

ORIGINAL ARTICLE

Metazoan/microbial biostalactites from present-day submarine caves in the Mediterranean Sea

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Keywords

Bioconstructions; bryozoans; cave communities; Holocene; Mediterranean; serpulids.

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Accepted: 1 September 2014

doi: 10.1111/maec.12229

Abstract

Biostalactites formed by metazoan–microbialite associations from three submerged marine caves in the Plemmirio Peninsula (south of Syracuse, Ionian Sea) are randomly distributed and show different sizes and morphologies, as well as variations in surface roughness/smoothness. The biostalactites consist of crusts a few centimeters thick of small serpulids and other metazoans, associated with fine-grained carbonate; the larger ones often include a nucleus of serpulid tubes (*Protula*). The metazoans include mainly serpuloids, sponges, bryozoans and foraminifers but microbial carbonates are also significant components. The composition of both the living communities and thanatocoenoses on the outer surfaces, as well as the composition and fabric of the internal framework, were analysed and used to reconstruct the history of the caves. All of the identified sessile faunas mainly consist of cryptic and sciaphilic dwellers that reflect cave conditions and their variations through time. The distribution pattern, composition and abundance of the present-day dwellers largely depend on the degree of roughness of the biostalactite surfaces and their positions within the caves. It has been suggested that the *Protula* specimens in the nuclei represent pioneer populations that formed aggregates during the early cave colonization phase, in response to relatively high food supply from seawater inflow and intruding continental waters. By contrast, the outer metazoan–microbialite carbonates reflect more confined conditions in the caves caused by Holocene sea-level rises. Hypotheses are proposed for biostalactite growth, taking into account information about the growth rates of some constituents, and evidence of dissolution effects. Similarities and differences between these biostalactites and other Holocene deposits previously described from submarine caves in the Mediterranean Sea and in tropical reefs are discussed.

Introduction

Biogenic stalactites formed by sessile metazoans and microbial carbonates have been found in three submerged caves on the Ionian coast of Sicily. These biogenic structures, termed ‘biostalactites’ (BSTs), are more or less elongate (cm-to-dm high) extensions from the ceilings and walls of caves. Serpulids, bryozoans and sponges are

the main macrofaunal constituents, in addition to the microbial component, which was already investigated by Guido *et al.* (2012, 2013, 2014).

Structures such as those found in the Plemmirio Marine Protected Area (PMPA) were previously known from present-day submarine caves in tropical seas. Macintyre & Videtich (1979) introduced the term ‘pseudostalactites’ to describe examples formed by serpulid tubes and

magnesium calcite projecting from the ceilings of submarine caves in the Caribbean (Belize). Similar structures were subsequently reported by Reitner (1993) from cryptic environments associated with coral reefs around Lizard Island, Australia. Similar BSTs have recently been studied by Onorato *et al.* (2003) and Belmonte *et al.* (2009) from Holocene caves in Southeast Italy.

In the fossil record, comparable bioconstructions are known from Jurassic to Cretaceous shallow-water caves and reef cryptic environments in Europe (Reitner 1993; Taylor & Palmer 1994a,b; Bertling & Insalaco 1998; Olivier *et al.* 2001, 2003; Olivier 2004; Reolid & Molina 2010).

The present paper aimed to: (i) describe the different morphologic types of BSTs from PMPA caves and their distribution patterns, if any; (ii) characterize the metazoan associations that constitute the entire framework of these BSTs, also clarifying their relationships with the micrite carbonates; (iii) study the composition of living and dead associations of sessile organisms on the outer surfaces of the BSTs, as well as their distribution patterns; (iv) highlight differences in metazoan composition/distribution, if any, among the BSTs within single caves and among the three caves examined; (v) compare the composition of the invertebrate faunas from the inner (earlier) parts of the framework toward the present-day surface in order to reconstruct possible environmental changes during the colonization history of these caves.

Material and Methods

Biostalactites were collected in September 2009 from the walls and ceilings of three submerged caves: the Gymnasium (GM), Mazzere (MZ) and Granchi (GR) caves, located in different settings along the Maddalena Penin-

sula, in the PMPA, south of Syracuse (Southeast Sicily), Ionian Sea (Fig. 1). The caves developed in Miocene biocalcarenes and biocalcirudites that are commonly thick-bedded, intensely faulted and karstified.

The three caves have blind terminations and developed subhorizontally. They open at about 20 m below the present-day sea level. The GR and GM caves are 53 and 65 m long, respectively, and do not exceed 3 m in height (Leonardi 1994). Both caves possess openings *c.* 8 m wide \times 3 m high. The MZ cave has a smaller entrance (3 m wide \times 1.5 m high) and consists of a still unexplored branch and a second narrowing branch (35 m long and 3–4 m wide) that ends in a small chamber less than 2 m high. The floors of all of the caves are nearly flat and largely covered by muddy deposits with an abundant bioclastic fraction. Light penetration decreases rapidly from the entrances, leading to total darkness within a few meters. The benthic communities are typical of the biocoenoses of dark caves (GO) and semi-dark caves (GSO) (Rosso *et al.* 2012, 2013, 2014a,b). Information exists about physical/chemical parameters only for the GM and GR caves (Pitruzzello & Russo 2008). Measurements during summer gave temperatures ranging from 22.9 to 23.5 °C for both caves, with a minimum at about 35 m (GR cave) and 18 m (GM cave) from the entrances. A comparable trend is shown by salinity, suggesting intrusion of continental waters (data not shown). Dissolved oxygen lowers sharply at about 50 m from the entrance for the GR cave and 33 m for the GM cave.

A total of 15 BSTs (six from MZ, five from GR and four from GM caves) were collected (Table 1). Sampling sites within each cave were at regular intervals from the entrances (Fig. 1).

The outer surfaces of BSTs were examined under a stereomicroscope to detect living and dead specimens of the various taxa.

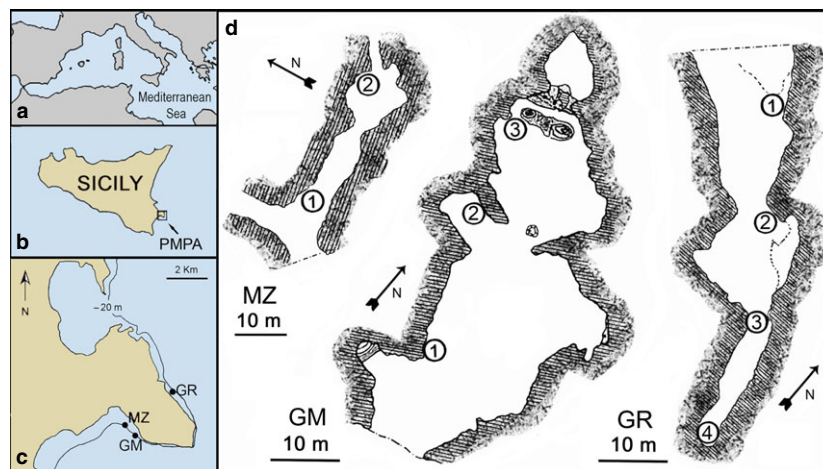


Fig. 1. Location of the studied area in the Mediterranean (a), Sicily (b), and Plemmirio Peninsula (c), and schematic maps of Mazzere (MZ), Gymnasium (GM) and Granchi (GR) caves. BST sampling sites are indicated.

Table 1. Morphologic types and main features of the 15 studied biostalactites. For the mushroom-shaped biostalactites, minimum and maximum diameters of the enlarged parts were measured.

cave	biostalactite	height (cm)	max and min diameters (cm)	shape	surface	distance from entrance (m)	position	nucleus
Granchi	GR 1p	7	7 × 9	Mushroom	S + R	10	Wall	Plaits of <i>Protula</i> tubes
	GR 2p	5	6 × 8	Dome	R	20	Wall	Coiled tubes of <i>Protula</i> , bored by <i>Litophaga</i>
	GR 3p	9	3 × 8	Conical	S + R	40	Wall	Plaits of <i>Protula</i> tubes
	GR 3v	7.5	3.5 × 6	Conical	R	40	Ceiling	Undifferentiated
	GR 4v	11	6 × 6	Cylindrical	S + R	60	Ceiling	Plaits of <i>Protula</i> tubes
Gymnasium	GM 1v	4.5	5 × 9	Dome	R	15	Ceiling	Coiled tubes of <i>Protula</i>
	GM 2v ₁	15	10 × 11	Conical	R	35	Ceiling	Undifferentiated, bored by <i>Litophaga</i>
	GM 2v ₂	5	5 × 6	Dome	R	35	Ceiling	Undifferentiated
	GM 3v	5	6 × 7	Dome	R	55	Ceiling	Undifferentiated
	Mazzere	MZ 1p	10	8 × 13	Mushroom	S + R	10	Wall
	MZ 1v	4	6 × 7	Dome	R	10	Ceiling	Coiled tubes of <i>Protula</i>
	MZ 2p ₁	5	6 × 8	Dome	R	35	Wall	Coiled tubes of <i>Protula</i>
	MZ 2p ₂	10	6 × 8	Conical	R	35	Wall	Plaits of <i>Protula</i> tubes
	MZ 2p ₃	9	8 × 8	Conical	S + R	35	Wall	Plaits of <i>Protula</i> tubes
	MZ 2v	14	5 × 7	Flabellate	R	35	Ceiling	Stalactite

R = rough side; S = smooth side.

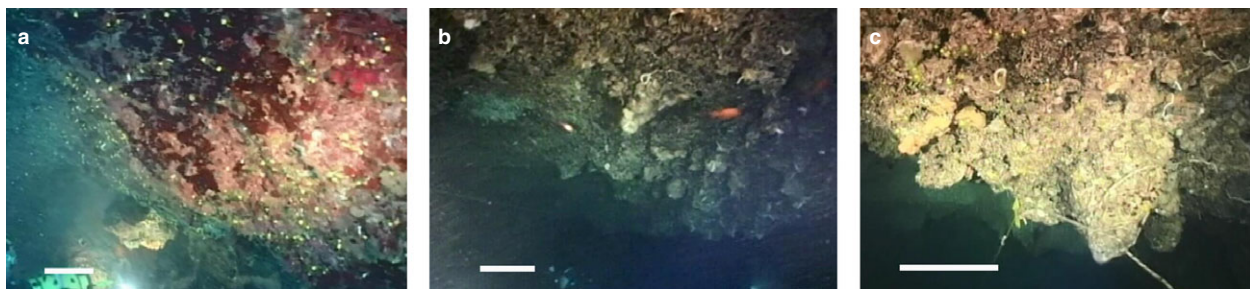


Fig. 2. Video images of Gymnasium Cave. (a) Rocky wall at the entrance, colonized by corals (light dots) and red algae. (b) Ceiling from the mid-part of the cave, showing closely spaced cylindrical BSTs, reaching densities of about 10 per square meter. (c) BSTs from the innermost parts of the cave, showing rough surfaces encrusted by sponges and serpulids and blackened by diffuse oxidation. Oxidation crusts and colonizers are also evenly distributed on the rocky surfaces of the cave (see upper part of image). Scale bars: 1 dm for all figures.

Serpuloideans, bryozoans and were determined to species level, and abundances were estimated for each species (Table 2). Identifications to family, genus or, where possible, species level were made for other co-occurring taxa (sponges, foraminifers, brachiopods, mollusks, corals, barnacles).

The composition of the invertebrate skeletons, as well as their relationships with associated autochthonous micritic carbonates and the fabric/structure of the internal parts were examined in cross-sections of broken basal parts and in longitudinal polished sections of selected BSTs.

Low magnification images were taken with a Zeiss Discovery V8A stereomicroscope equipped with an Axiocam MRC and Axiovision acquisition system.

Specimens are curated in the Paleontological Section of the Earth Science Museum at the University of Catania.

Results

Underwater observations

Biostalactites are absent close to the cave entrances, where scleractinian corals as well as coralline and squamariacean algae are conspicuous (Fig. 2a). BSTs start a few meters inside the entrances, and then occur throughout the caves. Video surveys revealed an apparently random distribution of BSTs inside the caves, although they tend to be more abundant in the mid-parts, where densities of up to 10 BSTs per square meter are reached (Fig. 2b). The BSTs develop from the rocky substrate, hanging from ceilings and projecting obliquely from walls, forming cm-to-dm-long frameworks that range from hemispherical, conical and cylindrical to flabellate in shape.

Table 2. Continued

	Granchi cave						Gymnasium cave						Mazzere cave					
	1p	2p	3p	3v	4v	1v	2v ₁	2v ₂	3v	1p	1v	2p ₁	2p ₂	2p ₃	2v			
	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C			
Sponges	**	**	*	**	*	**	**	*	*	*	*	*	*	*	**			
<i>Petrobiona massiliana</i> (Vacelet & Lévi, 1958)										*	*	*	*	*	*			
Aka sp.										*	*	*	*	*	*			
Hydrozoans spp.	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			
Scleractinians spp.																		
<i>Madracis pharensis</i> (Heller, 1868)										*	*	*	*	*	*			
Terebellids spp.										**	**	**	**	**	*			
Molluscs																		
<i>Acar clathrata</i> (DeFrance, 1816)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			
<i>Litophaga litophaga</i> Linnaeus, 1758										*	*	*	*	*	*			
Vermetids	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			
Barnacles	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			
<i>Verruca spengleri</i> Darwin, 1854	**	**	*	*	*	*	*	*	*	*	*	*	*	*	*			

p, BST from the wall, v, BST from the ceiling. Asterisks indicate the number of specimens/colonies for each taxon: one star = one to two; two stars = three to 10; three stars = >11.

Sizes and shapes of the BSTs do not seem to be closely related either to their distances from the cave entrance or to their positions on the ceilings or walls. BSTs of different morphologies and sizes often co-exist close to each other (Fig. 2b, c). No substantial differences were observed among the three caves with respect to the abundance, size and morphology of the BSTs.

The BSTs had a generally rough outer surface, more or less encrusted by sessile organisms, among which only sponges and serpulids were obvious in the underwater surveys. The BSTs observed were grey to whitish in color, often blackened by diffuse oxidation. The remaining cave surfaces in general appeared to be evenly and uniformly coated by oxidation crusts and colonizers (Fig. 2c).

Morphology

Four morphologic types were distinguished among the 15 sampled BSTs (Table 1, Figs 3–5):

- 1 Cylindrical to conical (7.5–15 cm in height, 3.5 × 6 to 10 × 11 cm in cross-section), circular or elliptic in cross-section. The outer surface is uniformly rough (GR3v, GM2v₁, MZ2p₂), or shows distinctive smooth and rough appearances on opposite sides (GR3p, GR4v, MZ2p₃), rough areas having a millimetric patterned relief;
- 2 Mushroom (7–10 cm in height, 7 × 9 to 8 × 14 cm in cross-section in the largest part), showing a smooth surface near the base and a prevalently rough surface in their distal parts, characterized by cm-sized, downward-directed digits (GR1p, MZ1p);
- 3 Dome (4–5 cm in height, 5 × 6 to 6 × 8 cm in cross-section), with uniformly rough surfaces (GR2p, GM1v, GM2v₂, GM3v, MZ1v, MZ2p₁). Rough areas have millimetric radial protrusions;
- 4 Flabellate, elliptic in cross-section (14 cm in height, 5 × 10 cm in cross-section), with rough areas developed as elongated branches, obliquely and downward directed and iso-oriented (MZ2v). Digitats are cylindrical to flabelliform, centimetric in diameter and separated by furrows up to 2–3 cm deep.

BST surface communities and thanatocoenoses

The rough and smooth outer surfaces of the BSTs are encrusted by living and dead specimens/colonies belonging to different invertebrate groups, forming communities and thanatocoenoses, respectively (Table 2, Figs 3–5). Communities are scarce. Subsequent thanatocoenoses occur within the same BSTs, superimposed through time, and detectable thanks to the different darkness and thickness of the Fe/Mn coatings of the skeletons, as well as their covering relationships.



Fig. 3. External surfaces and sections of BSTs from the PMPA caves. (a–c) Dome-shaped biostalactite GR2p from Granchi Cave. a: Lateral view, b: cross-section, c: distal view with a *Protula tubularia* specimen (long black arrow) and several tubes of *Semivermilia crenata* (one indicated: short black arrow). A coral (white arrow) and sponges are also visible. d–f: Mushroom-shaped BST MZ1p from Mazzere Cave. d: Cross section with a small *Protula* nucleus embedded within a thick outer metazoan-microbial crust. A large scleractinian skeleton and a *Lithophaga* borehole are also visible. e, f: Lateral smooth and rough sides near the base and in the enlarged distal part, respectively. Serpulids are among the most obvious encrusters. g: Longitudinal section of the BST MZ2p3 from Mazzere Cave, with a large nucleus of *Protula* tubes and a relatively thin (1–2 cm) outer microbial edge. h–j: Flabellate BST MZ2v from Mazzere cave. h: Outer extremely rough surfaces with elongate digitats, colonized by very rare metazoans. Longitudinal- (i) and cross- (j) sections showing the nucleus, including a stalactite at the base (short arrow) and a celleporiform bryozoan colony near the tip (long arrow).

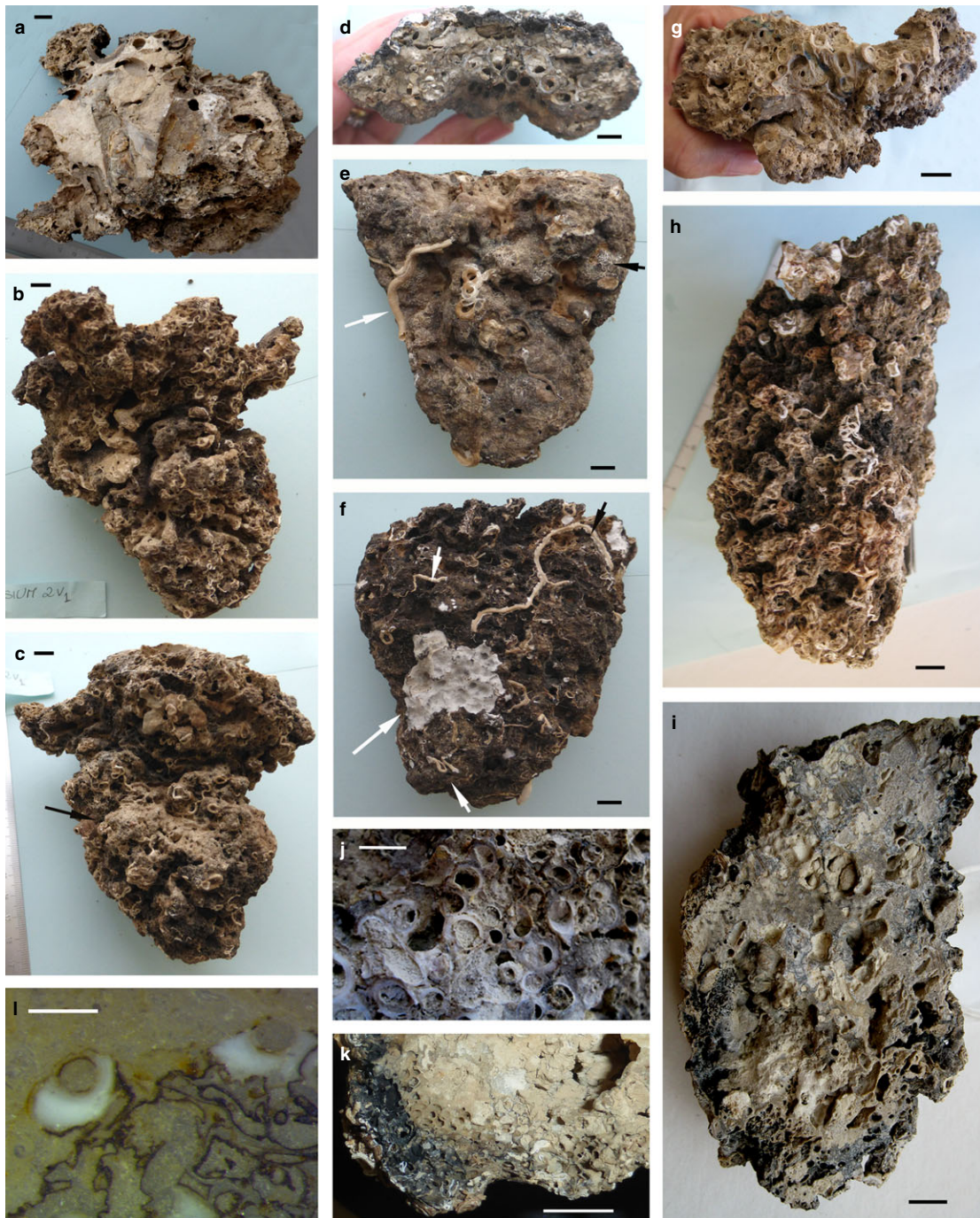


Fig. 4. External surfaces and sections of BSTs from the PMPA caves. a–c: Cone-shaped BST GM2v1 from Gymnasium Cave. a: Elliptical basal cross-section showing undifferentiated nucleus and bivalve boreholes partially filled by sediment. b, c: Lateral rough black-coated surfaces encrusted by rare, small serpulids and sponges (arrow). d–f: Cone-shaped BST GR3p from Gymnasium Cave. d: Basal cross-section with an elongated nucleus of *Protula* tubes. e: Lateral smooth side with encrusting foraminifers (short black arrow) and rare serpulids (long white arrow). f: Lateral rough side with *Semivermilia crenata* (short white arrows), *Protula* sp. 2 (black arrow), and a large encrusting sponge (long white arrow). g–k: Cylindrical BST MZ2p2 from the Mazzere Cave. g: Basal cross-section showing the inner *Protula* nucleus. h: Rough side blackened by oxidation and heavily colonized by serpulids. i: Longitudinal section showing the inner framework with a nucleus of a few widely-spaced *Protula* tubes embedded in and grading to a dominant metazoan/microbial concretion. j: Detail of the basal cross-section in g: with several *Protula* tubes arranged side-by-side. k: Detail of the outer metazoan-microbial BST's edge, blackened by oxidation. Cavities, mainly mm-sized, are partly filled by micrite. l: Thin section of the metazoan-microbial frame. Brown Fe/Mn crusts and corrosive surfaces are visible, partly dissolving calcareous tubes of serpulids.



Fig. 5. Present-day colonizers of the BST surfaces. a: Coiled tubes of the gregarious serpulid *Spiraserpula massiliensis* encrusted by several tubes of the microserpulid *Josephella marenzelleri*. BST GR2p. b: Detail of a smooth surface densely encrusted by the foraminifer *Cornuspiramia adherens*. BST GR3p. c: The serpulid *Sermivermilia crenata* and a lichenoporidae bryozoan on the rough surface of the BST MZ1v. d: Tube of the serpulid *Semivermilia pomatostegoides* on BST GR4v. e: The bryozoan *Lagenipora* sp. On BST GR4v. f: Tiny colony of the bryozoan *Puellina (Glabrilaria) pedunculata* on BST GR4v. g: The brachiopod *Tethyrhynchia mediterranea* and a tubuliporidae bryozoan on BST GR1p. h: The brachiopod *Argyrotheca cuneata* attached to the bryozoan *Onycoella marioni* from the rough side of BST GR1p. i: The brachiopod *Joania cordata* on BTS GR1p. j: Colony of the scleractinian *Madracis pharensis* on BST MZ1v. k: Individuals of the small bivalve *Acar clathrata*, nesting within a small crevice in BST MZ2p3.

Serpuloideans and bryozoans are the dominant taxonomic groups, followed by sponges and foraminifers. Other invertebrates, *i.e.* mollusks, brachiopods, hydrozoans, scleractinians, barnacles and terebellids, are quite subordinate or even rare, and occur in only a few BSTs. Furthermore, these last groups are represented by very few species, whose specimens and colonies usually are only very small to small in size, except for the scleractinian *Madracis pharensis*, which has colonies as large as 2 cm. Most species occur in both the living community and the thanatocoenoses of the same BST. Nevertheless, several bryozoans and serpuloideans may be present exclusively as either only living or dead specimens.

Serpuloideans include 13 living and 18 dead species. *Semivermilia crenata*, *Josephella marenzelleri* and *Semivermilia pomatostegoides* are the most common species, with living specimens and quite abundant dead ones occurring on most BSTs. Some species live only on a few BSTs, where they may be dominant. This is the case for the gregarious serpulid *Spiraserpula massiliensis* (GR3v) and the spirorbid *Spirorbis cuneatus* (MZ1p and MZ2p₂) (Table 2).

Bryozoans are more diversified than serpuloideans, consisting of 31 living species, plus a further one in the thanatocoenoses. Nevertheless, they are subordinate when the total number of colonies, the surfaces encrusted and skeletal carbonate production are considered. Only a few species are common or very common. They include the cyclostomes *Annectocyma indistincta* and *Annectocyma major*, the cheilostomes *Aetea truncata* and *Puellina (Glabrilaria) pedunculata*, the cyclostomes *Diplosolen obelia* and *Disporella hispida*, and the cheilostomes *Onychocella marioni* and *Cosciniopsis ambita*. All other species are more subordinate and often restricted to single BSTs.

Encrusting growth is the dominant morphology, and most species develop small unilaminar colonies (*e.g.* *Escharoides mamillata*) and even dot-like colonies named spots [*e.g.* *Setosella cavernicola*, *P. (G.) pedunculata*] or are uniserial runners (*A. truncata*). Only a few species develop multilaminar colonies, often through frontal budding, such as *Stephanollona armata* and *O. marioni*. Erect, both rigid (*Reteporella*, *Schizoretepora*) and flexible (*Crisia*), morphologies are very subordinate.

Contrary to the inner frame, sponges are very abundant, being important constituents of the present-day community, with a variety of species. They form relatively large crusts, 50–1000 µm thick (Figs 3c, 4c,f). Among other invertebrates (Table 2), encrusting foraminifers are also abundant, mainly represented by the agglutinated species *Cornuspiramia adherens* (Figs 4e, 5b). Brachiopods such as *Novocrania anomala*, *Tethyrhynchia mediterranea*, *Argyrotheca cuneata*, *Joania cordata* and *Megathiris*

detruncata are present as rare living and dead specimens on a few BSTs (Fig. 5g–i). Similarly, the scleractinian *Madracis pharensis* (Fig. 5j) only occurs in two BSTs as either living or dead colonies. Among mollusks, a few specimens of the boring bivalve *Lithophaga lithophaga* are present, together with some nesting arciids belonging to *Acar clathrata* (Fig. 5k), and rare vermetid gastropods. Finally, some terebellids and the barnacle *Verruca spengleri* occur in some BSTs, also as living specimens.

Degree and pattern of colonization

No difference in degree and pattern of colonization was observed among BSTs from different caves, or among differently sized/shaped BSTs from the same cave. Conversely, slight differences exist in relation to the position of the BSTs within caves, and mostly in relation to the smoothness/roughness of their outer surfaces. In particular, in all BSTs the colonization degree is relatively high in the outermost sites and in some BSTs from the middle parts, where hydrozoans, vermetids, bivalves and barnacles are more abundant than in BSTs from the inner caves (Table 2). Colonization degree may also be high, as in BSTs GR2p, MZ3v and GM2v₁, which are extensively covered by large sponges, as well as by numerous serpulid tubes and laminar bryozoan colonies (Figs 3a and c, 4c, f, h).

Interestingly, serpuloideans and bryozoans show a non-uniform distribution (Table 2). In addition to a group of species common to all the BSTs [the serpulids *Semivermilia crenata*, *Josephella marenzelleri*, *Semivermilia pomatostegoides* and the bryozoans *Annectocyma major*, *Aetea truncata* and *Puellina (Glabrilaria) pedunculata*], some other species occur solely on a few BSTs within a single cave, or even on a single BST. *Spiraserpula massiliensis* is locally dominant (Table 2, Fig. 5a).

Similarly, different degrees of colonization were observed within single BSTs, with the rough sides of cylindrical-conical shaped BSTs being more densely colonized than the smooth sides. Colonizers of the rough sides are more diverse at a high taxonomic level. Brachiopods and mollusks, such as vermetids and small nesting arciids (Fig. 5g–k), exclusively or mainly occur on rough portions within small cavities and crevices. In addition, serpulideans and bryozoans are also more abundant in terms of both species and specimens/colonies on rough sides (Fig. 4b,c,f,h). By contrast, the smooth sides show low diversity and lower coverage and abundance of specimens/colonies compared with the rough sides, particularly in the living associations (Fig. 4e). Foraminifers show an opposite trend, with *Cornuspiramia adherens* covering large surfaces with specimens that form an intricate network of very thin, tubular chambers (Figs 4e and 5b).

Composition and fabric

Biostalactites consist of invertebrate skeletons that are cemented by carbonates (Figs 3–5), whose precipitation is induced by microbial activity (see Guido *et al.* 2013). The invertebrate component of the bioconstructions consists of serpulid tubes, which represent the main skeletal constituent, primarily contributing to the framework (Fig. 4g). Bryozoan skeletons are subordinate whereas foraminifer, scleractinian and sponge remains are rare (Fig. 4d and g). Due to diffuse partial dissolution and micritization, skeletons of serpulids and other invertebrates often appear incomplete and/or altered with respect to their original contours and shapes (Fig. 4l); as a result, they can rarely be identified. Cementation mostly occurs at the base and in the innermost parts of the BSTs (Figs 3d and 4a,d,g). The framework has numerous mm-sized cavities, mainly formed by lumina of large serpulid tubes and by convolute microbialite laminae that often open outwards (Fig. 4k). Cavities are locally filled with loose-to-cemented micrite. Fe/Mn crusts are common, largely coating external surfaces (Fig. 4e and f) and are also visible in the internal fabric as irregular thin dark-brown layers alternating with frame-builders and microbialites (Fig. 4k and l).

Serpulid tubes are about 200 µm to 4 mm in diameter, with circular or triangular cross-sections, demonstrating that they belong to different species. Locally tubes form dense aggregates of numerous specimens. Bryozoans were hardly recorded on natural and polished sections. Their presence may have been underestimated due to their poor preservation caused by early diagenetic processes. In a few instances multilaminar, millimetric colonies (seemingly belonging to *Schizomavella* and/or *Stephanollona*) prevail, as well as thinner laminae belonging to undetermined species that are usually a few tens of microns thick and do not exceed 100 microns. Celleporiform colonies are rare but the BST MZ2v is partly constructed by a bryozoan species (probably *Celleporina caminata*) developing this type of colony growth (Fig. 3j, arrowed), together with multilaminar bryozoans. Benthic foraminifera are also rare, encrusting on serpulid and bryozoan skeletons. More rarely, isolated specimens were found, embedded within more or less cemented pelites. Remnants of sponge spicules are obvious in some parts within microbial carbonates. A few scleractinian calices were detected, only one of which was large in size: 1.5 cm in diameter (Fig. 3d).

Most BSTs, particularly those showing elongate morphology (either conical or cylindrical) possess an inner nucleus, more (Fig. 3 g) or less (Fig. 4i) readily distinguishable from the surrounding outer portion by its different composition and fabric (Table 1). When differentiated in this way, the nuclei are mostly composed of large serpulid tubes (1.5 to 4 mm diameter). They clearly belong to *Protula* (Figs 3d,g

and 4d,g,j) and are here tentatively assigned to *Protula tubularia* by comparison with specimens that occur on the outer surfaces of some BSTs (GR2p, GR3p: Fig. 3a–c). These nuclei are formed by bunch-shaped aggregations of tubes oriented sub-vertically from the ceiling and walls. *Protula* aggregations are usually elongated parallel to the axes of BSTs, but do not reach their outer surfaces. By contrast, in dome-shaped BSTs the cores are less obvious and consist of irregularly coiled tubes of *Protula*. Finally, some BSTs completely lack a differentiated nucleus (Table 1, Fig. 4a). A single BST (MZ2v) has an elongated inorganic core formed by a karstic stalactite (Fig. 3h–j).

All the BSTs (where a differentiated nucleus is lacking) and their outermost 1–3 cm part (when a nucleus is present) are characterized by a more massive framework (Figs 4 and 5). *Protula* is occasionally present, whereas other small serpulids make up the bulk, and other metazoans are also present; all are often connected by autochthonous micritic carbonate. In particular, some BSTs can be nearly entirely formed by thick crusts of inter-twined tubes belonging to the gregarious serpulid *Spiraserpula massiliensis* (Fig. 5a).

Discussion

Composition, degree and pattern of colonization on BST surfaces

Only slight differences were observed among BSTs from the different sampling sites within the caves. The overall trend was a general decrease in total biotic diversity at a high taxonomic level and in serpulid species richness, from the entrances toward the more obscure recesses. This trend is shared with metazoan associations on comparable BSTs in Apulian caves (Onorato *et al.* 2003; Belmonte *et al.* 2009) and with cave communities in general (Laborel & Vacelet 1958; Harmelin 1969, 1980, 1985, 1986, 1997, 2000; Harmelin *et al.* 1985; Balduzzi *et al.* 1989; Bianchi & Morri 1994; Balduzzi & Rosso 2003, *etc.*). These depend mainly on factors related to the degree of confinement, such as decreasing illumination, reduced water flow, and depletion in oxygen and food/larval supply.

Surprisingly, the expected outward–inward gradient was not clearly observed here for bryozoans, which instead showed a patchy distribution as noted by Rosso *et al.* (2012), probably due to their particular sensitivity to small-scale variability in environmental parameters. Furthermore, living bryozoans on BST surfaces accounted for less than one half of the total number of species colonizing hard surfaces in the same caves in a previous study (Rosso *et al.* 2012). This could be related simply to the smaller number of samples analysed in the present study, but also to the particular location of the exploited sub-

strata (*i.e.* available BST surfaces) and local microenvironmental conditions, which differ between the bases and the tips of BSTs (see discussion in Harmelin 1980; Harmelin *et al.* 1985). This could also be responsible for a certain patchiness also observed for other metazoans, with slightly different compositions between BSTs and sites from a single cave, and especially from different caves.

The observed differentiation, in both species richness and specimen/colony abundance and coverage, between entirely rough BSTs and those characterized by extensive smooth surfaces seems clearly related to the onset of microenvironmental conditions. The higher metazoan biodiversity and colonization on the rough sides (mostly observed for bryozoans and serpuloids) could be related to enhanced larval settlement and recruitment as well as to the preference of some species for sheltered microhabitats such as crevices (Rassdmussen & Brett 1985; McKinney & Jackson 1989; Taylor & Wilson 2003). Interestingly, not all species select crevices; some prefer the elevated rough tips (Fig. 4h; fig. 3a,c in Guido *et al.* 2013), probably as an adaptation to intercept water flow (Harmelin 1985).

The resulting metazoan polar distribution, with smooth surfaces characterized by fewer serpulids and other metazoans and the rarity or even the absence of bryozoans but the dominance of *Cornuspiramia adherens* networks compared with the rough surfaces, suggests differences in hydrodynamic conditions on the opposite sides of some BSTs. A comparable polarity has been observed by Toscano & Raspini (2005); Rosso *et al.* (2014a,b) in Mediterranean deep-sea Fe/Mn crust-grounds. This constitutes a further similarity between bathyal and cave environments (Zibrowius 1971; Harmelin *et al.* 1985; Harmelin 1997). Interestingly, *C. adherens* encrustations are common on bathyal flat firm- and hard-grounds exposed to clay deposition (Rosso *et al.* 2010, 2014c).

Ecological significance of metazoan associations

As expected, communities and thanatocoenoses on the outer surfaces of the studied BSTs include a number of species typical of cave environments, *i.e.* characteristic of 'dark and semi-dark cave biocones' (*sensu* Pérès & Picard 1964), and they also constitute the cave invertebrate associations (see discussion in Rosso *et al.* 2012; for bryozoans). In particular, nearly 60% of both bryozoans (19 species out of 32) and serpuloids (11 species out of 18) are species considered diagnostic of caves by Rosso *et al.* (2013), *i.e.* they are either cave, sciaphilic and/or 'coralligenous' species and deep-water species.

Also the few species recognized from the internal parts, and mostly from the nuclei of the BSTs have the same

ecological significance, as *Protula tubularia* is known to be typical of cave environments (Bianchi & Sanfilippo 2003).

Frame-building capability of metazoans

Serpulids and bryozoans do not usually build large-sized bioconstructions in submarine caves but commonly live as isolated specimens or form thin organogenic coatings over a period of time (Harmelin 1985; Bianchi & Sanfilippo 2003), despite being among the dominant sessile skeletal metazoans in these environments (Laborel & Vacelet 1959; Pérès & Picard 1964; Zibrowius 1971; Harmelin *et al.* 1985). This is particularly true for blind caves where stagnation leads to biomass impoverishment and oligotrophy (Harmelin 1969; Harmelin *et al.* 1985; Fichez 1990, 1991a,b). Nevertheless, in favorable settings they can exceptionally form cm-thick concretions. This is the case for the gregarious serpulid *Spiraserpula massiliensis*, whose irregularly coiled tubes form extensive centimetric crusts in both present-day (ten Hove & van den Hurk 1993) and fossil caves (Rosso *et al.* 2014c). Analogously, some long-living plurilaminar bryozoans occasionally develop cm-size digitate reliefs, crests and nodules (Harmelin 1985, 1986; Harmelin *et al.* 1985), as in the case of some species in the PMPA caves (fig. 2c, d in Rosso *et al.* 2013).

In particular, the serpulid *Protula tubularia* (and congeneric species) usually occurs as a few isolated individuals within caves (Zibrowius 1968; Bianchi 1981; Bianchi & Sanfilippo 2003), but is one of the main frame-builders in the Plemmirio caves, where it was able to form aggregations similar to those in a few present-day caves from the Mediterranean area (ten Hove & van den Hurk 1993; Bianchi *et al.* 1995; Onorato *et al.* 2003; Belmonte *et al.* 2009).

Similarly to other serpulids, the gregarious behavior of *Protula* species is controlled by environmental factors and may be enhanced by local conditions in the extreme and/or unstable environments that it occupies (ten Hove 1979; ten Hove & van den Hurk 1993). In the studied caves, it is reasonable to hypothesize that formation of the BSTs' *Protula*-rich nuclei was promoted by gregariousness triggered by the local increase in food availability. Due to its large-size, *Protula tubularia* probably has trophic requirements higher than other smaller cave-dwelling serpulids. In submarine caves, food is mostly supplied by water inflow from the open sea, and specimens (and the plaited structures they form) tend to project downwards as far as possible from the substratum. This behavior increases the exposure of the worms' branchial crowns to the often weak flow of incoming water, as suggested by Belmonte *et al.* (2009). In karst caves an

additional source of food could locally and temporarily be organic matter in water entering through fractures in the cave roof. Such additional resources may have enhanced the initial growth of *Protula* specimens near open fractures (Fig. 6), and these populations could then have persisted as a result of the selective settlement of new generations of recruits from outside or, even more probably, from the adults in the area. In fact, *P. tubularia* has an unusual reproductive strategy involving: (i) the production of lecithotrophic larvae brooded in gelatinous masses near the parental tube mouth (see Kupriyanova *et al.* 2001 for a review) and (ii) the settlement of young individuals close to parents (especially in still waters) leading to self-sustaining populations that may persist over time. The possibility of nutrient inflow from fractures, outlined above, is supported by the incorporation of terrestrial biomarkers within the micrites of the BSTs examined (Guido *et al.* 2013). Underwater surveys showing cave roofs locally 'bleached' due to the absence of present-day marine colonizers, and the *in situ* salinity measurements in some PMPA caves (Pitruzzello & Russo 2008), suggest that this phenomenon is still active, although probably reduced.

It therefore seems likely that nucleation and growth of the Plemmirio BSTs could have been promoted by nutrient-rich waters. This is paralleled by the formation of unusual bioconstructions of the large serpulid *Serpula vermicularis* in deep-water Mediterranean habitats (Sanfilippo *et al.* 2013), benefitting from food supplied by cascading North Adriatic Deep Water.

Plaits of living *Protula* specimens have been reported from Cyprus by ten Hove & van den Hurk (1993) and from a few Italian caves (Bianchi *et al.* 1995; Onorato *et al.* 2003). These aggregations are actively growing and either lack the metazoan–microbial coatings observed in the Plemmirio BSTs, or only have short concretionary sleeves around their basal parts.

Bioconstructions more similar to those at Plemmirio have been described from an Apulian cave (Belmonte *et al.* 2009). These are larger (up to 2 m long), but include *Protula* nuclei covered by 'brownish calcareous matrix largely composed of tiny tubes'.

Although Belmonte *et al.* (2009) did not investigate the origin and nature of these coatings, they could well include microbial carbonates comparable to the cemented carbonates of the Plemmirio BSTs that are made up by autochthonous, peloidal to clotted peloidal micrites widely assumed to reflect bacterially induced mineralization processes (Guido *et al.* 2012, 2013, 2014). The presence of biomarkers derived from sulfate-reducing bacteria confirmed a microbial influence in the formation of the clotted peloidal micrite in the Granchi and Mazzere BSTs (Guido *et al.* 2013).

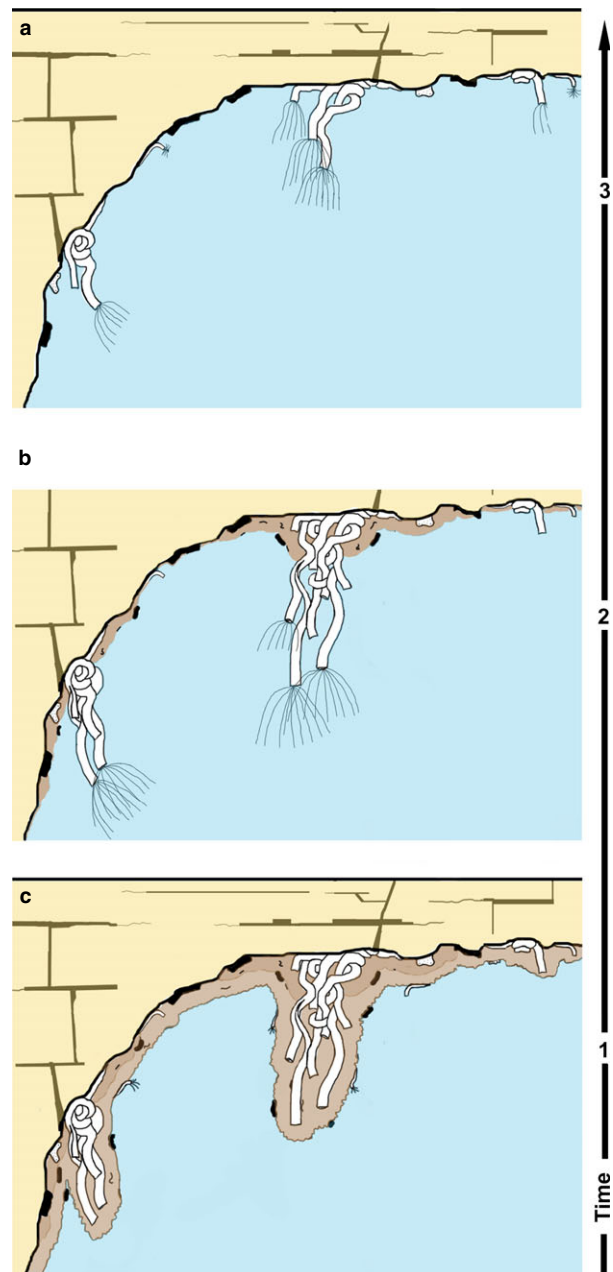


Fig. 6. Inferred progressive phases of colonization during Holocene flooding of the cave and a growth model for the metazoan–microbial BSTs. a: Pioneer metazoan encrustation with conspicuous *Protula tubularia* specimens. b: Development of *Protula* plaits by successive populations, and early formation of microbial crusts. c: Death of *Protula* populations and progressive thickening of the microbialite-metazoan crusts which engulf empty tubes. *Protula* plaits play an essential role in the formation of pendants. Fractures in the bedrock, through which food-rich continental waters could have intruded are indicated.

Analogous bioconstructions occur in c. 10-m deep present-day caves in Australian reefs (Reitner 1993), where a 'metazoan/microbialite facies' was recognized

that includes coralline sponges, serpulids (other than *Protula*), bryozoans and other sessile faunas inter-growing with calcifying microbes. These irregular and slow-growing bioconstructions, up to 50 cm high and coated by Fe/Mn bacterial biofilms, occur in the innermost parts of the caves as a result of dark conditions and reduced sedimentary input. Comparable conditions were inferred for metazoan–microbial ‘pseudostalactites’ in Jurassic intra-reef paleocaves (Olivier *et al.* 2003).

BST life history

Marine ingressions and final flooding of the Plemmirio caves occurred at the beginning of the Holocene, as indicated by biogenic carbonates in speleothems from the Gymnasium cave dated 8229 ± 242 years BP (Scicchitano *et al.* 2008). The settlement and growth of *Protula tubularia* aggregates, constituting BST nucleation, therefore took place at or after that time. *Protula* aggregates some 2 m long and up to 6.5 kyr old occur in the Apulian caves (Belmonte *et al.* 2009). By contrast, the BSTs studied here rarely exceed 1 dm. Consequently, even if they started to grow immediately after flooding, they appear to exhibit a very low mean growth rate, possibly with highest values of $1\text{--}2 \text{ cm} \cdot \text{kyr}^{-1}$, although growth rate probably differed between the nuclei and external portions (see below).

Protula tubularia is probably a long-lived species, like other large serpulids. According to Kupriyanova *et al.* (2001), individuals have life spans of between 10 and 35 years. Information about their growth rates and even total tube length is lacking, but tubes 20–25 cm long have been observed in Pleistocene mid-shelf silty settings in central and eastern Sicily (A. Rosso & R. Sanfilippo, personal observations). The only available data come from estimates of the growth of *Protula* specimens forming the nuclei of the Apulian aggregates, where tubes grow $2.7\text{--}4 \text{ cm} \cdot \text{year}^{-1}$ (Belmonte *et al.* 2009). Interestingly, these estimates overlap with those reported for the early stages of *Serpula vermicularis* that form deep-water coral/serpulid build-ups in the Bari Canyon (Sanfilippo *et al.* 2013). As for this latter species, it could be that the growth rate of *Protula* slows considerably with age, and eventually stops during senescence. Based on these assumptions, the dimensions of the studied nuclei (which do not exceed 12 cm for the longest BSTs) could result from tube aggregation over a few *Protula* generations, covering a time span of possibly one or a few hundred years. This would imply a mean growth rate of 1 mm per year, or less for the *Protula*-rich nuclei, also taking into account possible stasis in the growth. This growth rate fits well with that reported for large-sized, cave-dwelling, frame-building metazoans (Schmid 1996).

Even slower growth rates are possible for the metazoan–microbial crust developed on *Protula* aggregates as well as over the whole cave surfaces (Fig. 6). This is because it is rich in small serpulid tubes and other invertebrate remains that are intermingled with microbial micrites formed by sulfate-reducing bacteria (Guido *et al.* 2013). Metazoans generally grow slowly in submarine caves and Harmelin (1985) hypothesized that 2–3-cm-high nodules constructed by the thickly layered bryozoan *Onychozella marioni* need several centuries to form. Other species, such as the micromorphic bryozoans *Setosella cavernicola* and *Herentia hyndmanni*, are probably able to withstand periods of starvation by slowing or even stopping growth (see discussion in Berning *et al.* 2008). The crusts that coat the *Protula* plaits also occur generally on the cave surfaces. Like the ‘metazoan–microbial facies’, they include black/brown coatings representing Fe/Mn bacterial biofilms, seemingly analogous to those described by Reitner (1993) as strongly corrosive for carbonates (due to the activation of particular electrochemical processes). For the studied BSTs this is supported by the diffuse partial dissolution of skeletal remains and micrite carbonates (Fig. 4I) in the frame, often including half-preserved serpulid tubes or even their internal micrite coatings. Thus, dissolution produced by Fe/Mn biofilms may help to explain the extremely slow growth rates observed in the BSTs, whose volume is significantly lower than the pristine carbonates produced earlier in the Holocene. To conclude, a mean growth rate of $50\text{--}120 \mu\text{m} \cdot \text{year}^{-1}$ can be inferred, taking into account the variability in thickness of the metazoan–microbial crusts. This rate is consistent with the results of Reitner (1993).

The transition from *Protula* aggregates to metazoans and biomicrites testifies to environmental changes that occurred within the caves through time (Fig. 6), leading to the death of *Protula* populations replaced by other serpulid and invertebrate populations typically of cave environments which still live on the outer surfaces of the BSTs. A possible explanation is progressive reduction in food supply as a consequence of confinement resulting from deepening of the cave during the Holocene sea-level rise. This is also supported by the rough surfaces of BSTs, which are comparable to mesoscopic ‘dendritic’ outer morphologies of microbial–metazoan concretions, considered as characteristic of low water energy and low sediment supply (Schmid 1996; Olivier *et al.* 2003), and could reflect the onset of these conditions. Thus, the community replacement sequence observed in the BSTs could be interpreted as indicative of a transgression, as was suggested by Reitner (1993) for cryptic microbialites of present-day Australian intra-reef caves that exhibit outward–inward diachronous vertical facies succession (from corals to thick coralline red algae crusts to microbialites).

Conclusions

This study of BSTs from the Plemmirio caves led to the following results: (i) BSTs appear to be randomly distributed within caves and show different sizes and morphologies depending on what they encrust, including true stalactites, *Protula* tubes and flat rocky surfaces; (ii) metazoan communities and thanatocoenoses on the external surfaces of BSTs (here investigated in detail for the first time) reflect present-day cave conditions and gradients, as do the recognizable metazoans that constitute their nuclei, all belonging to the semi-dark and dark cave biocoenosis classifications; (iii) the degree of colonization and the distributional patterns of present-day encrusters on the outer surfaces partly depend on BST roughness, which is related to microenvironmental conditions; (iv) the nuclei of the BST frameworks are often formed by *Protula* tubes, while the outer portions and present-day surfaces consist of other smaller cave invertebrates (mainly serpulids and bryozoans); (v) authochthonous micritic carbonates are significant components of the BSTs; (vi) the *Protula* populations represent pioneer metazoan colonization of the cave, reflecting significant food availability during the first phase of caves history, at least in areas that may also have benefited from additional food supply by intruding continental waters; (vii) the outer metazoan–microbial association, including strongly corrosive Fe/Mn microbial coatings, is shared with all cave surfaces, and indicates a slowdown in BST growth due to the onset of confined conditions; (viii) the transition in BST metazoan composition relates to major changes in the cave environment caused by the Holocene sea-level rise.

We conclude that metazoan–microbialite bioconstructions can be regarded as a confined facies of the dark cave biocoenosis. Metazoan–microbial associations are still relatively poorly known in present-day environments, but ongoing studies have revealed that they are more common in caves and in other extreme environments than previously thought. These intriguing, ecologically complex and environmentally sensitive constructions deserve further study to assist their better understanding.

Acknowledgements

The following people are acknowledged: V. Incontro, former Director of the Plemmirio MPA, for facilitating sampling activities; V. Di Martino (Istituto per l'Ambiente Marino Costiero, Catania) for underwater sampling; R. Leonardi (Dipartimento Scienze Geologiche, Geologiche e Ambientali, Università di Catania) for providing underwater videos and additional information. This research was financially supported by the CoNISMa Project 'Study of the submarine cave environments - Codice Habitat 8330 -

in the Marine Protected Areas of Pelagie, Plemmirio and Capo Caccia' and also in part by grants from the University of Catania to A. Rosso and R. Sanfilippo. This is Catania Paleocological Research Group: contribution no. 392. We are grateful to G. Belmonte (University of Bari) for useful discussions and to the reviewers for the constructive comments that helped us to improve the manuscript.

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