

Serpulid communities from two marine caves in the Aegean Sea, eastern Mediterranean

ROSSANA SANFILIPPO¹, ANTONIETTA ROSSO¹, ADRIANO GUIDO² AND VASILIS GEROVASILEIOU³

¹Department of Biological, Geological and Environmental Sciences, University of Catania, Corso Italia, 57, I-95129 Catania, Italy,

²Department of Biology, Ecology and Earth Sciences, University of Calabria, Via Bucci, cubo 15b, I-87036 Rende, Cosenza, Italy,

³Institute of Marine Biology, Biotechnology and Aquaculture, Hellenic Centre for Marine Research, 71500 Heraklion, Crete, Greece

This paper is a first detailed contribution to the knowledge of serpulid diversity from marine caves of the eastern Mediterranean Sea. A total of 27 taxa were recorded in two submerged caves of Lesvos Island, in the Aegean Sea. A clear trend of variability was observed with serpulid abundance, specifically that of sciaphilic and deep-sea species, increasing inwards while the number of taxa and species diversity did not change significantly across the two caves. In the innermost sectors of the studied caves two types of bioconstructions were observed: (a) 'coiled doughnuts' of Protula, recorded for the first time in Mediterranean caves; and (b) 'biostalactites' mainly consisting of skeletal metazoans recorded for the first time from the eastern Mediterranean. The results of the present study revealed new faunal elements and type of bioconstructions for the Mediterranean marine caves, showing that several aspects of their communities are still poorly known and deserve to be further investigated.

Keywords: Annelida, Serpulinae, Spirorbinae, tubeworms, bioconstructions, biostalactites, cave-dwellers, biodiversity, colonization pattern, Holocene

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INTRODUCTION

Marine caves are characterized by environmental gradients generating spatial variability of sessile colonizers (Harmelin, 1985, 1986; Bianchi & Morri, 1994; Bussotti *et al.*, 2006). These complex habitats constitute 'biodiversity reservoirs' of high conservation value, harbouring endemic species and 'ancient' forms (Bianchi *et al.*, 2012; Gerovasileiou & Voultsiadou, 2012). Although Mediterranean marine cave communities have been the subject of research in several studies, considerable knowledge gaps still exist, with regard to certain regions (e.g. eastern and southern Mediterranean sectors) and taxonomic groups (Gerovasileiou *et al.*, 2015, 2016a).

Serpulid polychaetes are among the dominant sessile taxa in confined marine cave systems (Zibrowius, 1968, 1971; Belloni & Bianchi, 1982; Bianchi, 1985; Harmelin *et al.*, 1985; Bianchi & Sanfilippo, 2003), sometimes forming bioconstructions that resemble pseudo-stalactites. Such formations have been observed to date in the Caribbean Sea (Macintyre *et al.*, 1982), the Tyrrhenian Sea in the western Mediterranean (Antonioli *et al.*, 2001) and the southern Adriatic and Ionian seas in the central Mediterranean (Belmonte *et al.*, 2009; Quarta *et al.*, 2010; Sanfilippo *et al.*, 2015).

The diversity of serpulids in marine cave habitats has been investigated mostly in the western Mediterranean Sea (e.g. Zibrowius, 1968; Di Geronimo *et al.*, 1993; Taddei-Ruggiero

et al., 1996; Bianchi & Sanfilippo, 2003; Harmelin *et al.*, 2003; Rosso *et al.*, 2013). To date, a total of 51 serpulid species have been reported from Mediterranean marine caves in the literature (V. Gerovasileiou, unpublished data).

The research effort recently invested in marine caves of the eastern Mediterranean has raised the regional biodiversity known from this habitat type (Gerovasileiou *et al.*, 2015). Most studies, however, focused on other taxa, which dominate in marine caves, such as sponges (e.g. Gerovasileiou & Voultsiadou, 2016). Bailey (1969) recorded eight Spirorbinae species from a small submerged cave in Chios Island (North Aegean Sea) but most serpulid species known from the Aegean ecoregion have been reported from habitats other than caves (Knight-Jones *et al.*, 1991; Koçak *et al.*, 1999; Arvanitidis, 2000; Bianchi & Morri, 2000; Çınar *et al.*, 2014).

The aim of this paper was to (1) provide a first detailed record of the diversity of serpulids in submerged caves of the under studied eastern Mediterranean; (2) examine the structure of serpulid assemblages in this area, focusing on aspects of their morphology, ecology and growth form; and (3) investigate their distribution patterns along different cave sectors.

MATERIALS AND METHODS

Study areas

The surveyed caves are located off Lesvos Island (Aegean Sea, eastern Mediterranean) (Figure 1A). Agios Vasilios cave

Corresponding author:
R. Sanfilippo
Email: sanfiros@unicat.it

(38.969°N 26.541°E) is a blind cave located at a depth range of 24–40 m (Figure 1B). Fara cave (38.969°N 26.477°E) is 32 m long and has the shape of a tunnel, ending in a dark chamber connected to a second cave through a fissure (Figure 1B). The entrance of the cave is located at 18 m while the average depth inside the cave is 14 m. Both caves are formed in Triassic carbonate rocks (Katsikatsos *et al.*, 1982). The two caves were mapped and depicted in three-dimensional models with ‘cavetopo’ software (Gerovasileiou *et al.*, 2013a). The structure of their sessile communities has been previously described (Gerovasileiou *et al.*, 2013b, 2014; Gerovasileiou & Voultsiadou, 2016) but their serpulid diversity has not been studied.

Sampling process and sample analysis

Three replicate quadrats of 400 cm² (20 × 20 cm) were scraped at 10 sampling stations in the surveyed caves (six in Fara cave and four in Agios Vasilios cave) in 2010 by scuba diving using the quadrat sampler designed by Chintiroglou & Koukouras (1992). Sampling stations (Figure 1B, Table 1) represented different assemblages of the sidewalls and ceiling at different distances from the entrance of the caves. Photographs of serpulid bioconstructions were also taken *in situ*. Samples were sieved (0.5 mm) and preserved in 10% formalin. After the sorting process, serpulids were identified at the species level under a stereomicroscope.

For each station, living communities and thanatocoenoses (empty tubes) were examined, and the serpulid abundance (N), number of taxa (S) and Shannon–Wiener diversity

index (H') were calculated. Moreover, all taxa were assigned to six ecological groups according to Rosso *et al.* (2013 and references therein), specifically: (1) ‘Cave species’ including sciaphilic species which thrive in caves as well as in other cryptic micro-habitats (cavities or crevices); (2) ‘Sciaphilic and/or coralligenous species’ which show preference for shadowy and sheltered biotopes such as overhangs, coralligenous concretions, and the lower surface of small-sized hard substrata lying on soft bottoms; (3) ‘Deep-water species’, which are usually found on the outer shelf and upper slope (lower circalittoral and upper bathyal zones); (4) ‘Shelf species’, including more or less euryoecious species which are widely distributed in shelf environments; (5) ‘Shallow-shelf species’ including light-tolerant species able to colonize infralittoral to upper circalittoral habitats; (6) ‘Unplaced species’ which cannot be placed in any of the above groups. The latter group includes species for which no distributional preference is known and taxa identified at high taxonomic levels.

Low magnification images of selected specimens were taken with a Zeiss Discovery V8A stereomicroscope equipped with an Axiocam MRC and Axiovision acquisition system. Specimens are deposited in the Palaeontological Section of the Earth Science Museum at the University of Catania (Italy).

Statistical analysis

One-way permutational ANOVA (perANOVA) was used in order to investigate the variability of the above biotic measures across the stations of each cave (factor, Station; fixed with six

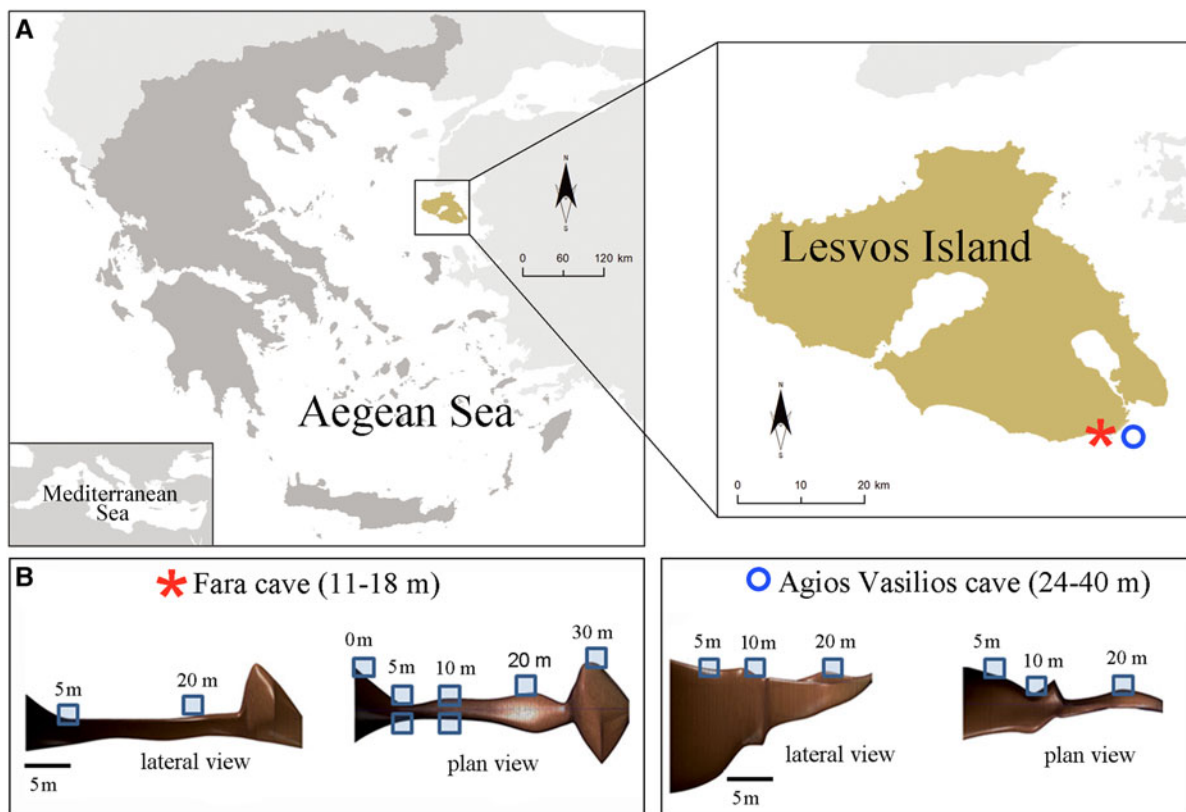


Fig. 1. Map of Lesvos Island in the Aegean ecoregion, showing the locations of the studied caves (A). Scaled three-dimensional depictions (lateral and plan views) of Fara and Agios Vasilios caves produced with ‘cavetopo’ software (Gerovasileiou *et al.*, 2013a) and location of sampling sites (B).

Table 1. Description of the sampling sites for all stations (i.e. distance from the entrance and position on the walls of the cave) and their basic community structure (F: Fara cave, V: Agios Vasiliios cave).

Stations	Site description	Community
F1	Left wall (vertical), at the cave entrance	Coralligenous community, dominated by calcareous rhodophytes
FC1	Ceiling, 5 m from the entrance	Semi-dark cave community, dominated by scleractinians and sponges
F2	Left wall (vertical/positive inclination), covered with a layer of sediment, 5–10 m from the entrance	Semi-dark cave community, dominated by sponges
F3	Right wall (overhanging), 5–10 m from the entrance	Semi-dark cave community, dominated by scleractinians and sponges
FC2	Ceiling, 15–20 m from the entrance	Transitional zone between the semi-dark and dark cave community, dominated by serpulids and bryozoan nodules
F4	Cave walls (vertical), covered with a black coating of Fe-Mn oxides, 20–30 m from the entrance	Dark cave community, dominated by serpulids and sponges
VC1	Ceiling, 5–10 m from the entrance	Semi-dark cave community, dominated by scleractinians and sponges
V1	Cave walls (vertical), 5–10 m from the entrance	Semi-dark cave community, dominated by sponges
VC2	Ceiling, 15–20 m from the entrance	Dark cave community, dominated by scleractinians, sponges and serpulids
V2	Cave walls (vertical), 15–20 m from the entrance	Dark cave community, dominated by sponges and serpulids

levels for Fara cave and four levels for Agios Vasiliios cave). Resemblance of the serpulid community in the different sampling stations of the caves was examined with multidimensional scaling (MDS), based on the Bray–Curtis similarity index (fourth root transformed mean abundance data).

The contribution of serpulid taxa to the similarity of samples within the resulting groups was estimated with SIMPER (SIMilarity PERcentages). Statistical analysis was undertaken using PRIMER-E v6 software package (Clarke & Gorley, 2006).

RESULTS

Taxonomic composition

A total of 27 serpulid taxa were identified in the two caves (19 Serpulinae and 8 Spirorbinae), 21 of which were common in both caves (16 Serpulinae and 5 Spirorbinae). Living serpulid assemblages consisted of 14 taxa (10 Serpulinae and 4 Spirorbinae), 6 of which (5 Serpulinae and 1 Spirorbinae) were found in both caves (Table 2). The thanatocoenoses

Table 2. Systematic list of serpulid taxa recorded in the studied Aegean caves (bold font indicates a living community).

	F1	FC1	F2	F3	FC2	F4	VC1	V1	VC2	V2
Serpulinae										
<i>Serpula cavernicola</i> Fassari & Mòllica (1991)		2		6		4	2	9		11
' <i>Serpula vermicularis</i> ' Linnaeus, 1767	4		2							
<i>Serpula vermicularis</i> f. <i>echinata</i> Linnaeus, 1769							3	3		
<i>Serpula concharum</i> Langerhans, 1880	2	3+2	1		4		1			
<i>Serpula concharum</i> (deep form) Langerhans, 1880								3		
<i>Spiraserpula massiliensis</i> (Zibrowius, 1968)						6		6	10+6	
<i>Vermiliopsis labiata</i> (O.G. Costa, 1861)	4					8		7+2	3	36+5
<i>Vermiliopsis</i> sp.			2	2	2		2	1	1	
<i>Metavermilia multicristata</i> (Philippi, 1844)	3	3	30+8	5	16+6	45+4	2	20+4	40+3	38
<i>Semivermilia crenata</i> (O.G. Costa, 1861)		30	58+8	36	145+18	185	70+12	93	78	77
<i>Semivermilia pomatostegoides</i> (Zibrowius, 1969)					31				8	8
<i>Filogranula calyculata</i> (O.G. Costa, 1861)	1						3			2
<i>Filogranula gracilis</i> Langerhans (1884)						1			1	1
<i>Janita fimbriata</i> (Delle Chiaje, 1822)					13	6	3	2	10	20
<i>Spirobranchus polytrema</i> (Philippi, 1844)	5	6	1	4			5	2	2	3
<i>Spirobranchus triqueter</i> (Linnaeus, 1758)	2									1
<i>Hyalopomatus</i> cf. <i>variorugosus</i> Ben-Eliahu & Fiege, 1996	2				6					6
<i>Josephella marenzelleri</i> Caullery & Mesnil, 1856	42	18		60	5+35	140	16+20	70+18	60	35+35
' <i>Protula tubularia</i> ' (Montagu, 1803)	2		3		9+1	6+3	12+2		8+6	25+2
<i>Protula</i> sp.1					2	12		4		8
Serpulinae sp.1								2	1	
Spirorbinae										
<i>Spirorbis cuneatus</i> Gee J.M., 1964		4		5					3	3
<i>Pileolaria heteropoma</i> Zibrowius, 1968		2								
<i>Pileolaria militaris</i> Claparède, 1870		1	1					3		
<i>Protolaeospira (Protolaeospira) striata</i> (Quievreux, 1963)			4				4+6	6		
<i>Vinaria koehleri</i> (Caullery & Mesnil, 1897)				3				3	1	
<i>Janua (Dexiospira) pagenstecheri</i> (Quatrefages, 1866)		2			2		3		3	3
Spirorbinae sp.1		1			1					
Total number of specimens	67	74	118	121	296	420	166	258	244	319

consisted of 26 taxa (19 Serpulinae and 7 Spirorbinae), of which 18 were common in the two caves (15 Serpulinae and 3 Spirorbinae). The most widely distributed and abundant species were *Semivermilia crenata*, *Josephella marenzelleri* and *Metavermilia multicristata*, in all cases. The remaining taxa presented much lower abundances. Selected photographs of serpulid specimens are presented in Figure 2.

Spatial patterns

Serpulid abundance increased inwards in both caves (Table 3); however, this variability was significant only in Fara cave, for the living community ($df = 5$, Pseudo-F = 3.5903, $P < 0.05$),

the thanatocoenosis ($df = 5$, Pseudo-F = 10.185, $P < 0.01$), and the total community ($df = 5$, Pseudo-F = 8.2601, $P < 0.01$). The number of taxa and the Shannon–Wiener diversity index did not change significantly in either of the two caves. Higher numbers of taxa were recorded in all stations of Agios Vasiliou cave compared with those of Fara cave (Table 3).

Multivariate resemblance analysis revealed three major groups of stations with similarity greater than 60%, as shown in the MDS plot (Figure 3): (1) stations from the semi-dark sector of Fara cave (F₃ with FC₁); (2) stations from the semi-dark sector of Agios Vasiliou cave (VC₁ with V₁); and (3) stations from the dark sectors of both caves (FC₂, F₄,



Fig. 2. Photographs of serpulid specimens from different stations of the studied marine caves (in parentheses): (A) *Serpula cavernicola* (V₁); (B) '*Serpula vermicularis*' (Fara cave); (C) *Serpula vermicularis* f. *echinata* (V₁); (D) *Serpula concharum* (FC₂); (E) *Spiraserpula massiliensis* (VC₂); (F) *Vermiliopsis labiata* (V₁); (G) *Metavermilia multicristata* (F₄); (H) *Semivermilia crenata* (V₂); (I) *Spirobranchus polytrema* (FC₁); (J) *Hyalopomatus* cf. *variorugosus* (V₂); (K) *Josephella marenzelleri* (V₁); (L) '*Protula tubularia*' (F₄); (M) *Pileolaria heteropoma* (FC₁); (N) *Vinearia koehlerii* (V₁). Scale bars: 1 mm for A–K and M–N, 1 cm for L. Photos by R. Sanfilippo (A, C–K, M–N), T. Dailianis (B) and V. Gerovasileiou (L).

Table 3. Number of taxa (S), mean abundance (N) and Shannon–Wiener diversity (H') per sampling station for the total and living communities and for the thanatocoenoses, respectively.

Stations	Total community			Living community			Thanatocoenosis		
	S	N	H'	S	N	H'	S	N	H'
F1	10	22.3	1.444	2	15.3	0.295	8	7	1.976
FC1	11	24.7	1.792	2	2	0.693	9	22.7	1.597
F2	8	38.7	1.09	5	7.3	1.327	5	31.3	0.903
F3	7	39.7	1.331	1	1.3	0	6	38.3	1.225
FC2	11	113	1.379	4	17.3	0.909	11	93	1.23
F4	10	140	1.417	2	2.3	0.683	10	137.7	1.391
V1	15	85.7	1.752	7	12.7	1.593	11	73	1.563
VC1	12	54.3	1.582	5	14.3	1.229	10	40	1.472
VC2	14	81	1.874	4	24	0.624	12	55	1.623
V2	16	106.3	2.151	3	14	0.55	16	92.3	2.201

VC2 and V2), regardless of the position on the cave walls. The two outermost stations of Fara cave, F1 and F2, differed from the above groups. According to the results of SIMPER analysis, the taxa which contributed by 60% to the similarity of samples within the above groups were respectively (in order of appearance): (1) *S. crenata*, *J. marenzelleri* and *Spirobranchus polytrema*; (2) *S. crenata*, *J. marenzelleri*, *Protolaeospira (P.) striata* and *Serpula vermicularis f. echinata*; (3) *S. crenata*, *J. marenzelleri*, *M. multicristata* and '*Protula tubularia*'. On the other hand, the taxa which contributed to 60% of the dissimilarity between the above groups could be categorized as follows: (a) taxa with higher abundance in the inner dark cave sectors (e.g. *Vermiliopsis labiata*, '*P. tubularia*', *Spiraserpula massiliensis* and *M. multicristata*); (b) taxa recorded exclusively in the dark cave sectors (*Semivermilia pomatostegoides*); (c) taxa with higher abundance in the semi-dark cave sectors (e.g. *P. striata*).

Ecological groups

Sciaphilic/coralligenous serpulids prevailed in terms of number of taxa (8) in both caves, followed by deep-water (8), shallow-shelf (5), shelf (3), cave (2) and unplaced taxa (Table 4). The same order was recorded with regards to abundance. The abundance of the three first groups increased towards the dark interior of both caves (Figure 4). However,

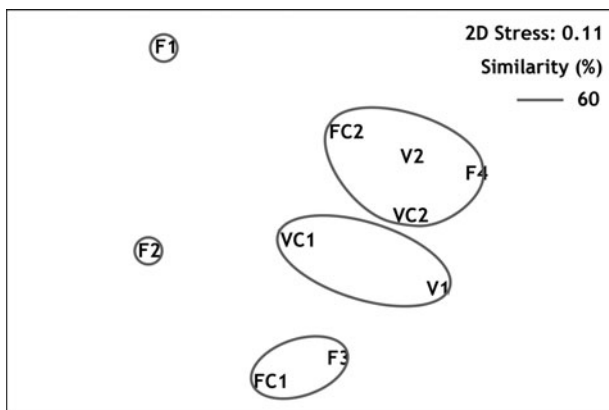


Fig. 3. Resemblance of sampling stations demonstrated in MDS plot.

Table 4. Assignment of the serpulid taxa recorded in the studied caves to ecological groups according to the classification scheme by Rosso *et al.* (2013) and newly acquired data.

Ecological groups	Taxa
Sciaphilic and/or coralligenous taxa	<i>Filigranula calyculata</i> , <i>Josephella marenzelleri</i> , <i>Metavermilia multicristata</i> , <i>Protolaeospira (P.) striata</i> , <i>Semivermilia crenata</i> , <i>Serpula concharum</i> (deep form), <i>Vermiliopsis labiata</i> , <i>Vinearia koelheri</i>
Deep-water taxa	<i>Filigranula gracilis</i> , <i>Hyalopomatus cf. variorugosus</i> , <i>Janita fimbriata</i> , ' <i>Protula tubularia</i> ', <i>Semivermilia pomatostegoides</i>
Shallow-shelf taxa	<i>Serpula concharum</i> , <i>Spirobranchus polytrema</i> , <i>S. triqueter</i> , <i>Janua (Dexiospira) pagenstecheri</i> , <i>Pileolaria heteropoma</i>
Shelf taxa	<i>Serpula vermicularis f. echinata</i> , <i>Spirorbis cuneatus</i> , <i>Pileolaria militaris</i>
Cave taxa	<i>Serpula cavernicola</i> , <i>Spiraserpula massiliensis</i>
Unplaced taxa	<i>Protula sp.1</i> , <i>Serpulinae sp.1</i> , ' <i>Serpula vermicularis</i> ', <i>Spirorbinae sp.1</i>

variability was significant only in Fara cave, for the sciaphilic/coralligenous (df = 5, Pseudo-F = 9.0973, P < 0.01) and deep-water groups (df = 5, Pseudo-F = 3.0735, P < 0.01).

Bioconstructions and aggregates

Serpulids were more abundant in the innermost dark sectors where the rock was only partially covered by serpulids and coated by diffuse black oxide crusts (Figure 5A). They were mostly found as isolated tubes, but in the innermost sectors of the caves some taxa aggregated to form three-dimensional structures. 'Giant' isolated tubes (up to 1 m long) possibly belonging to the genus *Protula* (observed *in situ*) were among the largest encrusters in the inner dark edge of Agios Vasilios cave. Some '*P. tubularia*' specimens were locally aligned (Figure 5B), or aggregated, forming bioconstructions, often associated with nodular bryozoan concretions

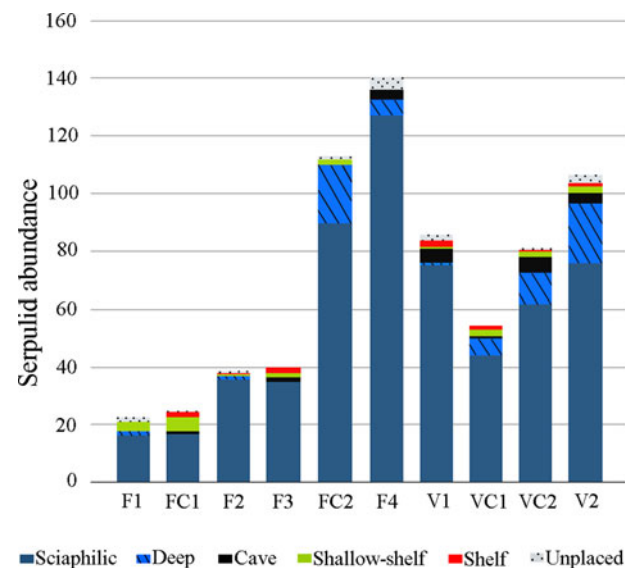


Fig. 4. Contribution of the different ecological groups to the abundance of serpulids in the sampling stations of the studied caves.

(Figure 5C). Thick crusts of tubes, resulting from the superimposition of successive generations of different serpulid taxa, were obvious at places (Figure 5D).

Bioconstructions of '*P. tubularia*' had two forms: (1) coiled 'doughnuts' of tubes (Figure 6A), up to 6 cm in diameter, resulting from the superimposition of tube whorls strictly adhering to each other (Figure 6B), sometimes presenting straight tube end (the diameter of tube whorls was often progressively increasing); and (2) plait-like aggregates, ~8 cm high and 4 cm wide, formed by irregularly coiled and intermingled tubes (Figure 6C–E). The doughnut-like formations were larger and more frequent inwards (Figure 6F). The plait-like structures were hanging from the ceilings and projected obliquely from the walls in inner semi-dark and dark cave sectors (Figure 6G).

The microserpulid *J. marenzelleri* locally formed mm-thick crusts of intermingled tubes, resulting in three-dimensional intricate nets. They occurred in samples from the semi-dark and dark cave communities, coating the surface of bryozoan concretions and *Protula* tubes, and filling small cavities (Figure 6H). These *Josephella* 'nets' were locally recrystallized, with secondary large crystals substituting the tube walls and filling spaces between tubes (Figure 6K).

DISCUSSION

The results of the present study showed that the surveyed Aegean marine caves host a rich serpulid fauna (14 living and 27 dead taxa), comparable to that from marine caves in the

western and central Mediterranean Sea, which had been thoroughly studied for their serpulid diversity; notable examples include: Bagaud cave (19 living taxa), in South France (Harmelin *et al.*, 2003); Mitigliano (27 living taxa) and the semi-submerged Accademia (2 living and 20 dead taxa) caves in the Tyrrhenian Sea (Belloni & Bianchi, 1982; Bianchi, 1985; Balduzzi *et al.*, 1989; Di Geronimo *et al.*, 1993; Rosso *et al.*, 2013); Mazzere, Gymnasium, and Granchi caves (13 living and 32 dead taxa) in the Ionian Sea, Sicily (Rosso *et al.*, 2013); the semi-submerged Ciolo cave (20 living) in the Ionian Sea, southern Apulia (Denitto & Licciano, 2006).

The species *Hyalopomatus* cf. *variorugosus* is reported for the first time from the marine cave habitat. This species had been reported from bathyal bottoms of other Mediterranean regions, with living and dead specimens (Ben-Eliahu & Fiege, 1996; Sanfilippo, 1998, 2009; Rosso *et al.*, 2010), and from Pleistocene bathyal deposits of southern Italy (Di Geronimo *et al.*, 1997). The remaining taxa have already been reported from other marine caves in the Mediterranean Sea (Di Geronimo *et al.*, 1993; Taddei-Ruggiero *et al.*, 1996; Bianchi & Sanfilippo, 2003; Rosso *et al.*, 2013). Serpulid communities from caves located at comparable depths along the Tyrrhenian and Ionian coasts of Sicily had a similar structure, with the species *Semivermilia crenata* and *Josephella marenzelleri* dominating (Rosso *et al.*, 2013). Interestingly, some taxa (i.e. *Serpula vermicularis* f. *echinata*, *Filogranula calyculata*, *H.* cf. *variorugosus*, *Serpulinae* sp.1 and *Spirorbinae* sp.1) found in the studied Aegean caves were absent from marine caves of Sicily. On the other hand, several species that are known to be typical cave-dwellers (Rosso *et al.*, 2013 and references therein) e.g.

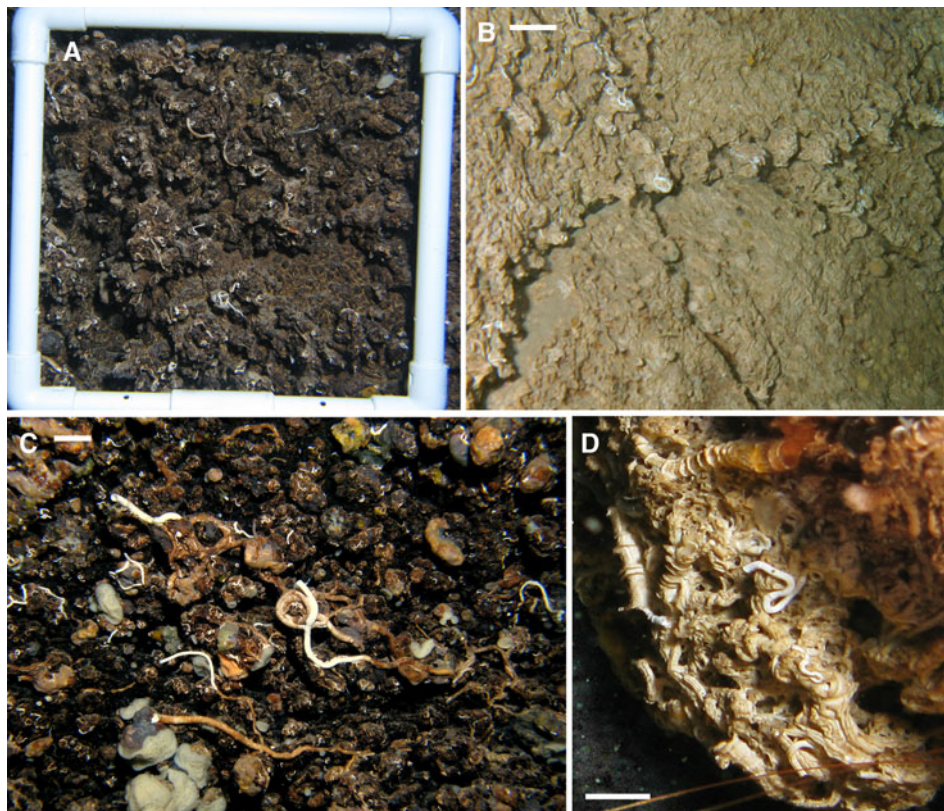


Fig. 5. (A) Wall of Fara cave from the dark zone, partially covered by different species of serpulids and coated by diffuse black oxide crusts (20 × 20 cm sampled surface F4, 30 m from the entrance); (B) Aligned biostalactites along a fissure of the right wall in Agios Vasiliou cave (20 m from the entrance); (C) Serpulid bioconstructions associated with nodular bryozoan concretions in the dark zone of Fara cave (25 m from the entrance); (D) Thick crusts of superimposed tubes formed by subsequent serpulid generations in Agios Vasiliou cave (20 m from the entrance). Scale bars: 5 cm for B, 1 cm for C, D. Photos by V. Gerovasileiou.

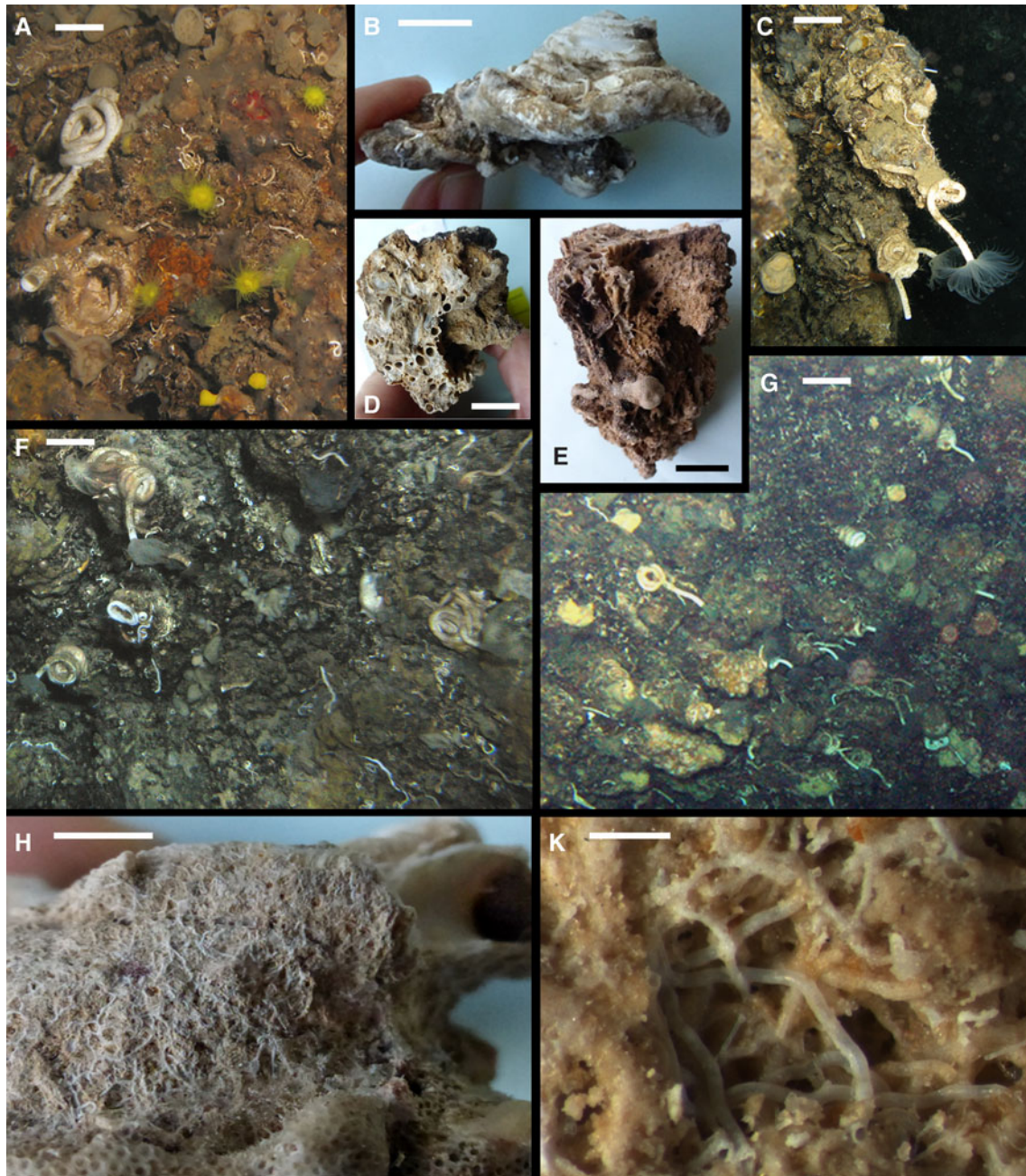


Fig. 6. (A) Coiled 'doughnuts' of tubes belonging to the large-sized serpulid '*Protula tubularia*' (15 m from the entrance, Agios Vasilios cave); (B) A doughnut-like *Protula* bioconstruction, showing several tube whorls of increasing diameter (5 m from the entrance, Agios Vasilios cave); (C) Biostalactites built by aggregated individuals of the serpulid '*P. tubularia*' (25 m from the entrance, Fara cave); (D, E) Subconical biostalactite formed by aggregated *Protula* tubes and cemented micrite: cross section and longitudinal view (32 m from the entrance, Fara cave); (F) Wall in the dark zone of Fara cave, covered with doughnut-like formations (30 m from the entrance); (G) Cave wall with densely spaced biostalactites (~10 formations/cm²), obliquely projecting towards the center of Fara cave (20–30 m from the entrance); (H) Intricate mm-thick tube nets formed by the microserpulid *Josephella marenzelleri* associated with bryozoans, developing on a doughnut-like tube of *Protula* (sample V2, Agios Vasilios cave); (K) Detail of H showing locally recrystallized micrite sediments between tubes. Scale bars: 1 cm for figures A–G, 5 mm for H, 1 mm for K. Photos by V. Gerovasileiou (A and F), R. Sanfilippo (B, D–E, H–K) and M. Sini (C and G).

Filigranula annulata, *Placostegus tridentatus*, *P. crystallinus*, *Semivermilia cribrata*, *Simplaria pseudomilitaris*, *Spirorbis marioni* and *Vermiliopsis monodiscus*, were not found among the scraped samples. These differences can be attributed to the high biogeographic heterogeneity of sessile taxa in Mediterranean marine caves (Gerovasileiou & Voultsiadou, 2012) coupled with the locally patchy distribution of taxa inside caves (Harmelin, 1986, 1997; Rosso *et al.*, 2013) or mere sampling biases. For instance, the species *P. tridentatus*

and *V. monodiscus* were recently recorded as infauna in the canals of the sponges *Agelas oroides* and *Aplysina aerophoba* in the studied Aegean caves (Gerovasileiou *et al.*, 2016b). The majority of taxa recorded in this study (18 taxa, 67%), are also new elements for the marine cave fauna of the Aegean Sea, according to the most recent biodiversity census in this habitat type (Gerovasileiou *et al.*, 2015).

Two of the species identified in this study, *H. cf. variorugosus* and *Serpula cavernicola* are new records for the serpulid

fauna of the Aegean ecoregion (Arvanitidis, 2000; Ben Eliahu & ten Hove, 2011; Çinar *et al.*, 2014). The latter species is a typical cave-dweller, restricted to dark sectors of marine caves (Sanfilippo & Mòllica, 2000). It has been rarely reported from the Ionian and Tyrrhenian seas, the Straits of Gibraltar and the southern coasts of Portugal in the Atlantic Ocean, usually found as empty tubes (Fassari & Mòllica, 1991; Taddei-Ruggiero *et al.*, 1996; Sanfilippo & Mòllica, 2000; Rosso *et al.*, 2013). In the studied caves, only dead specimens of *S. cavernicola* were found in several stations (Table 1).

It has been suggested that marine caves function as ‘islands’, supporting isolated populations of sessile taxa (Muricy *et al.*, 1996), which often exhibit morphological adaptations to the local environmental conditions (Harmelin *et al.*, 1985). Furthermore, several cave-exclusive species have been recorded from only one or very few caves (Gerovasileiou & Voultsiadou, 2012; Gerovasileiou *et al.*, 2016a). In this respect, a number of serpulid taxa recorded in the studied Aegean caves deserve further study from the taxonomic point of view (morphological and molecular). These include the serpulids identified only at higher-than-species taxonomic levels (i.e. *Protula* sp.1, *Serpulinae* sp.1, *Spirorbinae* sp.1) as well as the species ‘*P. tubularia*’ and ‘*S. vermicularis*’, whose cosmopolitan distribution has been questioned (Kupriyanova & Jirkov, 1997; ten Hove & Kupriyanova, 2009). Distinct forms of certain taxa (i.e. *S. vermicularis* f. *echinata* and *S. concharum* (deep form)), which belong to different ecological groups (Table 4), were found in the deeper Agios Vasilios cave. Targeted study of the above-mentioned taxa would also be interesting from an ecological and taxonomic point of view.

The results of the multivariate resemblance analysis, coupled with those of the distribution of the different ecological groups across the studied caves, revealed that the structure of the serpulid community in the inner zone differs from that of the more heterogeneous outer semi-dark sectors. Specifically, the abundance of sciaphilic, deep-water and cave taxa increased inwards, following the environmental gradients such as the loss of light and the increasing water confinement (Balduzzi *et al.*, 1989; Bianchi & Morri, 1994; Sanfilippo *et al.*, 2015). This variability was more conspicuous in Fara cave and is possibly related to the higher level of confinement in this cave, as it is characterized by a more elongated shape and a narrower cross-sectional area, compared with the wider and less confined Agios Vasilios cave (Gerovasileiou *et al.*, 2013a; Gerovasileiou & Voultsiadou, 2016). The considerably higher percentage of deep-water taxa in the inner dark cave sectors is in accordance with the hypothesis that dark caves form ‘deep-sea mesocosms’ in the shallow littoral zone, presenting faunal affinities to the deep-sea (Zibrowius, 1971; Vacelet *et al.*, 1994; Harmelin & Vacelet, 1997; Martínez *et al.*, 2013).

Serpulid bioconstructions in the form of ‘coiled doughnuts’ by ‘*P. tubularia*’ seem to be unknown from other Mediterranean caves and deserve to be further investigated. On the other hand, the plait-like aggregates are similar to biostalactites currently being studied in a cave in Cyprus (Guido *et al.*, unpublished data) and to those found in other caves at comparable depths in the Apulian (Onorato *et al.*, 2003; Belmonte *et al.*, 2009) and Sicilian coasts of Italy, central Mediterranean (Guido *et al.*, 2013, 2016a; Sanfilippo *et al.*, 2015). These biostalactites consist of skeletonized invertebrates and syndepositional-cemented micrite deposited *in situ* through microbial metabolic activity (Guido *et al.*, 2012, 2013, 2014, 2016b). The aggregation of

Protula specimens forming this type of biostalactite seems to be influenced by the local salinity gradients induced by the dilution of continental water inflows through fractures in the surrounding rocks (Guido *et al.*, 2014; Sanfilippo *et al.*, 2015). A similar process could be responsible for the formation of the numerous biostalactites aligned along fissures of the Agios Vasilios cave.

In conclusion, the present study provided a first record of the marine cave serpulid fauna in the Aegean Sea identifying basic community patterns and interesting faunal affinities with other habitats as well as new faunal element and forms of bioconstructions for the Mediterranean marine cave habitat. The results of the present study suggest that several aspects of the marine cave communities are still poorly known and deserve to be investigated.

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Correspondence should be addressed to:

R. Sanfilippo
 Department of Biological,
 Geological and Environmental Sciences, University of Catania,
 Corso Italia, 57, I-95129 Catania, Italy
 email: sanfros@unict.it