Benthic foraminifera as environmental indicators in extreme environments: The marine cave of Bue Marino (Sardinia, Italy)

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ABSTRACT

The coast of the Gulf of Orosei (Sardinia, Italy) consists of impressive cliffs set up on dolostones and limestones characterized by wide karst systems connected to the sea. Marine caves, which are part of these system flooded by seawater through marine entrances, may be considered as extreme environments because of wide spatial and temporal environmental variability due to changing marine and terrestrial contributions. This study presents the results of the third survey carried out in summer 2016 in the Bue Marino cave, as part of a research project started in 2014 aimed at the application of Benthic Foraminifera (BF) as ecological indicators in Mediterranean marine caves for the identification of different habitats and their environmental interpretation. Sediment and water samples were collected from a total of 25 stations from two distinct sectors of the cave (North Branch and Middle Branch); sediments were analysed for living and dead BF and grain size, while Temperature, Salinity, pH and Dissolved Oxygen were measured in water samples collected close to sediment water interface. Two main foraminiferal assemblages, with distinct characteristics with respect to the typical Mediterranean shallow-water ones, were recognized by means of Hierarchical Cluster Analysis and Non-metric Multidimensional Scaling, and a Canonical Correspondence Analysis deduced their environmental significance. A well oxygenated, less saline environment with coarse bottom sediment, correlated with a mixed calcareous-agglutinated assemblage (*Gavelinopsis praegeri*, *Rosalina* spp., *Eggerelloides advenus* and *Reophax dentaliniformis*) with high species diversity (H-index 2.32–3.57) and low foraminiferal density, was exclusive of the North Branch. A scarcely oxygenated, more saline environment with fine bottom sediment enriched in vegetal debris was related to a prevalently agglutinated assemblage characterized by low species diversity (H-index 1.60–2.68), with high dominance of *E. advenus* (up to 83.6%) associated to *Ammonia tepida*, and high foraminiferal density, recognized in the Middle Branch. These different environments were interpreted considering the different modes of feeding the karst systems of the two branches. They also corresponded to two distinct ecozones, Entrance and Confluence, already recognized in earlier studies. The environmental significance of the foraminiferal ecozones recognized in this study and their comparison with the ones identified in the previous years, helped to consider the ecological zonation as a tool for detecting seasonal and, possibly, long term annual environmental variability in the marine system.

1. Introduction

Extreme environments are affected by life-threatening stable or, alternatively, widely variable physical-chemical parameters, due both to natural conditions or anthropogenic impact, which need specific adaptation strategies by inhabiting organisms. For this, they are considered as natural laboratories where studying the response of such organisms to environmental variability, improving scientific knowledge on the effects of global changes. Several habitats may be recognized as extreme environments in the marine realm; they range from transitional zone to deep sea and include the intertidal belt, marshes and lagoons, hydrothermal vents, marine blue holes, but also extremely oligotrophic,
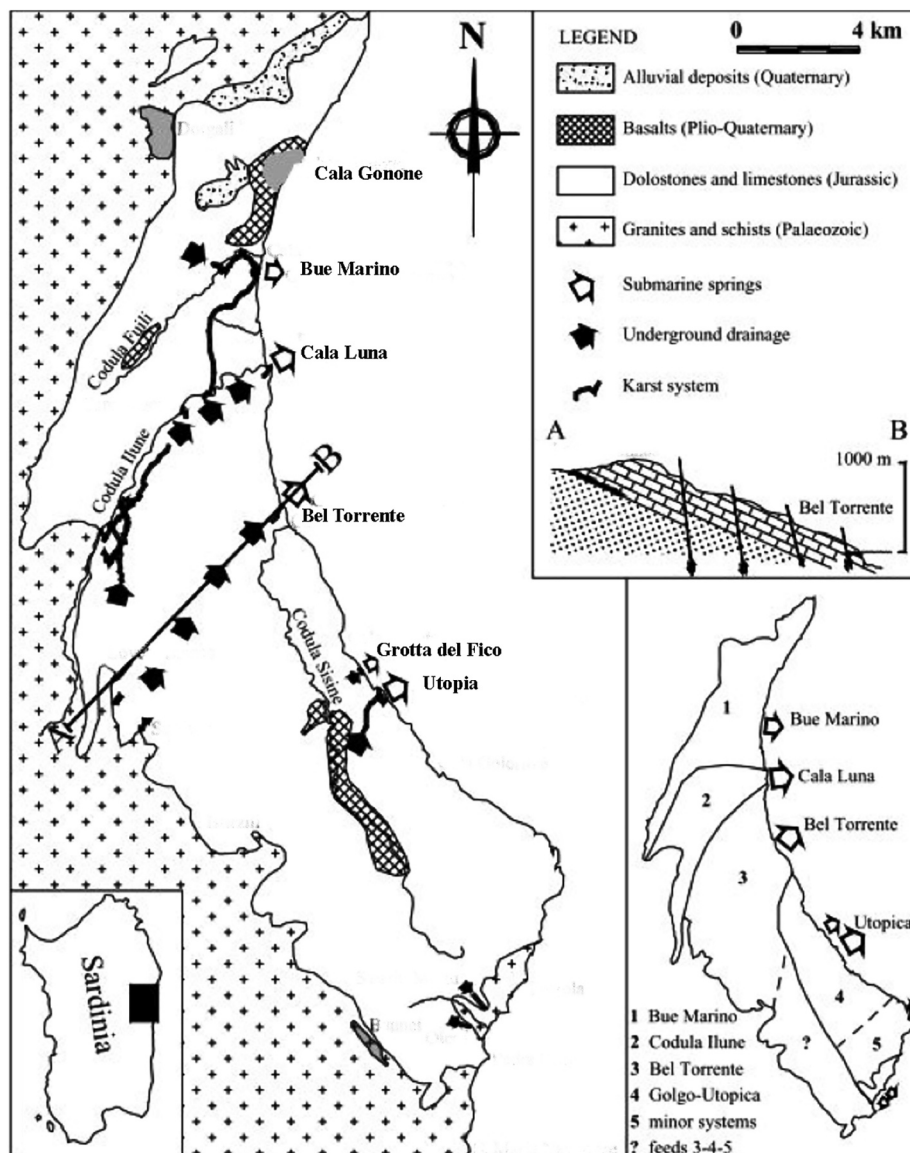

Fig. 1. Study area – geological and hydrogeological settings (from De Waele, 2008).

anoxic or highly contaminated areas and have been extensively studied in different research areas such as ecology, marine biology and microbiology (e.g. McMullin et al., 2000; Berois et al., 2012; Bang et al., 2018; Broman et al., 2020; Li et al., 2020). Also marine caves may be considered as extreme environments because, being at the boundary between marine and continental realms, they are affected by wide spatial and temporal environmental variability and extreme conditions as regards light and nutrients; moreover, another extreme character of these environments is the difficulty of access and data collection. Marine caves are of high scientific interest and object of many studies both in the areas of geoscience and life science; the first ones are mainly aimed at the identification of geological processes leading to their formation and development, especially under the influence of climate change (Antonioli et al., 2004; Florea and Vacher, 2006), while the second ones are mostly focused on the ecology of hard bottom communities, particularly sponges, serpulids, bryozoans and brachiopods (Rosso et al., 2013; Gerovasileiou and Voultsiadou, 2012; Gerovasileiou et al., 2015). Differently, sediments of marine caves have been rarely studied, both by biological and sedimentological viewpoint, although they are of high scientific interest, both because their texture is proxy for hydrodynamic conditions/water flow patterns and because they host rich benthic communities (Fornós et al., 2009; van Hengstum

et al., 2011; Navarro-Barranco et al., 2012). The common character of both hard and soft substrate communities is a decrease in species richness and biomass from the outermost to the innermost part of the cave which may depend on gradients of physical parameters (light, oxygen, salinity, etc.), trophic supply, as well as on the limited capacity of the larvae for dispersion and settlement (Gerovasileiou and Voultsiadou, 2012; Navarro-Barranco et al., 2012). This biotic decrease singles out successive ecozones, inhabited by distinct benthic assemblages with different ecological requirements (Bussotti et al., 2006).

Benthic foraminifera (BF), unicellular organisms mostly living in sediments, with epiphytic, epifaunal and infaunal microhabitat, from transitional and marine coastal areas to the deep-sea zones, have been increasingly recognized as reliable ecological indicators for the characterization and monitoring of marine habitats and for the assessment of the ecological status (Sousa et al., 2020). The advantage of studying BF in marine caves, where sampling is of particular difficulty, is linked to the collection of small sediment volumes allowing the census of statistically significant number of specimens, due to their small size and abundance. Moreover, due to their mineralized shell, called "test", they are preserved in the sedimentary record, being proxies of past environmental conditions.

The study of BF in marine caves has started in the last decade in

tropical karst systems of Yucatan peninsula (van Hengstum et al., 2008) and Bermuda (van Hengstum et al., 2011) and is still going on. The last research, conducted in two sites of the Bermudan karst system, identified different habitats based on different foraminiferal assemblages, in relation to water level variability from tidal forcing, which may be used as modern analogues in paleoenvironmental studies finalized to identify sea-level changes (Little and van Hengstum, 2019).

Only later, BF have been studied also in marine caves of the Mediterranean Sea which is, until now, the only temperate basin where this research has been developed. A project for the study of these environments using BF as environmental proxies, started in 2014 in Bel Torrente and Bue Marino caves (NE Sardinia, Italy), and is going on with other Mediterranean sites, with the aim of improving knowledge of ecology of these organisms in relation with natural and anthropogenic environmental changes (i.e. sea-level changes, acidification, water contamination). The first studies highlighted that BF may live inside the caves, not only close to the entrance but up to several hundreds of meters inside, responding to the environmental gradient due to the different rate of marine and terrestrial contributions and being useful for the ecological zonation (Bergamin et al., 2018; Romano et al., 2018b, 2020). The present work is aimed at improving the knowledge on the distribution of BF in the Bue Marino cave, sampling the sediments of inner sectors with respect to previous surveys, for better understanding the environmental factors determining the ecological zonation and the extent of marine influence in the cave. The foraminiferal response to the environmental variability in marine caves is of great importance if interpreted in the light of the global changes affecting the marine habitats, considering the huge biodiversity of BF, which account nearly 10,000 modern species and representing about 1/8 of the total, in the Kingdom Protoctista (Hammond et al., 1995).

2. Study area

In the mainland of the Gulf of Orosei (NE Sardinia, Italy), a crystalline Palaeozoic basement made out of granites and metamorphic rocks is overlaid by an almost 1 km-thick Middle Jurassic-Upper Cretaceous sequence, constituted by dolostones and limestones (Fig. 1; De Waele, 2008).

This carbonate succession belongs to the terminal part of the Supramonte karst plateau, one of the widest aquifers of Sardinia, and represents the geological context in which most of the present resurgences have been set (Cabras et al., 2008). The karst massifs greatly influence the hydrogeological structure, determining the absence of a superficial hydrographic network and favouring the development of underground water circulation that feeds numerous underground systems (De Waele and Melis, 2003, De Waele, 2004). The monoclinal structure, due to its inclination towards northeast, east or southeast, favours the conveyance of waters by underground routes towards the sea, where they flow through large underwater springs like as Bue Marino, Cala Luna, Bel Torrente and Utopia, that, due to a combination of karst and coastal processes, mainly in the mixing zone between fresh and salt water, are subjected to hyperkarst (De Waele and Nieddu, 2005).

Four main systems have been recognized among which Bue Marino-Codula Fuili (Fig. 1), which recharges around the Codula Fuili canyon and resurges from the northern branch of Bue Marino cave system, and Codula Ilune, which drains the homonymous canyon and resurges south of Cala Luna (Sanna et al., 2012).

In the area, the rainfalls are mainly concentrated between October and January, with average annual values ranging between 700 and 900 mm (Maxia et al., 2003; Bodini and Cossu, 2008); more detailed data collected by ARPAS (Agenzia Regionale per la Protezione dell'Ambiente – Dipartimento Meteoclimatico) and deriving from 4 rain stations located in the study area and related to the period 2014–2016 (Fig. 2), highlighted average annual values varying between 160 and 314 mm, with two periods of greater rainfall concentrated in February-

April (187–366 mm) and October-December (231–731 mm).

When intense rainfall occurs, the surface drainage of Codula Ilune and Codula Sisine, set on granites and basalts respectively, is activated while, only exceptionally, the smaller rivers, like as Codula Fuili (Fig. 1), almost completely set on carbonate lithotypes, are involved. In particular, Codula Fuili is the northernmost fluviokarst canyon of the Gulf of Orosei, along which many caves, representing remnants of past well-developed karst systems, have been documented. The underground drainage strongly contributes to the karst system of Bue Marino cave, explored for over 25 years by several speleologists for both emerged and submerged sectors, and extending for over 70 km, representing the largest cave in Italy (De Waele and Melis, 2003; De Waele and Nieddu, 2005; De Muro et al., 2006; De Waele, 2008). The cave is made up of three branches, with different hydrogeological characteristics: North, Middle and South Branch, which join together only close to the coast, in the central sector of the Gulf of Orosei between Cala Gonone and Cala Luna.

The North Branch (Fig. 3) is characterized by large fossil tunnels on whose walls the signs of higher sea level than today are still clearly visible. The active part of this branch consists of a complex of galleries, largely flooded, which develops for about 7 km, and which drains the waters from the Codula Fuili, with a base flow of $40 \, l \, s^{-1}$, coming from four underground springs (three freshwater inlets and a brackish one), located about 2 km far from the coast. During base flow, seawater penetrates up to 1,500 m, while during the flood periods the flow increases over $1,000 \, l \, s^{-1}$ (De Waele et al., 2009; Sanna and De Waele, 2010). Not data related to salinity are available for this branch, except for those measured by Hutňan (2013) in November 2006 who measured conductivity along the whole North Branch, detecting a general pattern from salt to freshwater with local influence of saline water.

The Middle Branch (Fig. 3), which extends for a total of 5,500 m, is poorly known by hydrogeological viewpoint, even if it is probably linked to some smaller sinks in the Codula Ilune river bed (Sanna and De Waele, 2010). It mainly develops at sea level in the direction of Codula Ilune, with brackish waters up to the inner parts, where Hutňan (2013) measured a conductivity of $14,900 \, \mu S \, cm^{-1}$.

The South Branch (Fig. 3) has the largest conduit reaching 32 m of water depth and a very low base flow (few litres per second), although during heavy rains the waters can go up to 3–4 m. When the water level is low, the salt water penetrates the branch for the first 300 m up to a barrier, which determines the boundary between the marine and fresh waters (Sanna and De Waele, 2010).

3. Materials and methods

3.1. Water and sediment sampling

The water and sediment sampling involved two different branches of the cave, North and Middle Branch, previously surveyed through specific procedures carried out by cave-diving skills of Global Underwater Explorers (GUE) divers. The North Branch was previously surveyed in 2014, while the survey of Middle Branch was carried out before the sampling phase according to the same procedures used for the North one (Romano et al., 2020). After that, at 30 m distance one from another, 19 sampling stations from the cave entrance to the inner zone of the North Branch, and 6 sampling stations in the Middle Branch from the connection to the inner zone, were positioned (Fig. 3). GUE divers collected sediment and water samples at all these stations.

In particular, water samples were stored in plastic containers, while the upper 2 cm layer of the cave bottom sediments were stored in two different containers: two aliquots of 50 and 100 cm³, respectively, were collected for grain size and foraminiferal analyses; the second one was immediately stained by means of an ethanol solution with Rose Bengal ($2 \, g \, l^{-1}$) recognized as a reliable method to distinguish living from dead foraminifera (Walton, 1952; Schönfeld et al., 2012). The station BM13 and BM6B were not sampled because of hard substrate. Water
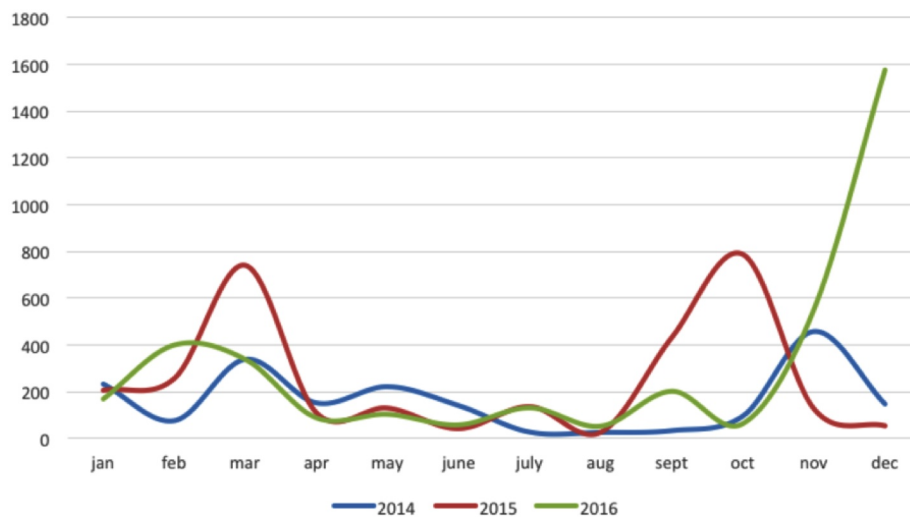
Fig. 2. Cumulated monthly rainfall over 4 stations of the Supramonte area in the period 2014–2016 (source ARPAS – Agenzia Regionale per la Protezione dell'Ambiente – Dipartimento Meteoclimatico).
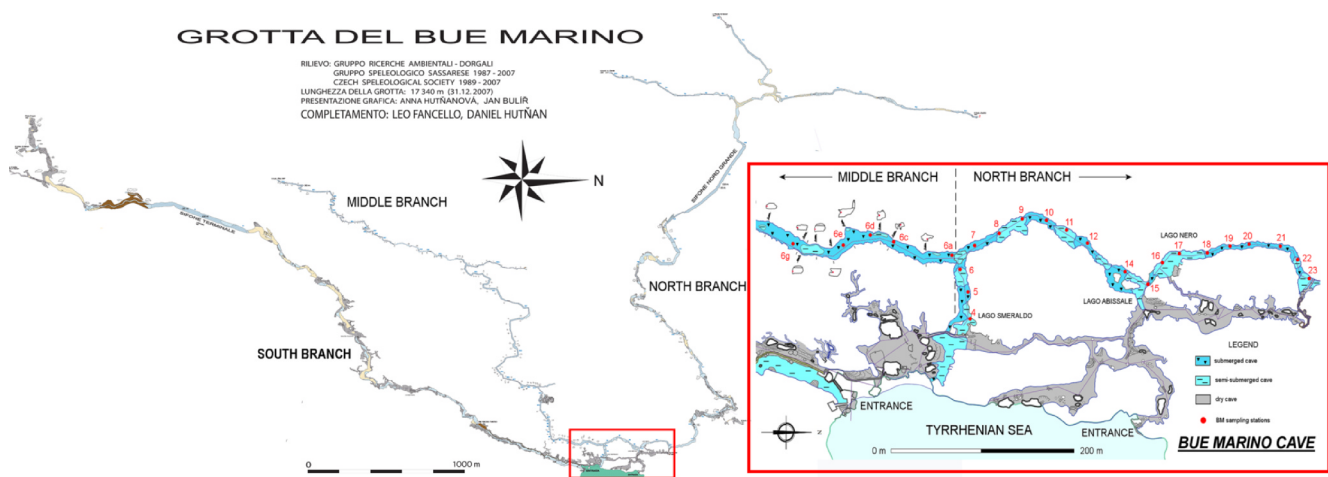

Fig. 3. Sampling station in the Middle and North Branch of Bue Marino system cave (survey map by Gruppo Ricerche Ambientali, Gruppo Speleologico Sassarese and Czech Speleological Society, modified).

parameters (temperature, T; salinity, Sal; pH; dissolved oxygen, DO) were measured by means of a multiparametric probe (Hanna HI 9828) with the following precision: T $\pm$ 0.15 °C; Sal $\pm$ 2%; pH $\pm$ 0.02 and DO 0.01 mg 1^{-1}.

3.2. Sediment analysis

Grain-size analyses were carried out according to Romano et al. (2018b) on pre-treated samples and then wet-separated into coarse (> 63 μm) and fine (< 63 μm) fractions. The coarse fraction was dry-sieved with meshes (ASTM series) ranging from -1 to $+4$ ϕ, while the fine fraction was analysed by means of a laser granulometer (HELOS, FKV) after being placed into a dispersant solution of sodium hexame-taphosphate. Results from the analysis of coarse and fine fractions were integrated by means of specific software in order to obtain the comprehensive distribution curve, ranging from -1 to $+10.5$ ϕ. In most cases, the fine fraction was not analysed because it was < 5% of the whole sample. Sediments were classified following Shepard (1954), modified according to Romano et al. (2018a). The > 63 μm fraction was also observed under a stereomicroscope for a qualitative study of the main inorganic and organic sediment components.

3.3. Benthic foraminiferal analysis

Samples were washed over a 63 μm sieve to eliminate staining solution and mud particles and then oven dried at 40 °C. Microfaunal analysis was conducted under a stereomicroscope Leica M205C up to 120 magnifications. The quantitative analysis of benthic foraminifera was separately conducted on living (rose Bengal stained) and dead assemblage and it was based on the count of all specimens present in the whole sample or in representative aliquots, obtained by microsplitter, containing at least 300 specimens for each sample. For the count of dead specimens, in order to prevent the inclusion of reworked or transported tests, only well-preserved tests, not re-crystallized and free of cracks and abrasions, were picked, counted and classified. Moreover, according to van Hengstum and Scott (2011), one species was considered as autochthonous in one sample and was included in the multivariate analysis only when at least one living specimen of the same species was found. The classification at the genus level was made according to the most used taxonomical study on foraminiferal genera (Loeblich and Tappan, 1987), while species were determined according to some important studies on the Mediterranean area (Cimerman and Langer, 1991; Sgarrella and Moncharmont-Zei, 1993) and to the World Modern Foraminifera Database (Hayward et al., 2011). Foraminiferal data were presented as both relative (%) and absolute abundance (see

Supplementary Material); due to the extremely different foraminiferal density through samples, the absolute abundance of species from samples of the North Branch was standardized at 50 g dry sediment, while it was at 1 g dry sediment for the Middle Branch (Dijkstra et al., 2020). The foraminiferal density of the total assemblage, represented by the Foraminiferal Number (FN), was calculated as the number of specimens per gram of the > 63 μm dry sediment fraction (Schott, 1935). The species diversity, in addition to the number of taxa per sample (S), was represented as the α-index (Fisher et al., 1943), which considers all counted species, included the rare ones, and H-index (Shannon, 1948), which considers both the abundance and evenness of species. Also, the Dominance (D) was determined, considering that stressed environments may be characterized by assemblages with low diversity and high dominance of one or few species (Magurran, 2004).

3.4. Statistical analysis

As regards abiotic data, a correlation matrix using Pearson's correlation was carried out to recognize significant correlations between pairs of water parameters. Also a Principal Component Analysis (PCA) was carried out on both water (T, Sal, pH and DO) and sediment (% gravel, sand, silt and clay) data as a descriptive method to investigate the comprehensive distribution of values of environmental parameters in the whole Bue Marino cave. Data were standardized using the z-score method in order to meet the effect of different scale range.

A two-way Hierarchical Cluster Analysis (HCA) was applied on the matrix with results of living + dead specimens in order to recognize groups of samples with homogeneous foraminiferal content, corresponding to distinct ecozones (Parker and Arnold, 1999). It included the relative abundance of commonly occurring species in a total of 16 samples (from BM4 to BM15 in the North Branch and from BM6A to BM6G in the Middle Branch) with > 50 total (living + dead) specimens (Barras et al., 2014). For the HCA, the Euclidean similarity coefficient to compare samples and the Ward's method of minimum variance to assemble clusters were applied (van Hengstum and Scott, 2011). In order to enforce the subdivision recognized by HCA, a Non-metric Multidimensional Scaling (NMDS) was applied, using a non-Euclidean similarity (Bray Curtis) for recognizing differences not detected by HCA (Legendre and Legendre, 1998). The four main sediment size fractions (gravel, sand, silt and clay) were considered in the analysis as environmental factors, but not included in the ordination, for highlighting the influence of sediment texture in the separation of clusters (Hammer et al., 2001; Taguci and Oono, 2005; Hammer and Harper, 2006).

A Canonical Correspondence Analysis (CCA), including the relative abundance of commonly occurring living species (i.e. species > 5% in at least one sample), together with sediment (grain size) and water (T, Sal, pH and DO) parameters, was carried out in order to highlight the effects of environmental conditions recorded at the sampling moment on living foraminifera (Bergamin et al., 2019). Due to the low number of living specimens, it was applied on a total of 8 samples (from BM8 to BM15 in the North Branch and BM6C in the Middle Branch) with a number of living specimens > 30 in the raw count. The statistical package PALaeontological STatistics-PAST was used for these analyses (Hammer et al., 2001; Hammer and Harper, 2006).

4. Results

4.1. North Branch

4.1.1. Water parameters

In the North Branch, both T and pH displayed a limited variability with a more or less evident decreasing pattern towards the inner cave (Fig. 4; see Supplementary Material). Temperature ranged between 24 °C in BM5 and 16 °C in BM22 and BM23; maximum pH was 8.05 at BM7, while the minimum (7.27) was recorded at BM23. Differently, Sal and DO showed wide variability, with a decreasing general pattern for

the first one, and the opposite for the second one. Sal had the maximum value of 36.12 at BM4, with local areas of low values between BM8 and BM10 (17.18–17.81), BM17 and BM18 (16.90–17.58), and at BM20 (17.50). DO was minimum at BM4 (2.69 mg l^{-1}) and maximum at BM23 (4.63 mg l^{-1}), with the exception of a peak value (4.98 mg l^{-1}) at BM17. Some significant correlations were recognized between parameters: T was positively correlated with pH (r 0.68583, p 0.0011883) and negatively correlated with DO (r −0.52182, p 0.021929); also, a negative correlation between pH and DO was recognized (r −0.5719, p 0.010516).

4.1.2. Sediment analysis

The sediments of North Branch did not show significant textural variations (Fig. 5). In almost all the stations, sand represented the predominant fraction, with maximum values in BM22 and BM23 (99.8%) and an average of 85% ± 19.5. Gravel was an important component only in BM5 (31.7%), BM10 (35.8%), BM12 (71.1%) and BM14 (30.1%), while the fine fraction (silt + clay) was always scarce, with values generally lower than 5%. Only in BM6, close to the confluence of the Middle Branch, a significant increase in the fine fraction, with percentages of 35.5% and 4.4% of silt and clay respectively, was registered (see Supplementary Material). A slight increase of pelitic fraction was also recorded in BM7 with 14.1% of silt and 1.8 of clay.

The qualitative microscopic analysis of the coarse fraction revealed fairly homogeneous compositional characteristics in all the samples. The sediments appeared brown-grey, with a medium to very coarse grain size, with sporadic organic fraction, widespread only in BM4 (plant debris, shells, fragments of bivalves, gastropods, echinoids, annelids, ostracods, foraminifers) and BM6 (plant debris, faecal pellets, foraminifers). Glassy quartz and colourless, from sub-angular to sub-rounded, hyaline or translucent granules, sometimes in euhedral forms, were prevalent and often associated with plagioclase, k-feldspar, biotite, muscovite, calcite, pyroxenes and amphiboles; in the gravelly fraction, lithic stones of granitoid origin were recognized (Fig. 6).

4.1.3. Benthic foraminiferal assemblages

In the North Branch, benthic foraminifera (living + dead) were found in samples from BM4 to BM17 (only one specimen was found in BM18), but they exceeded 50 specimens in 11 samples (from BM4 to BM15) and the FN ranged between 3 and 1,350. In BM16, BM17 and BM18, only few specimens were recorded, and the FN was < 2. Five samples from BM19 to BM23 were barren of foraminifera as well as of any kind of biogenic components. A total of 124 species was classified and the ones with higher relative abundance were (Fig. 7): *Ammoglobigerina globigeriniformis* (11.6% at BM15), *Ammonia tepida* (11.5% at BM6), *Cibicidoides lobatulus* (11.1% at BM4), *Eggerelloides advenus* (60.9% at BM10), *Lepidodeuterammina ochracea* (23.6% at BM16), *Patellina corrugata* (16.8% at BM14), *Reophax dentaliniformis* (27.7% at BM15) and *Rosalina bradyi* (13.7%) (see Supplementary Material).

The α -index ranged from 2.02 in BM16 to 12.42 in BM12, with a median of 5.49; the H-index ranged between 1.70 in BM16 and 3.57 in BM4, and showed a median of 2.60; finally, D varied between 0.04 in BM4 and 0.39 in BM10, with a median of 0.13 (Fig. 7).

Living foraminifera were present in 13 samples (from BM4 to BM6 and from BM8 to BM18); nevertheless, only in seven samples (from BM8 to BM15) the number of living specimens was higher than 20. The main living species were: *A. globigeriniformis, E. advenus, G. praegeri, L. ochracea, R. dentaliniformis* and *R. bradyi*.

4.2. Middle Branch

4.2.1. Water parameters

The water parameters, T, Sal and pH, displayed rather constant values along the Middle Branch (Fig. 4; see Supplementary Material). T was 23 °C in all the samples, Sal slightly varied between 34.74 in BM6D and 36.09 in BM6C, and pH was practically constant (7.91–7.99).
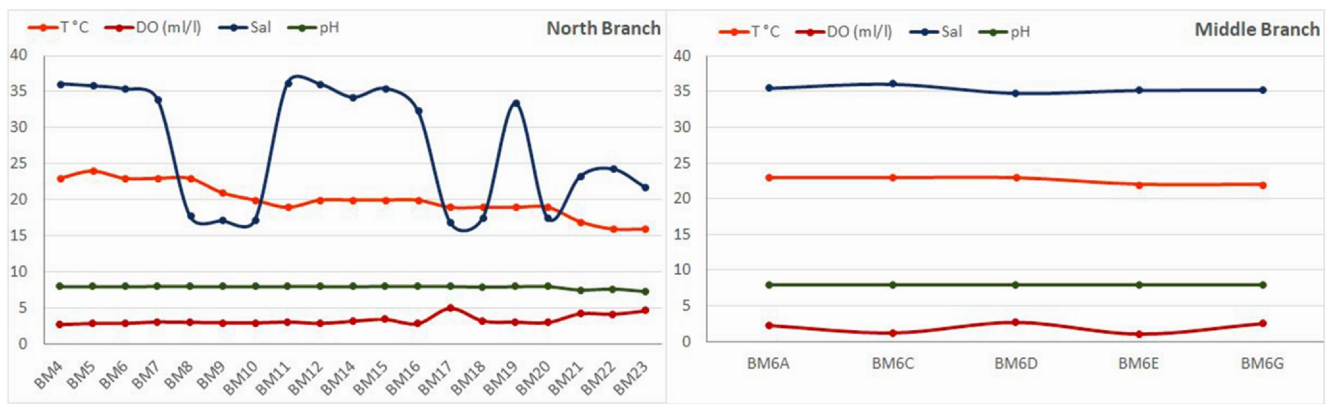
Fig. 4. Temperature, Dissolved Oxygen (%), Salinity and pH in the North and Middle Branch.
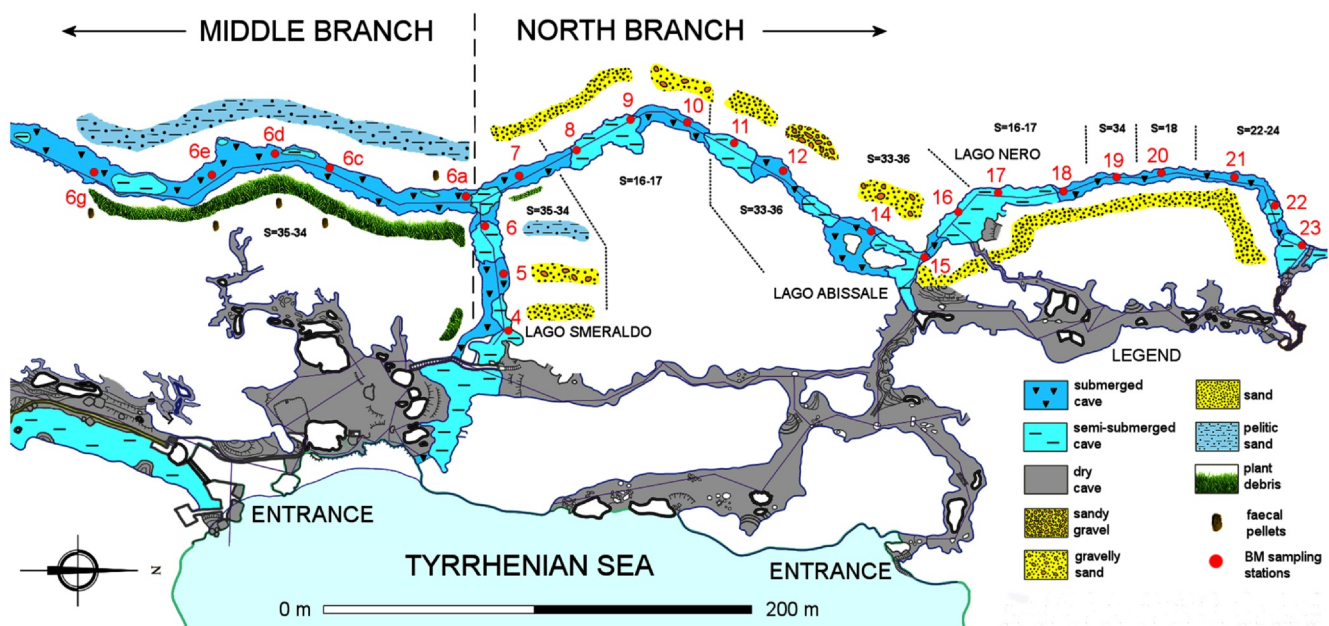

Fig. 5. Sediment classification according to modified Shepard and specific constituents (plant debris, faecal pellets) of the cave sediments. Also salinity (S) is reported.

Differently, DO showed considerable variability among samples, with the highest value of 2.65 mg l^{-1} in BM6D and the lowest one of 1 mg l^{-1} in BM6E. No significant Pearson correlations were recognized among water parameters.

4.2.2. Sediment analysis

Sediments in Middle Branch were markedly different from those of the North Branch and were classified as pelitic sand (Fig. 5). The sandy fraction, although almost always prevalent, significantly decreased, showing an average value of 59.4 ± 12.6%. The fine component, with silt fraction was prevalent if compared to clay, reaching its maximum value in BM6A (42.6%) and BM6G (42.1%). Instead, gravel was absent in all the analysed samples (see Supplementary Material). The microscope analysis highlighted brown-grey sediments, with a variable texture from fine to very fine and a predominant organogenic composition (plant debris, faecal pellets, shells and fragments of bivalves, gastropods, echinoids, annelids, ostracods, foraminifera). Quartz grains were prevalent while plagioclase, k-feldspar, biotite, muscovite, calcite, pyroxenes and amphiboles were subordinately present (Fig. 6).

4.2.3. Benthic foraminiferal assemblages

In the Middle Branch, dead benthic foraminifera were prevalent in

all the samples, whereas the living ones were present in BM6A, BM6C and BM6E. The FN was high, comprised between 148 and 3,483. In total 59 species were classified (see Supplementary Material): *E. advenus* dominated in all the samples with very high frequency (41.0–83.6%) while the other species showing percentages > 5% were *Ammonia inflata* (1.1–8.7%), *A. tepida* (8.2–30.2%) and *R. bradyi* (2.0–7.4%) (Fig. 7). The α-index ranged between 1.82 (BM6G) and 5.85 (BM6D), with a median of 3.31, while the H-index showed values between 0.66 (BM6G) and 2.18 (BM6D), with a median of 1.60; D was comprised from 0.22 to 0.72, with a median of 0.42 (Fig. 7). Living foraminifera were generally scarce, except in the sample BM6C, in which 42 specimens were recognised; the most abundant species were *E. advenus* and *A. tepida*.

4.3. HCA and NMDS of foraminiferal data

In order to compare foraminiferal assemblages from the North and Middle Branches, recognizing their degree of similarity, a two-way HCA was carried out on foraminiferal data of the whole cave. Moreover, to improve information on the clustering of samples, a NMDS was applied on the same matrix, including sediment fractions as additional environmental variables (Fig. 8). In the dendrogram obtained from the

Fig. 6. North Branch (up) – Prevalence of plant debris in BM6 (left) and quartz, plagioclase, k-feldspar, biotite and muscovite in sediment from station BM8 (right). Middle Branch (down) – Examples of textural characteristic of sediments.

HCA, two main clusters (A and B) may be recognized; this clustering corresponds to the main subdivision in the NMDS plot, where samples of cluster A display negative values for coordinate 1, associated with gravel and sand, while those of cluster B have positive values, associated with silt and clay. Cluster A grouped 6 samples all collected in the North Branch characterised by a heterogeneous calcareous-agglutinated mixed assemblage. The mean relative abundance of agglutinated, porcelaneous and hyaline taxa was 40.1%, 16.1% and 43.8%, respectively. The main species (median > 5%) were *R. dentaliniformis* (0–27.7%, median 15.9%), *E. advenus* (1.9–23.5%, median 14.0%), *Rosalina* spp. (1.3–14.2%, median 8.3%), *A. globigeriniformis* (0–11.6%, median 6.0), *G. praegeri* (1.0–9.7%, median 5.9%) and *Quinqueloculina* spp. (3.4–11.1%, median 5.4%). The diversity was enough high, with 31–54 species in each sample, except for BM15 where only 16 species were recognized. Consequently, the diversity indices were generally high: H-index ranged between 2.32 (BM15) and 3.57 (BM4); α-index varied from 4.48 (BM15) to 12.42 (BM12). Conversely, D was generally low (0.04–0.13). Among these samples, only BM4 showed high FN (1,350), while in the remaining ones it was extremely low, ranging between 3 and 6 (Table 1).

Different characteristics of BM4 from the other samples of cluster A, not detected by HCA, were recognizable in the NMDS plot, where BM4 displayed considerably lower values of coordinate 2 (Fig. 8); this was the only sample in which the presence of *E. advenus* was negligible (1.9%).

Cluster B comprised a total of 10 samples, among which all the 5 samples from the Middle Branch and 5 from the North one, located close to the confluence, strongly dominated by *E. advenus* (38.3–83.6%). The mean relative abundance of agglutinated, porcelaneous and hyaline taxa was 61.0%, 4.4% and 34.6%, respectively. In

the dendrogram, cluster B is divided into sub-clusters B1 and B2; the same subdivision is recognizable in the NMDS plot, where samples of cluster B show positive values of coordinate 1, with samples of B1 and B2 characterized by negative and positive values of coordinate 2, respectively. Sub-cluster B1 comprises 4 samples showing the dominance of *E. advenus* with percentages ranging from 38.3 to 43.9% (median 41.9%); other main taxa were *A. tepida* (2.6–30.2%, median 14.4%), *A. inflata* (1.3–9.0%, median 7.5%) and *Rosalina* spp. (3.9–12.9%, median 7.2%). In this sub-cluster, 19–46 species in each sample were classified. The H-index (Table 1) showed values from 1.60 (BM6A) to 2.68 (BM5), as well as α-index ranged between 3.31 (BM6A) and 7.09 (BM5), and D was between 0.18 (BM5) and 0.30 (BM6A). Six samples are included in sub-cluster B2 that was even more markedly dominated by *E. advenus*, with percentages ranging from 53.8 to 83.6% (median 61.9) in BM8 and BM6G, respectively. Among the other main taxa only *A. tepida* (3.4–18.9%, median 9.8%) and *Rosalina* spp. (3.0–11.2%, median 6.9%) were found. Sub-cluster B2 was less diversified than B1, with a number of species varying between 8 and 28 in each sample. H-index ranged from 0.66 (BM6G) to 1.89 (BM8); α-index was comprised from 1.82 (BM6G) to 4.49 (BM8); D increased with respect to B1, ranging between 0.31 (BM8) and 0.72 (BM6G) (Table 1). Among all the samples belonging to cluster B, the ones of the North Branch showed lower FN (from 13 in BM8 to 401 in BM7), except BM6 (FN 1,006), while higher FN (from 148 in BM6G to 3,483 in BM6E) was recorded in all the samples of Middle Branch.
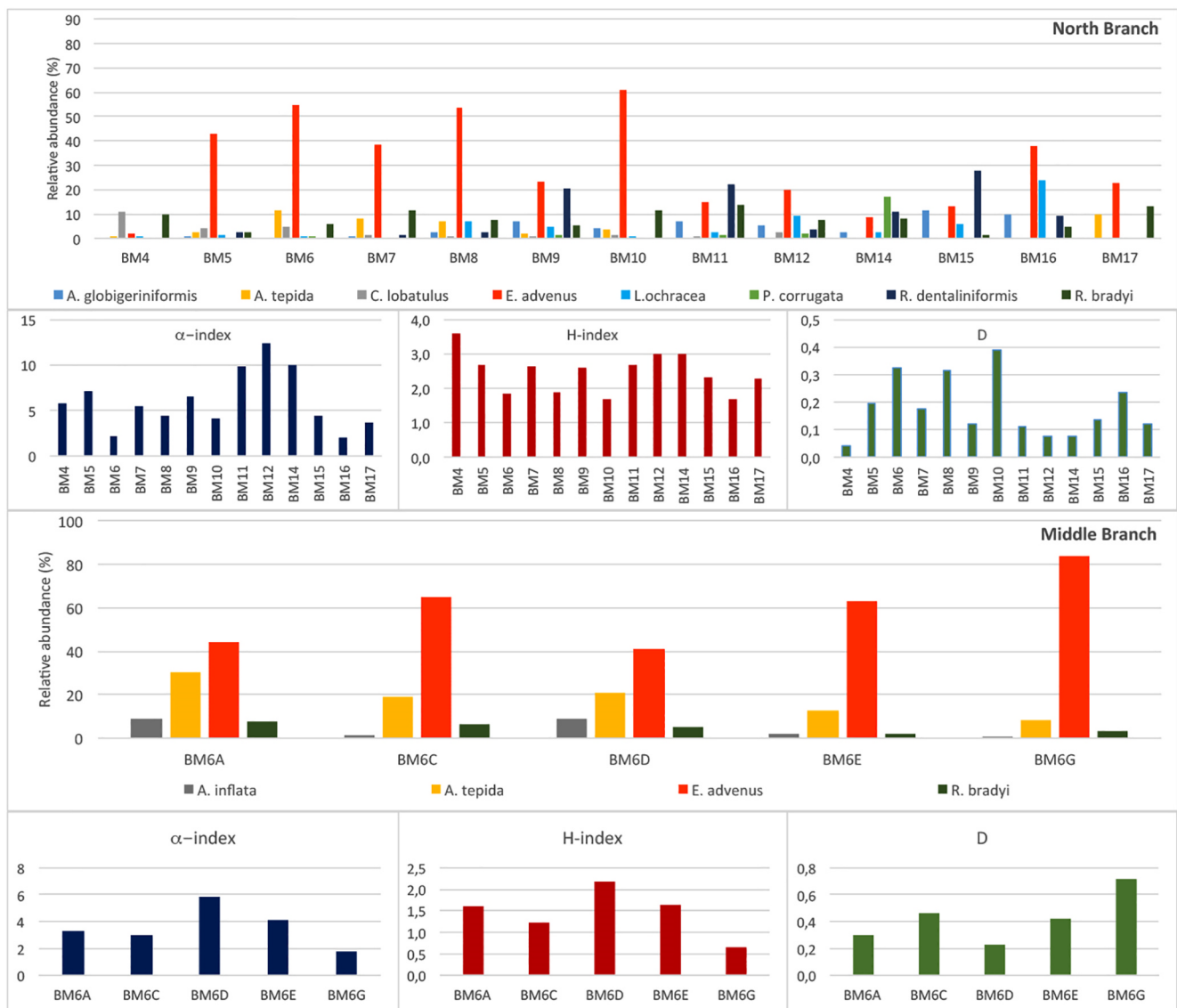
Fig. 7. Relative abundance of taxa exceeding 10% in at least one sample and faunal parameters samples in the North and Middle Branch.

5. Discussion

5.1. The environments of the cave

In order to characterize the Bue Marino cave by abiotic viewpoint, a PCA was carried out to identify how the abiotic parameters were distributed among samples collected in North and Middle Branches (Fig. 9). The scatter plot of PCA highlights T and Sal plotting on the positive side of PC1 inversely correlated with DO; pH, although with positive PC1 values, seems independent from the other parameters. As regards sediment variables, fine fractions show positive PC1 values, while sand has negative ones and gravel plots on the PC2 axis. A well-distinct environment (red ellipsis in Fig. 9) may be deduced for samples of the Middle Branch (PC1 > 0, PC2 < 0), strongly characterized by fine grained sediments and waters with higher Sal, T and pH, but lower DO. The same characteristics are also identified for BM6 and BM7, located close to the confluence of the two branches. Another environment (orange ellipsis in Fig. 9) is identified by stations of the North Branch on the negative side of PC1, characterized by very high sand content and higher DO.

Although a regular pattern with respect to the distance from the cave entrance cannot be identified, it is clear that the inner stations are those with the lowest PC1 values to indicate, as regards water parameters, higher DO and lower T, Sal and pH. In spite of a general low variability of pH in the whole cave, the inner stations (BM21-BM23), with the lowest PC1, were characterized by pH from 7.27 to 7.66, significantly below the value of 8.33 recorded in correspondence of the marine entrance in August 2014 (unpublished data) and the current average value of 8.1 for oceans (Millero et al., 2009).

Among samples not included in the two groups, BM4 shows water parameters similar to those of the Middle Branch, but considerably lower silt and clay percentages, while BM5, BM10, BM12 and BM15 are strongly characterized by high gravel content (Fig. 9).

Although the highest Sal of the whole cave was recorded in the samples of the first group (36.12–35.20), it was, however, significantly lower than the one (41.6) recorded in correspondence of the marine entrance in August 2014 (unpublished data) and lower than the normal marine salinity of the area (38.3, unpublished data). It is well known that, in general, there is inverse correlation between DO and T and this clearly emerges by the position of vectors in the PCA (Fig. 9). Nevertheless, the lower DO of these samples (1–2.84 mg l^{-1}) may not be attributed to warmer water temperature, because considerably higher DO was recorded in samples with similar T of the North Branch. More probably, lower DO was due to the decomposition of the high amount
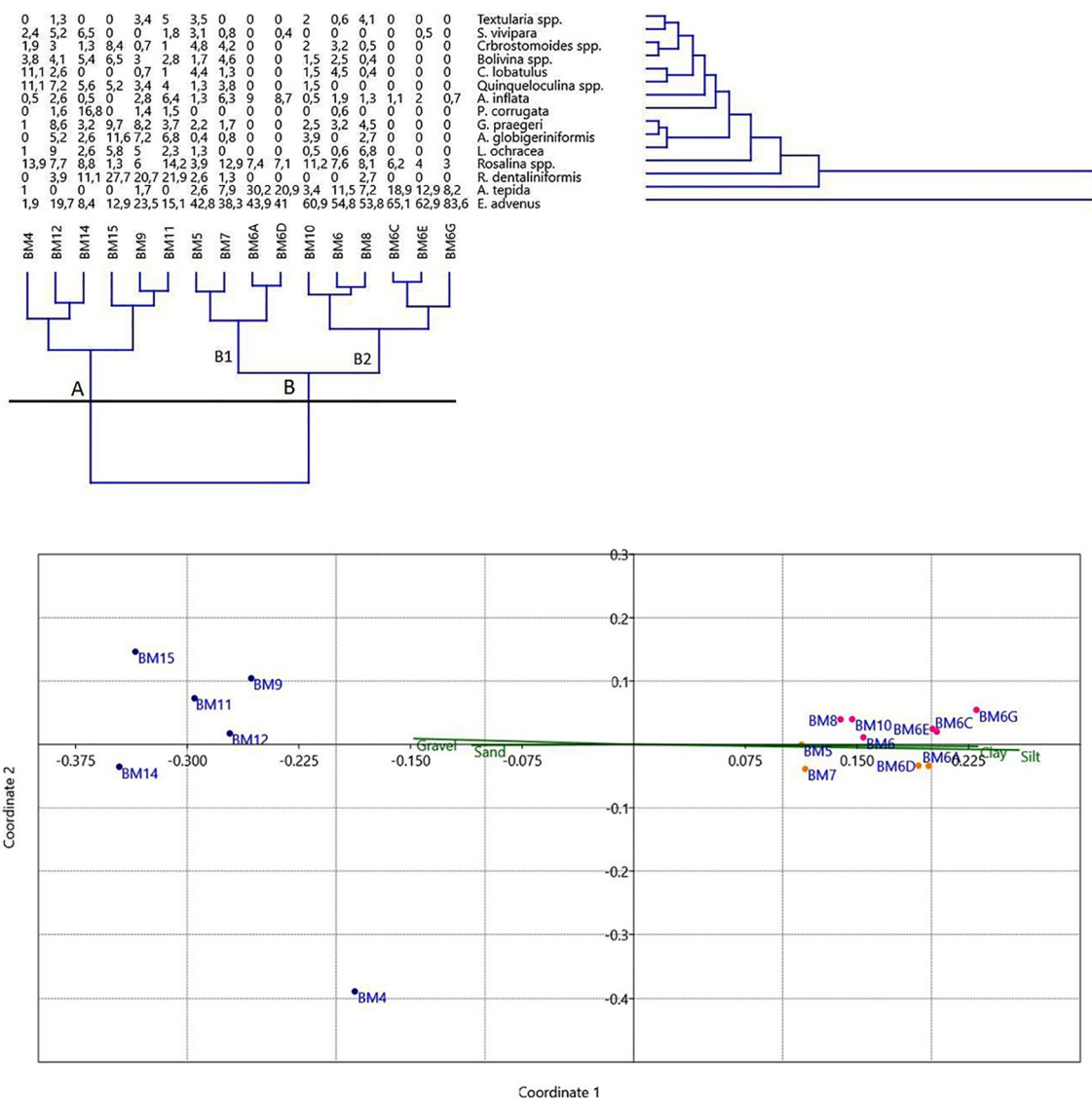
Fig. 8. Statistical analysis applied on total (dead + living) commonly occurring species of North and Middle Branch: two-way Hierarchical Cluster Analysis (HCA) on the top; Non-metric Multidimensional Scaling (NMDS) on the bottom. In the NMDS plot, blue, pink and orange dots correspond to cluster A, B1 and B2, of HCA dendrogram respectively.

Table 1
Faunal data characterizing cluster A and sub-clusters B1 and B2 identified by HCA and NMDS.

	MAIN TAXA (median relative abundance > 5%)		H-index		α-index		D		FN	
		Range	Median	Range	Median	Range	Median	Range	Median	Range	Median
A	*R. dentaliniformis*	0.0–27.7%	15.9%	2.32–3.57	2.83	4.48–12.42	8.21	0.04–0.13	0.09	3–1,350	5
	E. advenus	1.9–23.5%	14.0%								
	Rosalina spp.	1.3–14.2%	8.3%								
	A. globigeriniformis	0.0–11.6%	6.0%								
	G. praegeri	1.0–9.7%	5.9%								
	Quinqueloculina spp.	3.4–11.1%	5.4%								
B1	*E. advenus*	38.3–43.9%	41.6%	1.60–2.68	1.40	3.31–7.09	5.67	0.18–0.30	0.21	94–3,256	716
	A. tepida	2.6–30.2%	14.4%								
	A. inflata	1.3–9.0%	7.5%								
	Rosalina spp.	3.9–12.9%	7.3%								
B2	*E. advenus*	53.8–83.6%	61.9%	0.66–1.89	1.67	1.82–4.49	3.55	0.31–0.72	0.40	13–3,483	391
	A. tepida	3.4–18.9%	9.8%								
	Rosalina spp.	3.0–11.2%	6.9%								
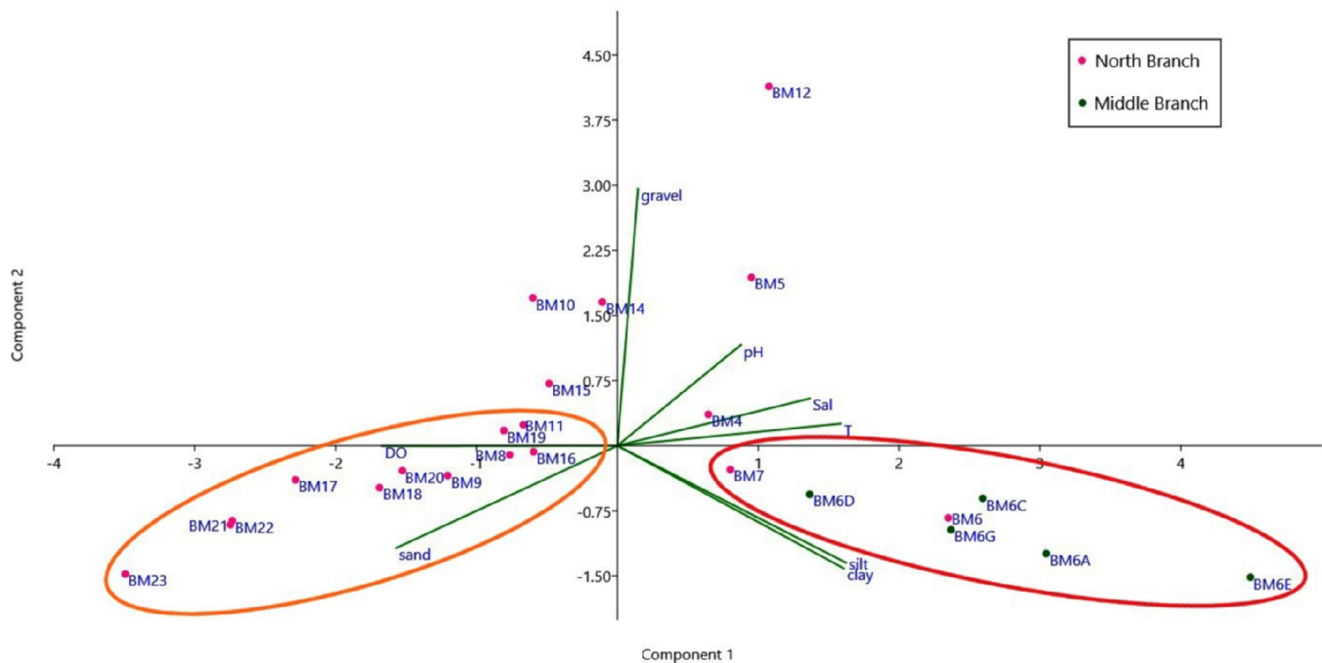
Fig. 9. Principal Component Analysis applied to abiotic parameters data. Component 1 and 2 account for 51% and 21% of variance, respectively. Red and orange ellipses identify the main environments of the Bue Marino cave (see text for more details).

of plant debris found in these samples (Fig. 6). According to Tyson and Pearson (1991), oxygen levels from 0.2 to 2 mg l^{-1} are to be considered as dysoxic and the corresponding biofacies as anaerobic.

Considering the distribution patterns of abiotic parameters among samples in the whole cave (Fig. 4, Fig. 9) it is clear that North and Middle Branch corresponded to different environments. The North Branch was characterized by higher variability of water parameters that displayed, albeit with different variability, a distinct pattern from the outer to the inner stations; moreover, effective hydrodynamic conditions may be deduced by the extreme scarcity of fine sediment fraction. Differently, the Middle Branch was rather homogeneous as regards both water and sediment parameters, with warmer, saltier but less oxygenated waters; lower water energy may be deduced by the high percentages of fine sediment and the associated plant debris. The influence of the Middle Branch was recorded also in the stations of the North one close to the confluence, up to BM7. The higher and steady salinity recognized in the Middle Branch suggests that contribution of marine water derives from still unknown independent connections to the sea, more than from the initial section of the North Branch. These findings are in accordance with conductivity measured by Hutňan (2013), who found highest values in the Middle Branch. Moreover, because the plant debris associated to the fine sediment is exclusive of the Middle Branch, it may be likely that it is supplied from a continental source area that feeds exclusively this sector. Indeed, the North Branch is exclusively fed by Codula Fuili system, mainly by infiltration processes, while surface drainage is activated only in case of exceptional rainfall. Differently, influences of Codula Ilune have been supposed for the Middle Branch; in this hydrographic basin, surface drainage is activated during seasonal rainfall periods and the penetration of water underground occurs through sinkholes (Sanna and De Waele, 2010). This mechanism allows the transport of washed-out fine sediment and plant debris, which are finally deposited in the Middle Branch under low-energy conditions.

5.2. Ecological response of benthic foraminifera

The abiotic parameters considered in this study are well known to influence the distribution of BF and, in case their values are far from the optimum, which is specific for each species, they act as environmental

stressors (Murray, 2006). Temperature has a strong influence on growth and reproduction (Saraswat et al., 2011; Kurtarkar et al., 2019), but also on foraminiferal density and size of specimens (Li et al., 2019). Limited availability of DO, often associated to high organic matter, favours the presence of selected tolerant opportunistic taxa and their vertical migration into sediment (Alve and Bernhard, 1995; Bernhard and Sen Gupta, 1999), while others survive with strongly decreased reproduction rates or reduced levels of metabolism (LeKieffre et al., 2017; Richirt et al., 2020). Lowered salinity of transitional environments promotes low diversity assemblages with euryhaline species (Debenay et al., 2006; Carboni et al., 2009), whereas elevated salinities in such environments result in abnormal growth of the foraminiferal test (Fiorini and Lokier, 2020); moreover, the sediment texture represents a discriminant factor for the assemblage composition (Celia Magno et al., 2012). Because, at a different extent, these parameters are correlated among them, the response of BF in natural environment is due to the concurrent effect of their variation (Charrieau et al., 2018; Dong et al., 2018). This is particularly true in marine caves, where all these parameters contribute to constitute an environmental gradient from the outer to the inner parts due to the different rate of marine and terrestrial influence. For this reason, a CCA based on commonly occurring living species was considered as a suitable tool to recognize the environmental drivers of foraminiferal species in cave environment, as regards water and sediment parameters (Fig. 10).

In the scatter plot, vectors of environmental parameters plot mainly on the first axis, silt and clay on the positive side, while DO, T, pH and sand are on the negative one; only Sal plots on the negative side of the second axis (Fig. 10). On the whole, some water parameters significantly varied in considered samples (Sal: mean 28.8 ± 9.4; DO: mean 2.8 ± 0.7), while other ones displayed scarce variability (T: mean 20.8 ± 1.5; pH mean 8.0 ± 0.03); the last ones did not supply reliable evidence about the response of foraminiferal species (Fig. 4). *Eggerelloides advenus* and *A. tepida*, dominant taxa in the prevailingly agglutinated assemblage of cluster B, show positive values of the first axis, resulting associated with higher values of silt and clay, and lower sand, DO, T, and pH. In these stations, DO corresponds to dysoxic conditions, associated to pelitic sediment enriched in plant debris. The ecological preferences of *E. advenus* and *A. tepida* are in accordance with these
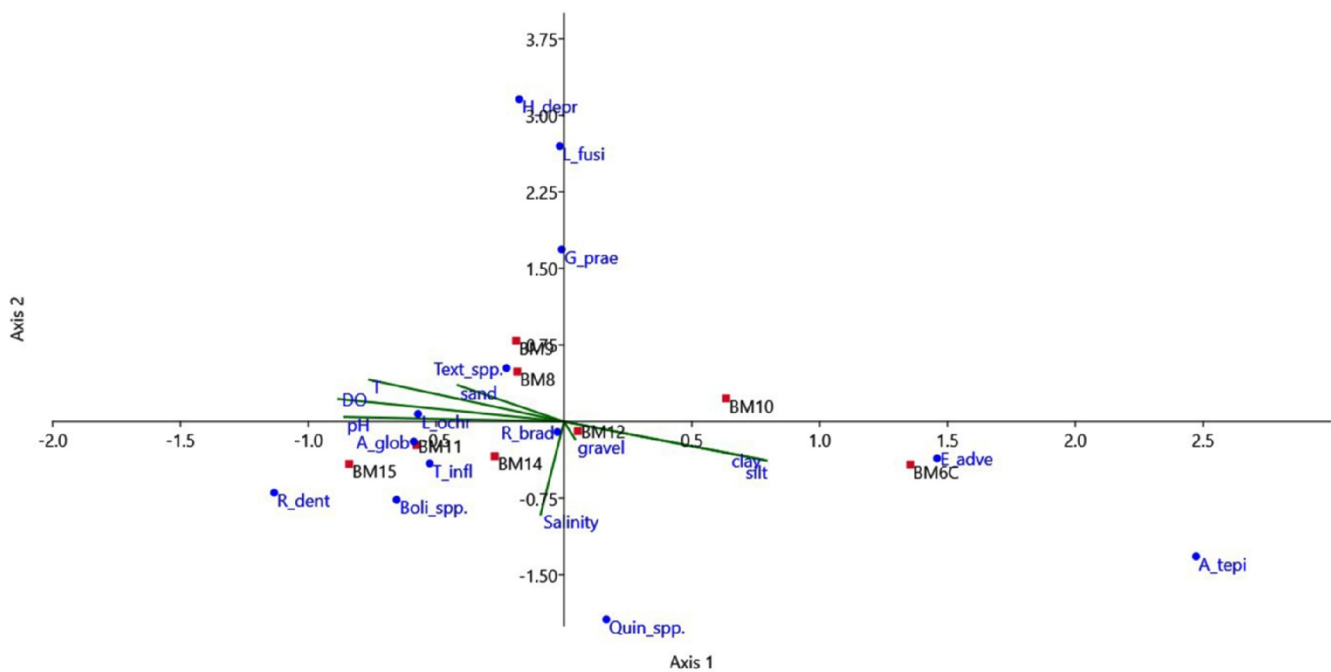
Fig. 10. Canonical Corresponding Analysis applied on living commonly occurring species of North and Middle Branch. Axis 1 and 2 account for 58% and 21% of the variance, respectively.

correlations. *Eggerelloides advenus* is known as an opportunistic infaunal species benefiting from degraded and refractory organic matter and being tolerant with the associated oxygen-depleted conditions (Alve, 1995; Patterson et al., 2000; Tsujimoto et al., 2006; Babalola et al., 2013, 2017). As regards *A. tepida*, it is a euryhaline species typically dominant in Mediterranean, often contaminated, brackish-water lagoons (Carboni et al., 2009; Frontalini et al., 2009; Damak et al., 2019; Dasgupta et al., 2020); nevertheless, in this study any correlations with low salinity are missing. However, it is considered by Jorissen et al. (2018) as a "second-order opportunist" species, i.e. strongly increasing with maximum organic enrichment and was also recognized as tolerating seasonal hypoxic/anoxic conditions (Petersen et al., 2019). Experimental studies on the response of BF to diatom detritus revealed that this species showed very high intake and turnover rates, being linked to high fluxes of organic matter (Wukovits et al., 2018).

Lepidodeuterammina ochracea, A. globigeriniformis, Trochammina inflata, R. dentaliniformis and *Bolivina* spp. (mainly *B. variabilis*), common species in the prevailingly calcareous assemblage of cluster A, display negative values for the first axis, resulting correlated with higher sand, T, pH and DO. *Reophax dentaliniformis* is an infaunal species recognized as a successful opportunistic species in re-colonization experiments (Kaminski et al., 1988), while *L. ochracea* is an epifaunal clinging species which was found at shallow water-depth in coarser oxygenated sediment of the Aveiro continental shelf and lagoon, associated to lower organic matter content (Murray, 2006; Alves Martins et al., 2019a, 2019b); it was also common in intertidal – subtidal and fjord environments of Norwegian coast (Murray and Alve, 2011). Both species were previously recorded in the caves of the Gulf of Orosei: the first one was, in association with *G. praegeri*, the characterizing species of the Entrance Ecozone of the Bel Torrente cave and also common in the Bue Marino cave, together with *A. globigeriniformis, T. inflata* and *B. variabilis*, while the second one was more abundant in the Transitional Ecozone of Bue Marino, dominated by *E. advenus* (Bergamin et al., 2018). *Trochammina inflata*, associated to *B. variabilis*, is typical taxon of the Subtidal Marine Assemblage in Bermudian marine caves, even if recovered in fine sediment (Little and van Hengstum, 2019). Generally, bolivinid species are associated to fine sediment with dysoxic up to anoxic conditions (Sen Gupta and Machain-Castillo, 1993; Bernhard

and Sen Gupta, 1999); in this study, the most abundant *Bolivina* species was *B. variabilis* that occurred in the North Branch correlated with higher DO. At today, only few data exist on its present-day distribution patterns; however, Schmiedl et al. (2003) deduced, from a Quaternary record, the preference of *B. variabilis* for eutrophic conditions without oxygen depletion, supporting our results on its preference of oxygenated environments. *Gavelinopsis praegeri* and *Rosalina* spp. (mainly *R. bradyi*), dominating cluster A, but ubiquitous in the whole cave (Table 1), are located on the second axis and on the origin of the axes, respectively (Fig. 10); the first one results indifferent to sediment characteristics, T and DO while, the second one also to salinity. This behaviour points to a high adaptive character already recognized for *R. bradyi*, which was common as living from the outer to the inner part of Bel Torrente cave (Romano et al., 2018b). *Gavelinopsis praegeri*, as well as *L. fusiformis* and *H. depressula*, are associated to lower salinity, while *Quinqueloculina* species show preference to higher salinity. No literature information was found about the response to this parameter for *L. fusiformis*, while *H. depressula* is well-known tolerating wide salinity variability, from hyper to hypohyaline conditions (Debenay et al., 2000; Carboni et al., 2009; El Kateb et al., 2018) as well as anthropogenic contribution of metals and organic pollutants (Vidović et al., 2016), and *G. praegeri* is generally recorded in a wide range depth in marine environments (Sgarrella and Moncharmont-Zei, 1993; Murray, 2006). The last one was commonly found by De Stigter (1996) as living in the shelf samples of the Adriatic Sea at a depth of 146 m, although occasionally it was also present at depths down to 1200 m. However, in the Sardinian cave, it was a very common species, together with *Rosalina* spp., in a wide range of salinity and associated to coarse sediment (Bergamin et al., 2018; Romano et al., 2018b, 2020).

5.3. Foraminiferal ecozones and their environmental significance

Two main assemblages, based on the total fauna, were recognized in the cave: the mixed calcareous-agglutinated assemblage corresponding to cluster A, exclusive of the North Branch, characterized by high species diversity and low foraminiferal density with abundant calcareous *G. praegeri, Rosalina* spp. and *Quinqueloculina* spp., and agglutinated *E. advenus* and *R. dentaliniformis* (Fig. 8); the prevailingly

agglutinated assemblage corresponding to cluster B, recorded in the whole Middle Branch and in the North one, close to the confluence, characterized by low species diversity and high foraminiferal density with high dominance of *E. advenus* accompanied by *A. tepida*, *A. inflata* and *Rosalina* spp.

From the NMDS plot (Fig. 8) it may be deduced that main separation between clusters A and B has a strong relationship with sediment texture, because grainsize fractions plot on coordinate 1. Cluster A is associated with higher gravel and sand, while cluster B with silt and clay. This agrees with sediment preference demonstrated by typical species of clusters A and B. In particular, *Rosalina* and *Quinqueloculina* species selected preferably sediment fractions from gravel to medium/coarse sand, while *A. tepida* lives mainly in very fine sand or silt (Celia Magno et al., 2012). Because organic matter has affinity with fine sediment, it may be supposed that also the different availability of nutrients linked to different grain size plays a role in clusters separation (Bergamaschi et al., 1997; Armynot du Châtelet et al., 2009). Another environmental factor, corresponding to coordinate 2, was responsible for the separation of sub-clusters B1 and B2, which is much less clear-cut than that between clusters A and B. The main faunal difference of these two subclusters is the abundance of *E. advenus*, which ranges from 38.8% to 43.9% and from 53.8% to 83.6% in B1 and B2, respectively. The more evident opportunistic behaviour of this species indicates higher environmental stress in B2; the tolerance to oxygen depleted conditions, associated to the ability of feeding on degraded refractory organic matter, may be the reason of its success (Thomas et al., 2000; Tsujimoto et al., 2006).

As regards assemblage A, it is exclusive of the North Branch, where the environment is characterized by colder, less salty and oxygenated waters, associated to sandy sediment, and well comparable to the assemblage of the Entrance Ecozone, recognized in summer 2014 and spring 2015 by Bergamin et al. (2018) and Romano et al. (2020) in the same cave, respectively. Assemblage B was recognized, in the present study, in the North Branch close to the confluence and in the whole Middle Branch, where warmer and saline waters characterized this environment, associated to pelitic, oxygen-depleted sediment with high organic content. A similar result, but limited to BM6, was recorded in summer 2014 by Bergamin et al. (2018), where an assemblage strongly dominated by *E. advenus* (58%), was found and interpreted as the response to the supply of fresh plant debris from the Middle Branch. However, for its ecological significance, assemblage B may be considered as corresponding to the Confluence Ecozone identified by Romano et al. (2020). Because this assemblage was recognized not only in samples from the Middle Branch, but also in the North Branch in proximity of the confluence, it may be supposed that, considering the total assemblage as the result of mean conditions over a monthly/yearly period, its influence was extended to part of the North Branch during this time span. Also samples BM16 and BM17, not included in the HCA and CCA for the low number of specimens, showed *E. advenus* as main species. Consequently, seasonal and annual differences have been recognized in extent of the Confluence Ecozone and in the type of the associated foraminiferal assemblage comparing this study with the previous ones. In particular, the wider extent of the Confluence Ecozone were recognized in summer 2016 with respect to 2014 could be explained by more intense rain during winter to transport fine sediment and organic matter from the mainland, followed by a dryer period (April-June) during which marine waters penetrated more efficiently in the Middle Branch (Fig. 2).

A more diversified agglutinated assemblage, characterized by several taxa such as *E. advenus*, but also *L. ochracea*, *R. dentaliniformis* and *Cribrostomoides jeffreysii*, corresponding to the Transitional Ecozone recognized in summer 2014, is not identified in this study. From BM18 to BM23 barren samples identify the Inner Ecozone, never recorded before in Bue Marino cave. The absence of foraminifera in these samples is not explainable by values of water parameters (T 16–19; Sal 17.50–33.43; pH 7.27–8.02; DO 2.98–4.63 ml l^{-1}) because it is well

known that BF inhabit extremely low and high salinity (Murray, 1991), low pH (Panieri et al., 2005; Di Bella et al., 2016) and may survive in hypoxic/anoxic conditions (Pucci et al., 2009). Then, other hypotheses should be advanced to explain the disappearance of BF in the inner stations. The increasing environmental instability (i.e. wide seasonal changes of water parameters and hydrodynamic conditions due to freshwater fluxes) in the inner cave sectors could be suggested as a possible explanation; however, several paralic environments experience wide changes of water parameters with temporal variability from seasonal to diurnal, according to tidal cycles, maintaining abundant foraminiferal communities (Debenay et al., 2000). Another hypothesis is that the colonization of BF in marine caves through the penetration of propagules, according to the mechanism illustrated by Alve and Goldstein (2003, 2010), is physically limited to the outer sector of the cave.

5.4. Wider significance of benthic foraminifera as environmental indicators in marine caves

In spite of the scarcity of living specimens in the studied cave, the short life cycle and rapid turnover of BF and the preservation foraminiferal test in sediments allowed to recognize that, on the whole during the year, BF develop well-diversified peculiar assemblages corresponding to ecozones. The yearly monitoring of these ecozones (Bergamin et al., 2018; Romano et al., 2020; this study) allowed recognizing that they responded to seasonal changes produced by the different rate of marine and terrestrial contributions. As a consequence, the study of BF in marine caves may be regarded not only in the light of increased knowledge of biodiversity of extreme environments, but also as a potential tool of investigation for short and long-term environmental changes. Moreover, the foraminiferal ecozones may be considered as modern analogues for reconstructing past environments in sediment cores (Little and van Hengstum, 2019). In addition, the response of BF to environmental stressors in cave environment is matter of interest also in the perspective of global changes in marine systems. In particular, the abundance of calcareous taxa is of great importance because they play an important role in the CO_2 cycle and several studies predicted their decline with increasing ocean acidification (Dias et al., 2010; Pettit et al., 2013). Romano et al. (2020) suggested that the higher rate of agglutinated taxa in the caves of the Gulf of Orosei, with respect to shallow water marine environments of Sardinia (Cherchi et al., 2009; Buosi et al., 2012, 2013a, 2013b) and, in general, of the Mediterranean Sea (Murray, 1991), was attributable to the reduced saturation of water with $CaCO_3$, in association with lower salinity and temperature. In fact, it is note that the mixing of seawater with freshwater from the karst aquifer produces a dissolution effect influencing both sedimentary calcareous rocks and organogenic carbonate (Radolović et al., 2015). This study indicates that, under these conditions, the addition of another stressor, like as the scarce oxygen availability, in the already stressed cave environment, once again favours agglutinated taxa which demonstrate higher opportunistic character than the calcareous ones.

6. Conclusion

This study improved information knowledge at different scientific levels. As first it provided new information at a local level, on the Bue Marino cave. In particular:

- characterization based on abiotic parameters helped to identify two distinct environments in the North and Middle Branch. The first one was characterized by colder, less saline and more oxygenated waters and coarser sediment pointing to higher hydrodynamic conditions; moreover, a clear pattern of environmental parameters was recognizable from the outer to the inner sector. The second one was a rather homogeneous environment with warmer, more saline and

oxygen-depleted waters associated to pelitic sediment, indicating scarce water flow. The influence of the Middle Branch was recognized in the North one, close to the confluence. This characterization helped to deduce different contributions for the two branches and unknown patterns of distribution of marine waters in the cave;

- the study on foraminiferal assemblages confirmed the stable presence of BF in sediment of marine caves of the Gulf of Orosei, with specific assemblages characterizing distinct habitats of the Bue Marino cave;
- sediment type and the associated oxygen levels were recognized as the main environmental factors influencing the distribution of foraminiferal ecozones, while salinity played a minor role;
- based on foraminifera distribution, two main ecozones were identified: the Entrance Ecozone, exclusive of the North Branch and already recognized in earlier studies, was characterized by a diversified mixed calcareous-agglutinated assemblage; the Confluence Ecozone, identified in the Middle Branch and in the North one, close to the confluence of two branches, was characterized by a prevailingly agglutinated assemblage with the high dominance of *E. advenus*, which displayed opportunistic behaviour in a stressed environment due to dysoxic conditions.

The lesson learnt from marine caves helped to deduce aspects of general interest about the study of BF in marine caves:

- the environmental significance of the foraminiferal ecozones recognized in this study and their comparison with the ones identified in the previous years, helped to consider the ecological zonation as a tool to recognize seasonal and, possibly, long term annual environmental variability in the marine system;
- the response of foraminiferal species to wide environmental parameters, as occurs in marine caves, is useful to understand possible response to global changes.

CRediT authorship contribution statement

Elena Romano: Conceptualization, Methodology, Investigation, Writing - original draft, Revision of the manuscript. **Luisa Bergamin:** Formal analysis, Methodology, Writing - original draft, Visualization, Revision of the manuscript. **Letizia Di Bella:** Investigation, Visualization, Writing - original draft. **Virgilio Frezza:** Investigation, Visualization, Writing - original draft. **Giancarlo Pierfranceschi:** Investigation, Visualization, Writing - original draft. **Andrea Marassich:** Sampling, Writing - original draft. **Claudio Provenzani:** Sampling, Writing - original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106977.

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