organisms in relation to natural and anthropogenic environmental changes (i.e. sea-level changes, acidification, water contamination). These studies have highlighted that BF may live deep inside the caves, not only close to the entrance but up to several thousand meters inside, responding to the environmental gradient and contributing to the ecological zonation (Romano *et al.*, 2020).

Brachiopods are bivalve, sessile benthic organisms with a calcite shell. They live by filtering food from the water current under low-light conditions. Up until the Cambrian Period (541 million years BP), brachiopods lived in many environments, from reefs to carbonate platforms down to abyssal depths. Now, these primarily sciaphilous organisms occur in the Mediterranean in a fairly limited number of taxa (14 species belonging to 10 genera), which live in shallow waters of restricted environments such as caves and clefts and tend to be more abundant in the circalittoral zone and at the shelf edge. In contrast to BF, Brachiopoda have been widely documented and studied in cave environments in different areas of the Mediterranean Sea (Taddei Ruggiero 1994, 2001, 2003; Logan *et al.*, 2004; Rosso *et al.*, 2013; Gerovasileiou & Bailly, 2016, Rosso *et al.* in press, among others); these organisms find ample hard substrates and scarce competition in this environment, making it suitable habitat and refuge. In fact, they are common enough to pave cave walls and ceilings at a density of up to 600 individuals per square meter (Taddei Ruggiero, 1994).

This study was aimed at obtaining environmental information from samples collected in the CT12 cave (Cabo Tiñoso, Spain) through the study of sediment characteristics, foraminifers and brachiopods in order to improve the knowledge about the benthic communities of cave environments and their ecological significance. This is the first study combining the ecological information obtained from a quantitative foraminiferal study (total assemblage) with dead brachiopod fauna (thanatocoenosis) found in the cave sediment.

Material and Methods

Study area

The CT12 cave is located on the coast of the Murcia region (Spain, Mediterranean Sea) close to Cabo Tiñoso, between Cabo Falcón and El Arco. Rainfall is scarce (< 200 mm yr^{-1}), so much so that Cabo Tiñoso represents one of the driest areas in the region. The predominant marine current shows a NE-SW direction and has an average speed of 0.5 knots. The average monthly surface water temperature registers a maximum in August (24.8°C) and a minimum in February (14.2°C). The average water salinity is 37.9, while the average values of the tidal amplitude oscillate around 0.6 m (Giménez Casalduero *et al.*, 2009). The thermocline, which generally starts in April-May, can reach a depth of 30 m.

The coast of Cabo Tiñoso is characterised by imposing cliffs overlooking the sea, interrupted only by a few inlets in which there are small stretches of sandy beach. The cliffs, at the base of which there are boulders and soft bottom with a steep slope, extend up to a depth of 20-30 m. The continental shelf has modest extension in the entire area; the escarpment, carved by several underwater canyons, starts from -300 m to 2,200 m (Giménez Casalduero *et al.*, 2009).

From a geological viewpoint, this coastal sector rep-

Medit. Mar. Sci., 21/3, 2020, 506-518

507

resents the southwestern end of the Betic Cordillera, where two overlapping tectonic complexes outcrop; one consists of mica-schist, quartzite, gneiss and marble, and the other is primarily composed of carbonate. In the study area, weakly metamorphosed rocks, fillades and quartzites outcrop, overlaid by a powerful succession of limestones and dolomites in which numerous caves of various dimensions and settings have developed, especially in connection to fractures related to tectonics (Garcia-Tortosa *et al.*, 2000). The region with the largest number of caves is Cartagena, with 48.3% of the total cavities in the inventory of the 'Federaciòn Murciana de Espeleologia'.

In particular, in the Cabo Tiñoso area there are six submerged cave systems: the cave of the lake (or of the Arco), that of La Virgen (or of Neptuno), the system of the Cuevas Gemelas (with two differentiated cavities CT11 and CT12), the Estalagmitas cave (CT17) and the Ovaza complex (Ros Vivancos, 1988).

Survey and sampling

Survey and sampling of the cave were carried out by Global Underwater Explorers (GUE) divers, who are specifically trained for scientific diving in marine caves, and ISPRA researchers according to GUE procedures. Divers positioned a permanent line from the entrance to the inner portion of the cave and the starting point was georeferenced through a Surface Marker Buoy. The line was used as a reference for the preliminary mapping of the cave by means of Mnemo device. Labelled cookies were positioned on this line, starting from the connection of the two entrances and following the cave morphology, for identification of the seven sampling stations, at which the distance to the entrance (DE) and water depth (W) were measured (Fig. 1, Table 1). Divers manually collected the superficial sediment samples (0-2 cm) at each station: two aliquots of 50 cc each were taken for grain size analysis and the faunal study, respectively.

Grain size analysis

For grain size analysis, samples were pre-treated twice with a solution of hydrogen peroxide (30%), then washed twice with natural water and wet-separated into two frac-

Table 1. Sampling stations in the CT12 cave. Distance to the entrance (DE) and water depth (W) were measured during the sampling.

	DE (m)	W (m)
CT1	0.0	14.7
CT2	35.0	7.9
CT3	45.0	9.1
CT4	65.0	6.7
CT5	75.0	7.1
CT6	95.0	9.7
CT7	120.0	13.4

tions (> 63 μm and < 63 μm), which were oven-dried and weighed. The coarser fraction (> 63 μm) was dry-sieved using ASTM series sieves with meshes ranging from -1 to +4 φ at intervals of 0.5 φ, and results were given as % weight. The fine fraction (< 63 μm) was analysed by means of x-ray sedigraph (Sympatech Helos). The results from two different instrument analyses were then merged to obtain the full distribution curve of the sediment (Romano *et al.*, 2018b). The > 63 μm fraction was also examined under a stereomicroscope (M165C, Leica) to qualitatively determine the composition of the biotic and abiotic components. Sediment was classified according to the ternary classification of Shepard (1954).

Foraminifera and Brachiopoda study

For the quantitative analysis of BF, samples were wet-sieved at 63 μm and split by means of dry Microsplitter into aliquots containing at least 300 specimens according to Schönfeld *et al.* (2012), then picked and counted under a stereomicroscope. The count of BF was carried out in the total assemblage and considered as the sum of several generations over time, including those that were possibly living at the time of sampling. This approach prevents seasonal variability from affecting foraminiferal species (Duchemin *et al.*, 2008), supplying information on mean environmental conditions (Leorri *et al.*, 2008) and allowing the identification of distinct environments (Little & van Hengstum, 2019). In order to prevent the inclusion of reworked or transported specimens, only well-preserved
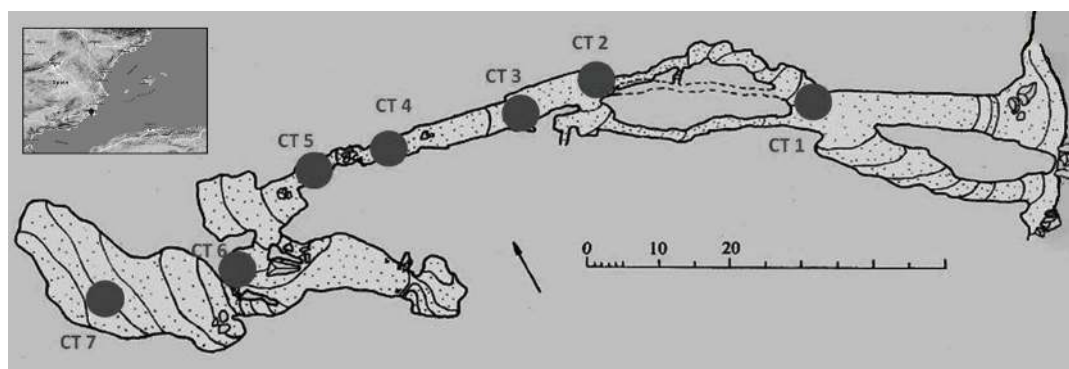

Fig. 1: Location of the study area and map of the CT 12 cave with sampling stations (from www.caveatlas.com, survey carried out by Centro Escursionista Cartagena, modified).

tests without breakages or abrasion signs were picked, counted and classified. The classification of BF at the genus level was done according to the most-used taxonomical study on foraminiferal genera (Loeblich & Tappan, 1987), while species were determined according to several important studies in the Mediterranean area (Cimerman & Langer, 1991; Sgarrella & Moncharmont-Zei, 1993) and the World Modern Foraminifera Database (Hayward *et al.*, 2011). The foraminiferal density was given as foraminiferal number (FN, the number of specimens per gram of dry sediment), as defined by Schott (1935). The species diversity was represented by H-index, which considers both the abundance and evenness of species (Murray, 1991; Shannon, 1948). The dominance (D) was also determined, taking into consideration that stressed environments may be characterised by assemblages with low diversity and high dominance of one or a few species (Magurran, 2004). Absolute species abundance was standardised with respect to 1 g sediment dry weight (Dijkstra *et al.*, 2020).

The census of Brachiopoda species was conducted by picking all specimens (at least 50) from the same sediment aliquot used for BF. For *Novocrania anomala* (Mueller, 1776) - considering that this species lives fixed to hard substrates and, once it dies, only the free valve falls to the bottom - only single sub-circular valves were counted and measured. The other species were counted as loose individuals with closed valves because their pedicle does not remain attached to the cave walls or ceiling upon death. The number of brachiopod individuals per station was counted and the changes in diversity and frequency along the distance from the cave entrance were determined.

Statistical analysis

Statistical analysis was applied only to quantitative data of BF because of the need to reduce the variability of a high number of recorded taxa, while it was not applied to brachiopod data due to low absolute numbers. Two-way (Q-mode and R-mode) Hierarchical Cluster Analysis (HCA) was applied to the relative abundance of the commonly occurring foraminiferal species (> 5% in at least one sample) to identify groups of samples with homogeneous foraminiferal content corresponding to the distinct assemblages (Scott *et al.*, 2001). The Euclidean distance coefficient was used to compare samples, and Ward's method of minimum variance was used for assembling clusters (Hammer *et al.*, 2001; Parker & Arnold, 1999). The canonical correspondence analysis (CCA) was carried out on the relative abundance of commonly occurring foraminiferal species, grain size results, water depth (W) and distance to entrance (DE) of each sampling station to determine the influence of sediment texture and position in the cave on species distribution. Finally, the correlation between the relative abundance of clinging/attached BF and the rate of sciaphilic/coralligenous brachiopod species, both considered as indices of estrangement from marine conditions, was determined by Pearson correlation coefficient. Statistical analysis was conducted using the statistical package PAleontological STatistics, PAST 3.18 (Hammer *et al.*, 2001; Hammer & Harper, 2006).

Results

Survey and cave description

The CT12 cave is characterised by typical features of a marine cave, with two entrances positioned at 12 and 23 m water depth. The shallow entrance has a relatively high ceiling and a canyon shape, while the deeper entrance is a low passage, quickly rising towards the other passage following a slope of organic sediment (Fig. 2). Once the two passages connect, the morphology quickly changes into a vertical passage where the presence of warmer freshwater is immediately noticeable. Between stations CT2 and

Fig. 2: CT 12 cave environment. The micrite coat is evident on the floor (photo courtesy of Belen Andres).

CT4, the passage assumes a regular elliptic cross-section, with some speleothems and obvious signs of chemical erosion on the upper portion of the cave. A minor restriction gives access to a wider room and finer sediment deposits, but an abrupt change in the direction of the cave identifies the progression. Another split towards the end of the cave distinguishes two very morphologically different areas; the left branch ends in a sediment pile, while the right branch drops down about 30 m into a breakdown room filled with large blocks and fine white sediment.

Grain size and mineralogical content

The textural characteristics of the sediments highlighted a mainly sandy composition for the sample closest to the entrance, CT1 (Table 2; Table S1; Fig. S1). In the CT2-CT4 section, the fine fraction prevailed, with sediments ranging from clayey silt (CT2) to sandy silt (CT3 and CT4). In CT5 the sandy component prevailed again (77%), while in CT6 the highest percentage of pelite was recorded (92.2% of silt and 5.5% of clay). Finally, in CT7 the sediment composition was classified as loam.

In all analysed samples, the compositional characteristics of the sandy fraction were quite similar. Sediments were made up almost exclusively of bioclasts, in particular the coarse shells of bivalves, gastropods, brachiopods, ostracods, foraminifers, spicules of sponges, serpulids and bryozoans. There were also dark lithic limestone fragments and calcite granules. A micrite coat covered bioclasts, and fragile pebbles of carbonate nature (concretions) and earthy consistency were observed, particularly in samples CT6 and CT7 (Fig. 3).

Table 2. Grain size results. Main grain size classes expressed as % dry weight.

	Gravel	Sand	Silt	Clay	Shepard classification
CT1	1.3	87.9	8.0	2.8	Sand
CT2	1.8	4.4	62.9	30.8	Clayey silt
CT3	3.4	29.7	47.4	19.5	Sandy silt
CT4	12.2	4.3	74.2	9.4	Sandy silt
CT5	11.0	66.0	15.4	7.6	Sand
CT6	0.0	2.3	92.2	5.5	Silt
CT7	25.0	27.2	27.9	20.0	Loam

Benthic Foraminifera

The absolute abundance of BF in the CT12 cave was generally high, with no linear pattern with respect to distance to the cave entrance (Fig. 4). The most evident difference was between the station at the entrance, which displayed a FN around 1,200, and those inside the cave, where the highest FN was recorded at CT2 (14,300); in
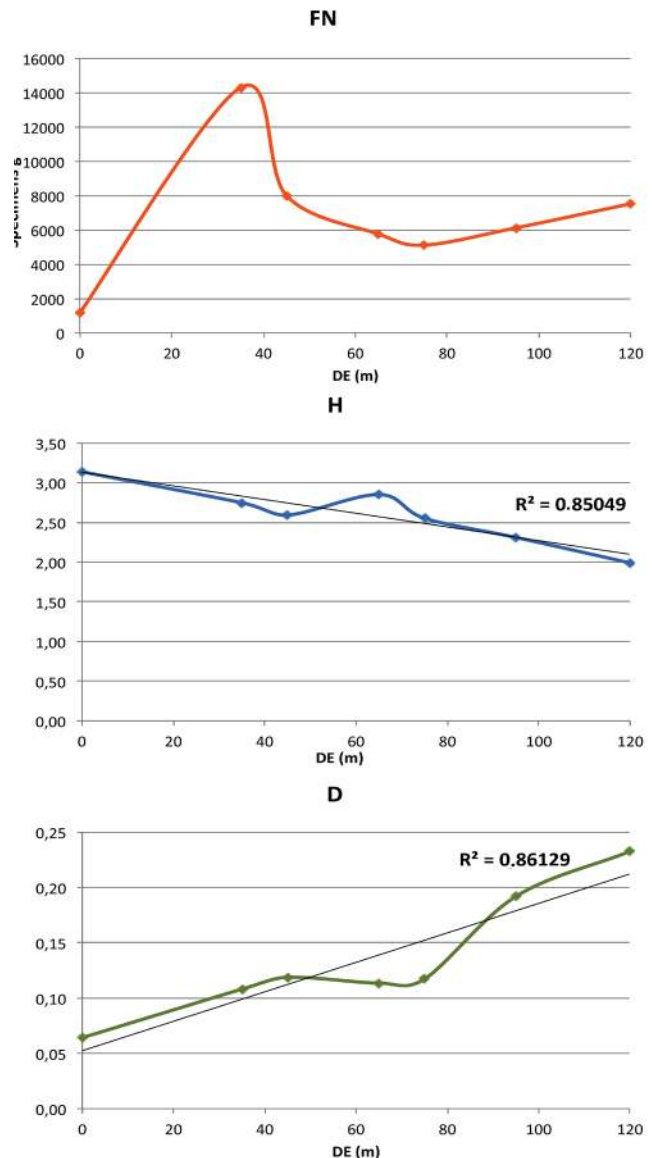
Fig. 4: Values of Foraminiferal Number (FN) Shannon index (H) and Dominance (D) along the cave profile.

Fig. 3: Sediment features of > 63 mm fraction in samples CT1, CT4 and CT7.

510

Medit. Mar. Sci., 21/3 2020, 506-518

the inner stations, FN was less variable (5,117-8,000). H, which is a proxy of species diversity, displayed a clear decreasing pattern in relation to DE, while D showed the opposite trend. A total of 100 species were classified and, in terms of absolute abundance, the species with the highest numbers were *Patellina corrugata* (Williamson, 1858), *Spirillina vivipara* (Ehrenberg, 1843) and *Tubinella inornata* (Brady, 1884). Other common species included *Miliolinella subrotunda* (Montagu, 1803), *Gavelinopsis praegeri* (Heron-Allen & Earland, 1930), *Spirophthalmidium emaciatum* (Haynes, 1973), *Rosalina* spp., mainly *R. bradyi* (Cushman, 1915), and *Sejunctella* sp. (Fig. 5; Table S2).

The HCA, carried out on relative abundance data of commonly occurring species (Table S3), identified one single sample and two distinct clusters characterised by similar faunal content, corresponding to a specific foraminiferal assemblage (Fig. 6) and distributed according to the succession of sampling stations and the morpholo-gy of the cave. Sample CT1 was clearly different from all other samples. The most abundant species in the assemblage were *G. praegeri* (14%), *M. subrotunda* and *Cibicidoides lobatulus* (Walker & Jacob, 1798) (10%), and *Textularia bocki* (Höglund, 1947) (9%). These samples were characterised by the highest H (3.1) and the lowest D (0.06) and FN (1,180), while all other samples shared the common characteristic of being dominated by *P. corrugata*, *S. vivipara* and *T. inornata* and were grouped into clusters A and B.

Cluster A, which is the most heterogeneous, included samples from the intermediate section of the cave; they showed similar percentages of two dominant species, *P. corrugata* at 16-26% and *S. vivipara* at 15-23%, while *T. inornata* was significantly lower (6-18%). Other common taxa in this cluster were *Sejunctella* sp. (2-7%) and, although widely variable, *Sigmoilopsis schlumbergeri* (Silvestri, 1904) (0.5-11%) and *S. emaciatum* (0.3-8%). In these samples, H ranged between 2.6 and 2.9 and D
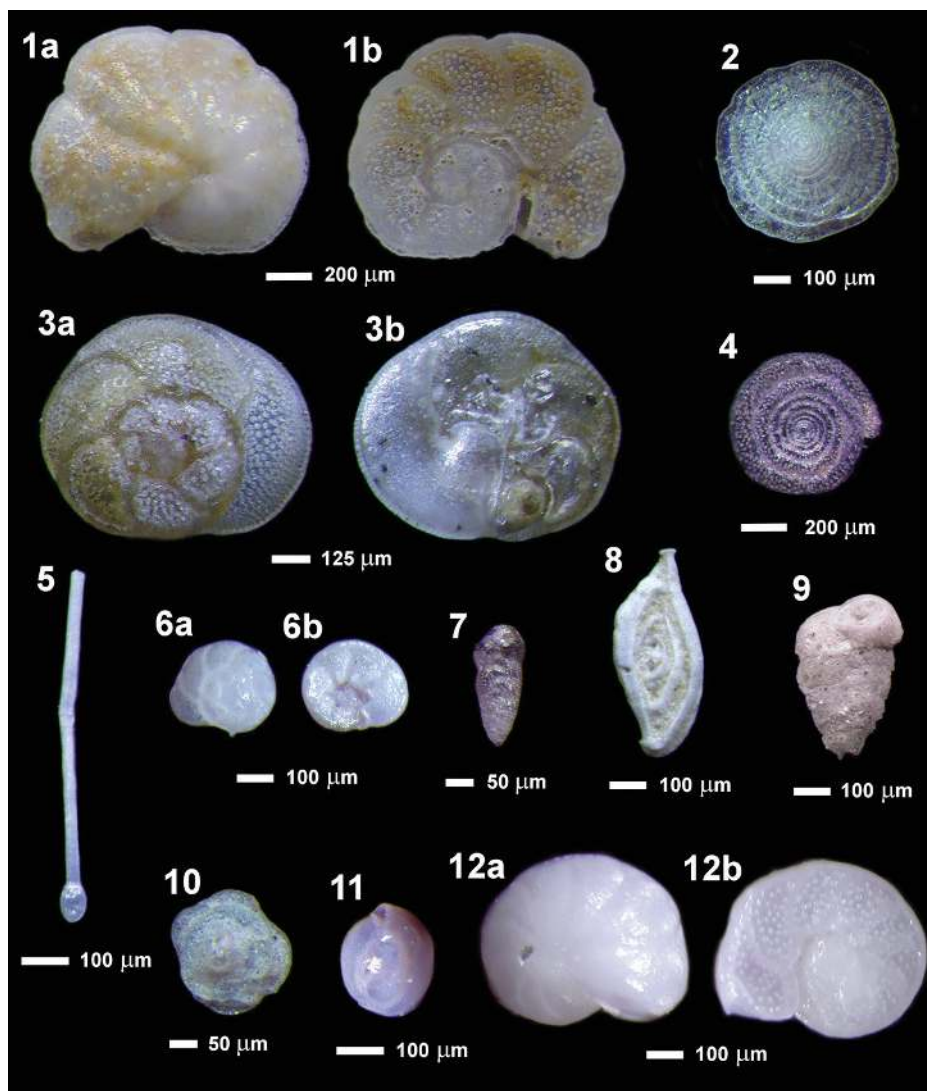

Fig. 5: Commonly occurring Benthic Foraminifera: 1) *Cibicidoides lobatulus*, ventral view (a), dorsal view (b); 2) *Patellina corrugata*, dorsal view; 3) *Rosalina bradyi*, dorsal view (a), ventral view (b); 4) *Spirillina vivipara*; 5) *Tubinella inornata*, lateral view; 6) *Gavelinopsis praegeri*, dorsal view (a), ventral view (b); 7) *Bolivina variabilis*, lateral view; 8) *Spirophthalmidium emaciatum*, lateral view; 9) *Textularia bocki*, lateral view; 10) *Sejunctella* sp., dorsal view; 11) *Miliolinella subrotunda*, lateral view; 12) *Cibicides refulgens*, ventral view (a), dorsal view (b).
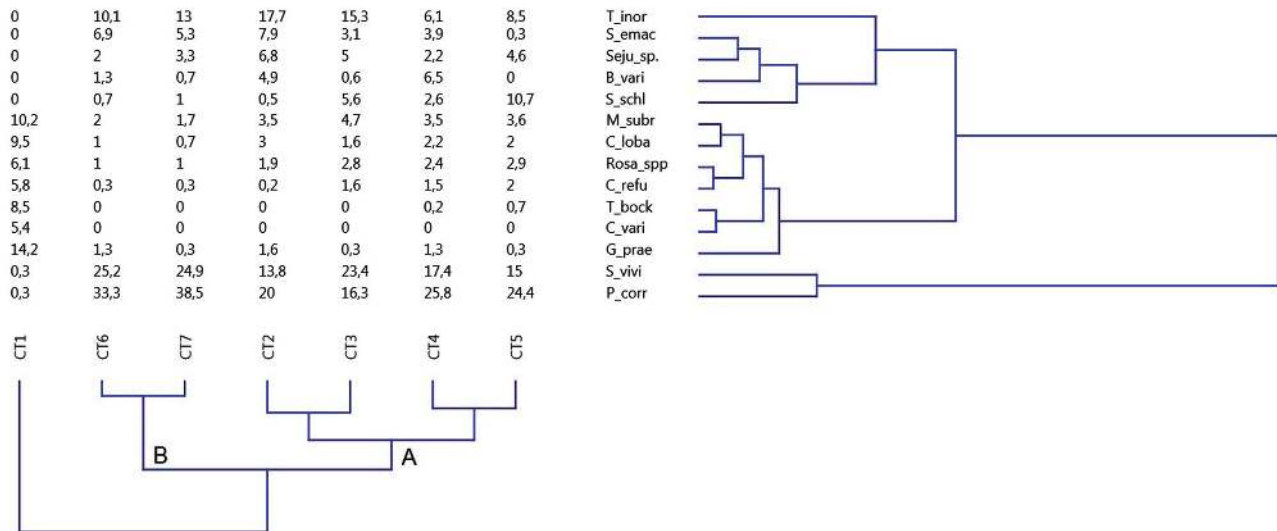
Medit. Mar. Sci., 21/3, 2020, 506-518

511

Fig. 6: Two-way (Q-mode and R-mode) Hierarchical Cluster Analysis (HCA) based on relative abundance of commonly occurring foraminiferal species.

was relatively stable at 0.11-0.12 while the FN was highly variable, ranging between 5,117 and 14,300. Cluster B included samples from the two innermost stations. Here, *P. corrugata* (33-39%) clearly became the dominant species at the disadvantage of the typical species at the cave entrance (CT1), which practically disappeared. *S. vivipara* (25% in both samples) and *T. inornata* (10-13%) showed similar abundance to cluster A. The lowest H (2.0-2.3) and highest D (0.19-0.23) values were recorded in these samples, while FN ranged between 6,120 and 7,525.

Brachiopoda

Overall, seven brachiopod species belonging to six genera were recognised: *Novocrania anomala* (Mueller, 1776), *Tethyrhynchia mediterranea* (Logan, 1994), *Megathiris detruncata* (Gmelin, 1791), *Argyrotheca cuneata* (Risso, 1826), *A. cistellula* (Searles-Wood, 1841), *Joania cordata* (Risso, 1826) and *Gwynia capsula* (Jeffreys, 1859) (Fig 7; Table 3; Table S4). The valves of *N. anomala* were sub-circular and 15 mm wide. The other species were much smaller, reaching the following sizes in shell diameter: 6 mm *M. detruncata*, 4 mm *A. cuneata* and *J. cordata*, 1.5 mm *T. mediterranea* and *A. cistellula*, and a mere 1 mm *G. capsula*. Species richness varied between three and six with a general decreasing trend from the entrance (CT1) to the innermost station (CT7). For absolute abundance, the most numerous were *A. cistellula* (173 specimens) and *A. cuneata* (150 specimens) followed by *T. mediterranea* (138 specimens) and *N. anomala* (119 specimens). The species were categorised according to Rosso *et al.* (2013) into the 'sciaphilic/coralligenous species' and 'cave species' ecological groups (Table 3). Two species of the first group, *A. cistellula* and *A. cuneata*, were recorded in all the stations. The first was very abundant throughout the cave with percentages ranging between 38.5% and 50.0%, with the exception of CT1 and CT5 where it was 12.4% and 10.5%, respective-

ly. Conversely, the second species displayed the highest percentages in CT 1 (39.8%) and CT4 (41.2%), while in the other stations the values ranged between 8.9% in CT7 and 22.7% in CT5. *N. anomala* was recorded from the entrance to CT5, where it showed the highest percentage (43.1%). *M. detruncata* was recorded in just three stations at low numbers, while *J. cordata* was present only in CT1 at 25.7%. Among the 'cave species', only two taxa were recognised. One of these, *G. capsula*, was exclusively found in CT6 at 10.9%. The other species, *T. mediterranea*, was found throughout the cave, with the lowest value at CT1 (1.8%) and variable values along the tunnel, with the highest value found at CT7 (51.8%).

Discussion

Morphological, textural and faunal characteristics were considered to identify different habitats within the cave environment. The grain size results revealed a great heterogeneity of sediment texture, with a prevalence of coarse sediment (gravel and sand) at the cave entrance (CT1) and an abundance of fine fractions (silt and clay) inside the cave, which reflects its morphology and bathymetric profile. Nevertheless, there were some exceptions to this general pattern (i.e. CT5), where the granulometric distribution had an inverse trend due to specific morphological features of the cave (Fig. S1). To interpret these results from a hydrodynamic viewpoint, it should be considered that coarse sediment fractions are nearly exclusively bioclasts derived from typical organisms of the cave environment, likely autochthonous and not transported from the sea by high-energy fluxes; this is confirmed by the absence of a decreasing pattern towards the inner stations of this component. Consequently, the high variability of sediment texture may not be attributed to high spatial variability of hydrodynamic conditions; actually, a low-energy environment may be supposed in the cave for the general presence of pelitic sediment (Table

Fig. 7: 1) *Novocrania anomala*, dorsal valve (a), outer (b) inner view; 2) *Tethyrhynchia mediterranea*; 3) *Argyrotheca cistellula*; 4) *Joania cordata*; 5) *Gwynia capsula*; 6) *Argyrotheca cuneata*, dorsal view (a), ventral view (b), internal view with septum and brachidium (c).

Table 3. Relative abundance of Brachiopoda. The two categories were defined according to Rosso *et al*. (2013): cave species, sciaphilic/coralligenous species.

	CT1	CT2	CT3	CT4	CT5	CT6	CT7
Gwinia capsula	0.0	0.0	0.0	0.0	0.0	10.9	0
Tethyrynchia mediterranea	1.8	30.8	33.6	9.8	17.7	25.0	51.8
Total cave species	**1.8**	**30.8**	**33.6**	**9.8**	**17.7**	**35.9**	**51.8**
Argyrotheca cistellula	12.4	38.5	40.8	39.2	10.5	50.0	39.3
Argyrotheca cuneata	39.8	17.9	17.6	41.2	22.7	14.1	8.9
Novocrania anomala	19.5	12.8	8.0	7.8	43.1	0.0	0.0
Joania cordata	25.7	0.0	0.0	0.0	0.0	0.0	0.0
Megathiris detruncata	0.9	0.0	0.0	2.0	6.1	0.0	0.0
Total sciaphilic/coralligenous species	**98.2**	**69.2**	**66.4**	**90.2**	**82.3**	**64.1**	**48.2**
Total # individuals	**113**	**39**	**125**	**51**	**181**	**64**	**56**
Number of species	**6**	**4**	**4**	**5**	**5**	**4**	**3**

2). Also, the micrite coat, which mainly constitutes the fine sediment fraction and is likely due to autochthonous carbonate precipitation as recognised in marine caves of Mallorca Island and Bermuda (Fornós *et al.*, 2009; Little & van Hengstum, 2019), confirms such conditions.

The clear succession of distinct foraminiferal assemblages along the cave also indicates the absence of significant post-mortem transport, which would have caused the mixing of fauna from different sections of the cave. The excellent state of conservation of small-sized and thin-walled foraminiferal fauna confirms the absence of high-energy water fluxes, which would have damaged the fragile tests. This reveals that, although samples were not stained for the recognition of living specimens, the total foraminiferal and dead brachiopod assemblages found in the sediments of the cave were not affected by significant post-mortem displacement. These results demonstrate that the environmental gradient along the cave influenced the composition of the assemblage. In fact, the decrease in species diversity and the increase in dominance indicate the rise of environmental stress moving towards the inner sector. This behaviour agrees with that commonly shown by other taxonomic groups in cave environments, depending on the physical gradients inside the cave (i.e. light, oxygen, salinity, etc.), the trophic supply gradient, and the limited capacity of the larvae for dispersion and settlement (Navarro-Barranco *et al.*, 2012). Although this study, due to logistical problems during the sampling activity, did not include the measurement of water parameters, some information on factors determining the distribution inside the cave of both Foraminifera and Brachiopoda may be deduced from the ecological characteristics of dominant species.

Epifaunal Foraminifera were prevalent in all samples and their abundance was positively correlated to DE (Fig. 8). In particular, a main faunal turnover from the cave entrance (CT1) to the tunnel (cluster A and B) was observed. Among the most abundant taxa in CT1, both *G. praegeri* and *Rosalina* spp. are epifaunal, attached or clinging to hard substrates; the first species is widespread on the continental shelf, while the second is generally epiphytic (Sgarrella & Moncharmont-Zei, 1993; Murray, 2006). They were both common in the marine caves of the Gulf of Orosei (Sardinia, Italy), more specifically in

the Entrance Ecozone, which extended up to 300 m inside the cave depending on season and cave morphology. *M. subrotunda* is an epifaunal species on plants or sediments, which was also found in the Entrance Ecozone of the Bel Torrente cave (Bergamin *et al.*, 2018; Romano *et al.*, 2018a; 2020). Among the other taxa, the common occurrence of *T. inornata*, which lives attached to hard substrates by an organic cement at the base of the proloculus (Cooke, 1978), should be mentioned. Two other assemblages were recognised, corresponding to samples from clusters A and B. Among the species abundant in both clusters, *S. vivipara* and *P. corrugata* live clinging to hard substrates such as rocks, large mineral grains, bioclasts or wood fragments (Murray, 2006). These two species were abundant in the Isolated Submarine Cave Assemblage recognised by van Hengstum & Scott (2011) in the most distal passages of Bermuda caves, completely flooded by marine water; they were thought to be gathering suspended food resources transported by saline groundwater circulation or, alternatively, using abundant high-quality, nitrogen-rich marine organic matter that is present in the distal cave benthos. This assemblage was dominated by *S. emaciatum*, which was also rather common in the CT12 cave. The same species, but also the less abundant *Sejunctella* sp., represented the characterising species of the Subtidal Marine Assemblage recognised in other Bermudian caves by Little & van Hengstum (2019) and thought to be associated with organic carbon from marine sources. Another common species in this assemblage was *S. emaciatum*, reported as an indicator of oxygenated saline groundwater, frequent also in the CT12 cave. The faunal change characterising the transition from cluster A to cluster B did not consist of a species turnover, but in a change of the assemblage structure due to a marked increase in D for increasing abundance of *P. corrugata* and the disappearance of species typical of the cave entrance (Fig. 4).

In the present study, the effects of sediment texture together with distance and water depth of each sampling station on species distribution were investigated by means of CCA (Fig. 9). From the scatter plot, it may be observed that DE and W, as well as sand, silt and clay, clearly plot on the first axis together with most foraminiferal species (Fig. 9). This suggests that these variables have a direct
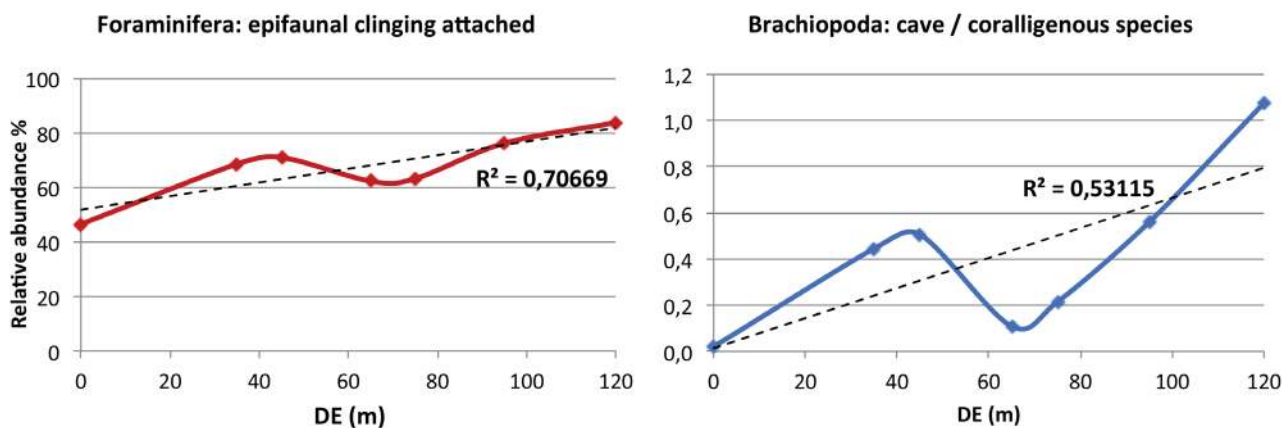

Fig. 8: Relative abundance of epifaunal clinging or attached foraminiferal taxa along the cave profile (left); rate between the two Brachiopoda groups A and B, according to Ross *et al.*, 2013 (right).
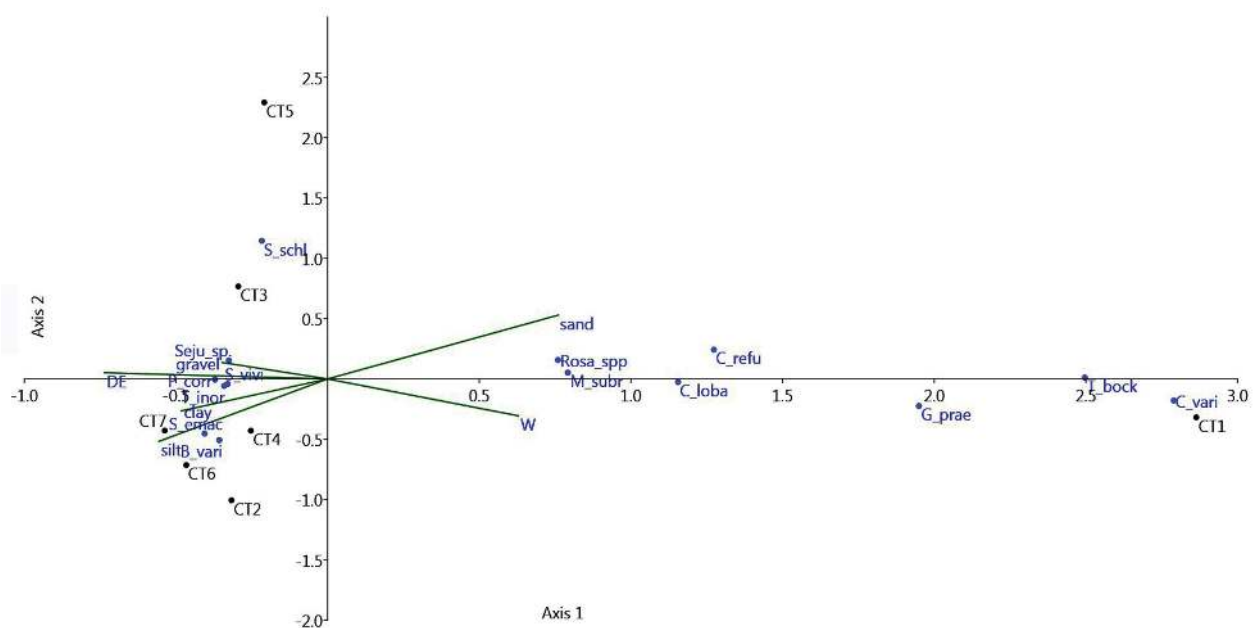
Fig. 9: Canonical correspondence analysis on relative abundance of commonly occurring species, with the main grain size fractions and cave data considered as environmental factors. The first and second axis account for the 79% and 11% of variance, respectively.

or indirect influence on foraminiferal distribution. Moreover, the clear separation of CT1 from all other samples along the first axis corresponds well to the HCA. Species characterising CT1 plot on the positive side of the first axis, associated with higher sand content and higher W. Among these species, *C. lobatulus* and *R. bradyi* were found to be correlated with sediment fractions ranging from gravel to coarse sand, indicating that these taxa use large grains as substrate (Celia Magno *et al.*, 2012). Species typical of clusters A and B plot on the negative side of the first axis and are associated with the fine sediment fractions (silt and clay), but also with gravel. The same preference by *P. corrugata*, *S. vivipara* and *S. emaciatum* for pelitic sediment was recognised by Little & van Hengstum (2019). This indicates that they prefer to attach to larger fragments associated with pelitic sediment. The CCA does not highlight the separation of clusters A and B recognised by the HCA, indicating that the parameters considered in this analysis are not responsible for the faunal transition from A to B. The high abundance of BF in these samples may indicate a high nutrient availability corresponding to cluster B, while the increasing opportunistic behaviour of *P. corrugata* moving away from the entrance may represent the response to increasing environmental stress (Alve, 1995, 2003). Consequently, the role of organic carbon recognised by Little & van Hengstum (2019) as a main factor influencing BF in the Bermudian caves may be supposed also for the CT12 cave.

The brachiopods in CT12 are all typical of Mediterranean cave environments, although the abundant *T. mediterranea* remains are not always commonplace in Italian marine caves. For instance, this species was not present in the Gulf of Naples (Taddei Ruggiero, 2001), whereas it was abundant in Sicily (Rosso *et al.*, 2013; Sanfilippo *et al.*, 2015). One noticeable exception is *G. capsula*, which has been never recorded in western Mediterranean

caves until now (Simon & Willems, 1999). Taking into account the distribution of species, three sectors may be recognised in the cave: a) the cave entrance, characterised by *J. cordata*, which was very abundant and only occurred here, represented by young individuals; b) the cave tunnel, where *Argyrotheca* spp. and *N. anomala* appeared as the best-represented taxa; and c) the large room in the inner cave, where a low-diversity assemblage was dominated by sciaphilic and micromorphic species and most 'sciaphilic/coralligenous species' disappeared. This subdivision of the cave coincides with the same sectors identified by the foraminiferal assemblages. Two of the ecological groups identified by Rosso *et al.* (2013), 'cave species' and 'sciaphilic/coralligenous species' were recognised in this study. The species of the first group are primarily sciaphilic species, typical representatives of marine cave communities though they also colonise other very sheltered microenvironments, often associated with species of the second group. In this study, they were represented by *T. mediterranea*, the only species exclusive to the cave environment, and *G. capsula* (Logan & Zibrovius, 1994; Logan *et al.*, 1997; Simon & Willems, 1999). The second group shows a preference for shadowed and sheltered biotopes such as cave overhangs, 'coralligenous' concretions, and the underside of small substrata lying on soft bottoms even at shallow depths. In this study, this group was represented by *N. anomala*, *M. detruncata*, *A. cistellula*, *A. cuneata* and *J. cordata*. Among these, *Argyrotheca* spp. and *J. cordata* fare better under more intense light, and can therefore occur in dim light conditions. This ecological characteristic would explain the exclusive presence of *J. cordata*, always represented by young individuals, in CT1. The rate of abundance between the two groups was positively correlated with DE, corresponding to an environmental gradient inside the cave in terms of light, nutrients, etc. (Fig. 8). Moreover,

Medit. Mar. Sci., 21/3, 2020, 506-518

515

the values of this parameter were distinct in the three sectors of the cave previously recognised; in particular, it was lowest at the cave entrance (0.02), had intermediate values (0.11-0.51) in the tunnel, and displayed the highest values in the terminal room (0.56-1.07).

The rate of two ecological groups of Brachiopoda and the relative abundance of clinging/attached BF, which may be considered as indices of the degree of estrangement from marine conditions, displayed a strong positive correlation (r = 0.92, p = 0.004). Because of the different lifestyles of the two groups, it is difficult to find a common environmental factor influencing both the abundance of brachiopod cave species and the epifaunal clinging/attached BF. Nevertheless, the environmental gradient inside marine caves is generally determined by different rates of marine and continental contributions in terms of light, nutrients, water and sediment, which are strictly correlated among them.

Based on Foraminifera and Brachiopoda distribution, while also considering the sediment texture, it is possible to recognise specific sectors of the cave, each one homogenous from an environmental viewpoint, which corresponds well to the cave morphology. These sectors consist of an entrance area, at the connection of the two passages, a tunnel sector, and a larger terminal room of the cave. The first sector corresponds well to the Entrance Ecozone recognised in the caves of the Gulf of Orosei (Bergamin *et al.*, 2018; Romano *et al.*, 2018a, 2020), while the other two sectors are comparable to the marine assemblages of the Bermuda caves (van Hengstum & Scott, 2011; Little & van Hengstum, 2019).

Conclusion

Sediment of the CT12 cave was found to originate *in situ* because it was constituted nearly exclusively of bioclasts of cave organisms for the > 63 μm fraction and by authigenic micrite for the < 63 μm fraction. Because of the autochthonous origin of the cave sediment and low hydrodynamic conditions deduced from high pelitic content, the textural variability does not reflect water fluxes supplying sediment, but rather is strongly conditioned by cave characteristics.

Diversity of the foraminiferal assemblages was negatively correlated with the distance to the cave entrance, indicating increasing environmental stress influencing the community structure, while the relative abundance of epifaunal clinging/attached taxa increased with the distance. Different foraminiferal assemblages were recognised according to the cave morphology, corresponding to the cave entrance, the tunnel, and the terminal room. Sediment texture and, possibly, nutrient availability, were identified as the main environmental driving factors for species distribution.

Brachiopods were somewhat abundant in sediments of the cave and fall into three distinct ecological assemblages, depending on the species tolerance to dim light conditions, the abundance of nutrients and cave morphology. The rate of cave and coralligenous taxa increased along the cave and was positively correlated to the distance to the cave entrance. The species *Gwynia capsula*, undocumented in the western Mediterranean to date, was sporadically found in the CT12 cave.

The independent study of BF and Brachiopoda led to the same ecological subdivision of the cave, and different indices of estrangement from marine conditions based on the two groups were found to be highly correlated. Despite the different lifestyles of these two groups, the strict correlation of environmental factors (light, nutrients, sediment texture, water parameters) changing along the cave for the different marine and continental contributions determine a comprehensive environmental gradient, causing the increasing environmental stress with similar effects on the different taxonomic groups.

The recognition of three distinct sectors of the cave, based on evidence obtained from the combined study of foraminifera, brachiopoda and sediment texture, lays the foundation for the recognition of specific ecozones. Further study, including more sampling stations and additional environmental parameters, will allow for better definition of these ecozones.

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516

Medit. Mar. Sci., 21/3 2020, 506-518

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Supplementary data

The following supplementary information is available on line for the article:

Fig. S1: Grainsize distribution curve; gravel (orange), sand (yellow), silt (green), clay (blue).
Table S1. Results of grain size analysis with sediment fractions at 0.5 φ interval.
Table S2: Foraminifera absolute abundance standardized at 1 g dry sediment. Faunal parameters are also given at the table bottom.
Table S3: Relative abundance of commonly occurring foraminiferal species.
Table S4: Absolute abundance of Brachiopoda.

518

Medit. Mar. Sci., 21/3 2020, 506-518