

The suspension-feeder communities of a Mediterranean sea cave

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SUMMARY: The zonation pattern of suspension-feeder communities in a 80 m long cave of the Gulf of Naples has been evaluated by standard, visually oriented, and photographic samplings. Light and water movement intensities have been measured and their gradients have been compared with the distribution of the considered taxa (Porifera, Hydrozoa, Bivalvia, Serpuloidea, and Bryozoa). The so-called "biocoenosis of semi-dark caves (GSO)" is restricted to the entrance and its presence seems mainly related to light values. On the contrary, the "biocoenosis of dark caves (GO)" occupies the rest of the cave, where light is almost absent, and is likely to be mainly influenced by water movement. The individuality of cave communities is discussed, stressing that also other habitats are colonized by species assemblages which are referable to GSO and GO. The evolution of species retained as "typical" of shallow water marine caves of the Mediterranean is hypothesized as having occurred mainly in cryptic or bathyal environments. The colonization of caves possibly occurred as a secondary event and therefore can be defined as "secondary troglobiosis". As a consequence, the denomination of cave-inhabiting communities should be reformulated.

Key words: suspension-feeders, Mediterranean benthos, submarine caves.

INTRODUCTION

Research on submarine caves has been greatly improved by SCUBA diving and direct investigation (see for references: LABOREL & VACELET, 1958, 1959; AA.VV., 1959; RIEDL, 1966; VACELET, 1964, 1967; BALDUZZI *et al.*, 1982; BIBILONI *et al.*, 1984). The results of such researches led to consider the very poor and scattered faunal assemblage of the inner parts of caves as an original biocoenosis, and not as a simplified or degenerated aspect of the one which is present near the entrances.

According to PÉRÈS & PICARD (1964) and PÉRÈS (1967), two biocoenoses are generally recognized in Mediterranean marine caves: the semi-dark cave biocoenosis (GSO) and the dark cave biocoenosis (GO). HARMELIN *et al.* (1985) synthesized the existing data on caves of both temperate and tropical seas, stressing the gradual decrease of species number and organismal cover along the outside-inside gradient, remarking that the specific richness near the cave entrances resembles that of cliffs and overhangs, often dropping even to zero in long caves.

Several authors (OTT & SVOBODA, 1976; CINELLI *et al.*, 1977; GILI *et al.*, 1986), investigating the causes of this impoverishment, could not directly relate the fauna decrement to the variations of environmental factors, owing to the difficulties in measuring and evaluating them. However, light and water movement are usually said to be two of the most important factors (CINELLI *et al.*, 1977).

Light obviously acts on algae distribution, but its drop should not negatively affect sciaphilous or nocturnal animals. Water movement, together with several other factors more or less depending upon it — such as sedimentation, organic matter and living preys supply, water exchange, dispersion and supply of larval stocks — directly affects the distribution of many organisms.

It can be reasonably supposed that, even for this sciaphilous fauna, the advantages of continuous darkness are balanced by the disadvantages due to the assumed decrease of water exchange. In fact, in caves with an active inside circulation, HARMELIN (1969) found an organismal cover exceeding 100% even in total darkness. A selection among trophic

groups, with a progressive decline and disappearance first of passive and then of active suspension feeders, occurs along caves with a complete gradient in biological cover (HARMELIN *et al.*, 1985). Overall water movement and related factors, however, cannot exhaustively explain the distribution of cave population, according to GILI *et al.* (1986). These authors advanced the hypothesis that along the walls of caves may exist boundary layers characterized by a particular stillness, affecting the normal trophic and physiological exchanges of the encrusting organisms.

The present research examines the faunal assemblages of a cave displaying sharp gradients of light, water movement and organismal cover, where suspension feeders represent the most important trophic group (OTT & SVOBODA, 1976). The aim of this study, which takes into account also the results of our previous contributions on this cave (BALDUZZI *et al.*, 1980, 1982, 1985; CATTANEO, 1981, 1982; BELLONI & BIANCHI, 1982; PANSINI & PRONZATO, 1982; BALDUZZI & CATTANEO, 1985; BIANCHI, 1985; BOERO, 1985; CATTANEO VIETTI & RUSSO, 1987), is to verify the individuality of the faunal assemblages and the consistency of the coenocline between GSO and GO biocoenoses in this horizontally developing cave.

METHODS

The Mitigliano cave (Fig. 1) opens near Punta Campanella, in the southern part of the Gulf of Naples. It is a completely submerged, almost straight, 80 m long diachase in a mainly calcareous rock. Its sandy bottom ranges from 16 m depth at the entrance to 8 m at the end. The generally high vaulted roof rises upper than the sea level forming air vaults. An inner room is separated by a low gully, whose height changes according to the variation of the sandy bottom level. A complete obstruction of the passage, occasionally isolating from the sea the inner part of the cave, could not be excluded.

Field activities have been performed in summer months (1979-1982). Irradiance has been measured

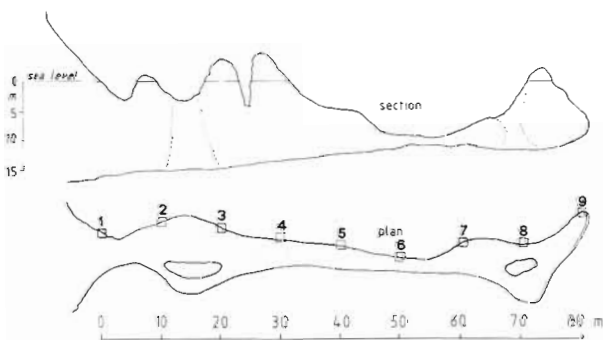


FIG. 1. — Topographic map of the Mitigliano cave. Numbered quadrats are standard sampling stations.

by a Kahlsico submarine photometer in $\mu\text{W cm}^{-2}$ and then evaluated as a percentage of the outside total solar energy. Water movement has been evaluated by the method of the gradual consumption of plaster balls (MUUS, 1968; PANSINI & PRONZATO, 1982).

The main part of the suspension-feeder fauna — sponges, hydroids, bryozoans, serpuloid polychaetes and bivalve molluscs — has been considered. Brachiopods and ascidians were scarcely represented in the cave, and have been neglected. Hydroids have been considered as passive suspension feeders, whereas the other taxa, being able of actively concentrating the food particles by means of ciliary currents, have been considered as active suspension feeders (WARNER, 1984).

The suspension-feeder assemblages have been studied by: a) visually oriented qualitative samplings; b) photographic surveys along transects at 5 m intervals (BALDUZZI *et al.*, 1985); c) quantitative sampling on standard surfaces (400 cm^2) along a longitudinal transect of 9 stations located 1 m above the bottom at intervals of 10 m (Fig. 1). The results yielded by the standard samplings have been statistically analyzed by using: Shannon-Weaver diversity index, evenness (DAGET, 1979), euclidean distances (CLIFFORD & STEPHENSON, 1975), factorial analysis of correspondences (BENZÉCRI *et al.*, 1982). Number of species, per cent cover and presence-absence of the individual species have been used in these analyses. Physical parameters and biological cover were reduced to a common scale in order to introduce both kinds of variables into a single ordination pattern of factorial analysis. To do that, their values have been divided among four size classes with the following upper limits: a) water movement (per cent weight of plaster consumption): 35, 55, 75, 100; b) light (percentage of the outside total solar energy): 0.01, 0.1, 1, 10; c) organisms (per cent area cover): 0.1, 1, 10, 100. This procedure also allowed to visualize on the graph resulting from correspondance analysis the different 'intensity states' assumed by the variables, which are of great interest especially for physical parameters. The significance of the axes has been evaluated by an extrapolation of LEBART's (1975) tables, while spatial density analysis (WILDI, 1979) has been used to identify clusters of stations.

RESULTS

The values of light penetration in the cave (Fig. 2) display a sharp gradient within a few meters and could not be recorded farther than 20 m from the opening. Water movement, instead, declines more gradually remaining well above zero till the end of the cave. The presence of the air vaults probably eases the propagation of water movement.

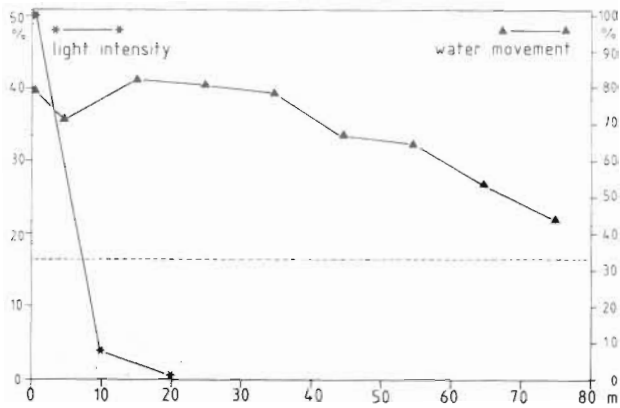


FIG. 2. — Measured values of light intensity and water movement. The dotted line represents the average consumption of plaster balls in still water.

The communities of the cave are sharply impoverished at a few meters after the entrance, with the disappearance of algae and their epiphytes and a remarkable reduction of massive and erect species (*Ircinia* spp., *Eudendrium racemosum*, *Halecium labrosium*, *Myriapora truncata*, *Caberea boryi*, *Scrupocellaria* spp.). The complex, stratified assemblage of the entrance is substituted by a simpler one, mainly composed by encrusting forms, within 10 m from the opening. A marked selection of trophic groups takes place in polychaetes and molluscs — two taxa which are more complex from a nutritional point of view — with a clear dominance of the suspension-feeding forms (BIANCHI, 1985; CATTANEO VIETTI & RUSSO, 1987).

The per cent cover of organisms — obtained by the photographic survey (BALDUZZI *et al.*, 1985) — generally declines towards the inner part of the cave, but the animal distribution is rather irregular (Fig. 3 a). High cover values correspond to monospecific

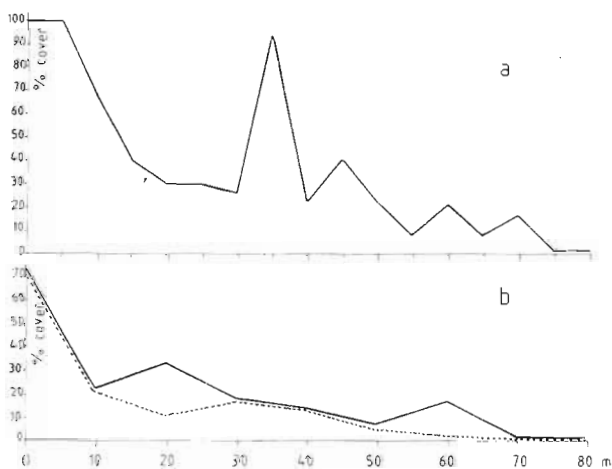


FIG. 3. — Evaluation of per cent cover: a) of all organisms, by photographic survey (after BALDUZZI *et al.*, 1985, modified); b) of suspension feeders, by standard samplings (solid line: with boring species; dotted line: without boring species).

or paucispecific facies, as the one formed by the sponge *Aaptos aaptos*, at about 35 m from the entrance (PANSINI & PRONZATO, 1982), and the one by the bryozoans *Celleporina caminata* and *Diaperoecia indistincta*, at 45-60 m and especially along the gully (BALDUZZI *et al.*, 1980, 1982, 1985). After the gully passive suspension feeders disappear, organismal cover drops to minimal values and animals are even more irregularly distributed, forming scattered patches on a bare rock covered by metallic oxides.

From the samples collected on standard surfaces, 134 species have been identified: 52 sponges, 9 hydroids, 45 bryozoans, 6 bivalve molluscs, 22 serpuloid polychaetes. Owing to the irregularities of the benthic distribution in the cave, to the intervals among the stations, and to their location near the bottom, only a part of the whole identified fauna — which actually totals 198 suspension-feeder species — is present in the standard samples (Table I). Some taxa are certainly underestimated. Most of the 39 hydroid species, for example, are concentrated at the entrance, on the upper parts of the walls and on the vaults (BOERO, 1985). Even the quantitative values may be underestimated, and the facies of sponges and bryozoans, which are easily observed *in situ* and in the photographic surveys, cannot be detected by the per cent cover values obtained from the standard samplings (Fig. 3 b).

The number of species decreases gradually (Fig. 4 a), while the per cent cover drops abruptly between station 1 and 2 (Fig. 3 b). The boring sponge *Alectona millari*, whose importance in the occupation of the superficial substrate is negligible, causes the peak in cover values of station 3 and 7. The decrease in substrate cover is regular, if the five boring species

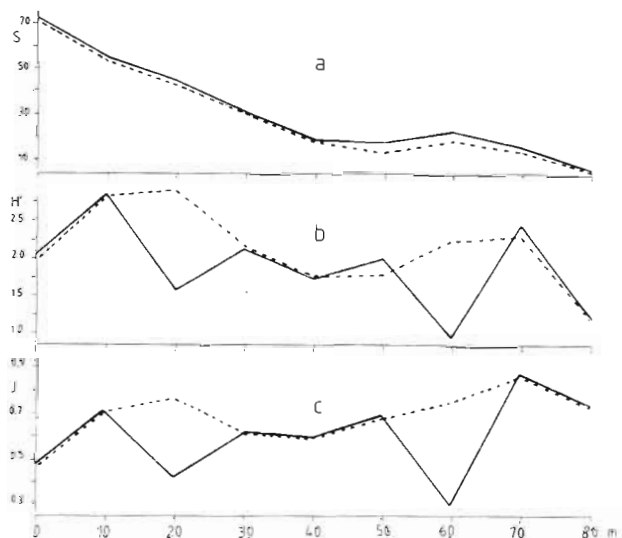


FIG. 4. — Parameters calculated from standard samplings: a) number of species, S; b) Shannon-Weaver diversity, H'; c) evenness, J. Solid line: with boring species; dotted line: without boring species.

TABLE I

List of suspension-feeder species collected in the Mitigliano cave. Numbered species were found in the samplings from standard surfaces (400 cm²).

PORIFERA								
1	<i>Aaptos aaptos</i> (Schmidt)	51	<i>Tricheurypon viride</i> (Topsent)	82	<i>Fenestulina malusii</i> (Audouin)			
2	<i>Acarinus tortilis</i> Topsent	52	<i>Triptolemus</i> sp.	83	<i>Hincksina flustroides</i> (Hincks)			
3	<i>Agelas oroides</i> (Schmidt)	HYDROIDA			84	<i>Lichenopora</i> sp.		
4	<i>Alectona millari</i> Carter		<i>Aglaophenia kirchenpaueri</i> (Heller)	85	<i>Margareta cereoides</i> (Ellis & Solander)			
5	<i>Aplysilla rosea</i> (Barrois)		<i>Aglaophenia octodonta</i> (Heller)	86	<i>Microporella ciliata</i> (Pallas)			
6	<i>Axinella damicornis</i> (Esper)		<i>Aglaophenia tubiformis</i> Marktanner-Turneretscher	87	<i>Microporella coronata</i> (Audouin)			
7	<i>Axinella verrucosa</i> (Esper)		53	<i>Antennella secundaria</i> (Gmelin)	88	<i>Mollia patellaria</i> (Moll)		
	<i>Batzella inops</i> (Topsent)			<i>Amphinema dinema</i> (Péron & Lesueur)	89	<i>Myriapora truncata</i> (Pallas)		
8	<i>Bubaris vermiculata</i> (Bowerbank)			<i>Bimeria vestita</i> Wright	90	<i>Nolella gigantea</i> (Busk)		
	<i>Chondrilla nucula</i> Schmidt			<i>Bougainvillia ramosa</i> (Van Beneden)	91	<i>Parasmitina rouvillei</i> (Calvet)		
	<i>Chondrosia reniformis</i> Nardo			<i>Campanularia hincksii</i> (Alder)	92	<i>Pentapora ottomulleriana</i> (Moll)		
9	<i>Clathrina</i> sp.			54	<i>Phylactella labrosa</i> (Busk)			
	<i>Cliona celata</i> Grant			<i>Clytia hemisphaerica</i> (L.)	93	<i>Plagioecia</i> sp.		
10	<i>Cliona levispira</i> Topsent			<i>Clytia linearis</i> (Thormely)	94	<i>Prenantia cheilostoma</i> (Manzoni)		
11	<i>Cliona schmidti</i> (Ridley)			<i>Clytia noliformis</i> (McCrary)	95	<i>Rhynchozoon</i> sp. A		
12	<i>Corticium bowerbanki</i> Sarà			55	<i>Clytia paulensis</i> (Vanhoffen)	96	<i>Rhynchozoon</i> sp. B	
	<i>Corticium candelabrum</i> Schmidt			<i>Coryne muscoides</i> (L.)	97	<i>Schizomavella auriculata</i> (Hassall)		
	<i>Corticium topsenti</i> Pouliquen			<i>Dynamena disticha</i> (Bosc)	98	<i>Schizomavella linearis</i> (Hassall)		
13	<i>Crella elegans</i> (Schmidt)			<i>Ectopleura larynx</i> (Wright)	99	<i>Schizoporella</i> sp.		
14	<i>Darwinella</i> sp.			<i>Eudendrium glomeratum</i> Picard	100	<i>Schizotheca fissa</i> (Busk)		
15	<i>Dercinus plicatus</i> (Schmidt)			<i>Eudendrium motzkossowskiae</i> Picard	101	<i>Scrupocellaria cf. reptans</i> (L.)		
16	<i>Diactinolopha moncharmonti</i> Sarà			<i>Eudendrium racemosum</i> (Cavolini)	102	<i>Scrupocellaria cf. scrupea</i> Busk		
17	<i>Diplastrella bistellata</i> (Schmidt)			56	<i>Eudendrium ramosum</i> (L.)	103	<i>Sertella couchii</i> (Hincks)	
	<i>Diplastrella ornata</i> Ruetzler & Sarà			57	<i>Filellum serpens</i> (Hassall)	104	<i>Tubulipora</i> sp.	
18	<i>Dictyonella</i> sp.				<i>Halecium beanii</i> (Johnston)	105	<i>Turbicellepora avicularis</i> (Hincks)	
19	<i>Dysidea tupa</i> (Martens)				<i>Halecium conicum</i> Stechow	106	<i>"Cardioecia" watersi</i> (O'Donogue & de Watteville)	
20	<i>Erylus discophorus</i> (Schmidt)				<i>Halecium halecinum</i> (L.)	BIVALVIA		
21	<i>Erylus euastrum</i> (Schmidt)				<i>Halecium labrosum</i> Alder	107	<i>Acar pulchella</i> Reeve	
22	<i>Eurypon major</i> Sarà & Siribelli				<i>Halecium mediterraneum</i> Weissman	108	<i>Anomia ehippium</i> L.	
23	<i>Fasciospongia</i> sp.				<i>Halecium nanum</i> Alder	109	<i>Arca noae</i> L.	
	<i>Geodia cydonium</i> (Jameson)				<i>Halecium petrosum</i> Stechow		<i>Chama gryphoides</i> L.	
24	<i>Grayella pulvinar</i> (Schmidt)				58	<i>Halecium tenellum</i> Hincks	<i>Chlamys varia</i> (L.)	
25	<i>Grayella</i> sp.				<i>Halocordyle disticha</i> (Goldfuss)	110	<i>Hiatella rugosa</i> (Pennant)	
26	<i>Halichondria contorta</i> (Sarà)				<i>Halopteris diaphana</i> (Heller)		<i>Lima lima</i> (L.)	
27	<i>Haliclona</i> sp.				<i>Obelia geniculata</i> (L.)	111	<i>Lithophaga lithophaga</i> (L.)	
	<i>Hemimycale columella</i> (Bowerbank)				<i>Plumularia obliqua</i> Johnston		<i>Musculus costulatus</i> (Risso)	
	<i>Ircinia pipetta</i> (Schmidt)				59	<i>Plumularia setacea</i> (L.)	<i>Mytilaster solidus</i> H. Martin in	
	<i>Ircinia variabilis</i> (Schmidt)				60	<i>Scandia gigas</i> (Heller)	Monterosato	
	<i>Ircinia</i> sp.				61	<i>Sertularella gaudichaudi</i> (Lamouroux)	<i>Spondylus gaederopus</i> L.	
28	<i>Jaspis johnstoni</i> (Schmidt)					<i>Sertularella gaudichaudi</i> f. <i>lagenoides</i> Stechow	112	<i>Siriarcia lactea</i> (L.)
29	<i>Leuconia</i> sp.					<i>Sertularella gaudichaudi</i> f. <i>ellisii</i> (Milne-Edwards)	SERPULOIDEA	
30	<i>Merlia normani</i> Kirkpatrick					<i>Stylactis fuculata</i> (Sars)	113	<i>Filograna</i> sp.
31	<i>Monocrepidium vermiculatum</i> Topsent					<i>Ventromma halecoides</i> (Alder)	114	<i>Filograna annulata</i> (O.G. Costa)
32	<i>Myriastru lactea</i> (Carter)					<i>Zanclaea costata</i> Gegenbauer	115	<i>Filograna calyculata</i> (O.G. Costa)
	<i>Oscarella lobularis</i> (Schmidt)				BRYOZOA			
33	<i>Penares helleri</i> (Schmidt)				62	<i>Aetea truncata</i> (Landsborough)	116	<i>Filograna gracilis</i> Langerhans
34	<i>Petrobiona massiliana</i> Vacelet & Lévi				63	<i>Alcyonidium gelatinosum</i> (L.)	117	<i>Hydroides pseudouncinata pseudouncinata</i> Zibrowius
35	<i>Petromica grimaldii</i> Topsent				64	<i>Amathia lendigera</i> (L.)	118	<i>Janita fimbriata</i> (Delle Chiaje)
36	<i>Petrosia ficiformis</i> (Poirct)				65	<i>Caberea borvi</i> (Audouin)	119	<i>Janua pagensecheri</i> f. <i>gnomonica</i> (Bailey)
	<i>Placospongia decorticans</i> (Hanitsch)				66	<i>Celleporina caminata</i> (Waters)	120	<i>Metavermlia multicristata</i> (Philippi)
	<i>Plakina dilopha</i> Schulze				67	<i>Celleporina hassallii</i> (Johnston)	121	<i>Pileolaria endoumensis</i> (Zibrowius)
	<i>Plakina trilopha</i> Schulze				68	<i>Chlidonia pyriformis</i> (Bertoloni)	122	<i>Pileolaria heteropoma</i> (Zibrowius)
37	<i>Raspaciona aculeata</i> (Johnston)				69	<i>Chorizopora brongniartii</i> (Audouin)	123	<i>Pileolaria koehlerii</i> (Caullery & Mesnil)
	<i>Reniera cratera</i> Schmidt				70	<i>Crassimarginatella crassimarginata</i> (Hincks)	124	<i>Pileolaria militaris</i> Claparède
38	<i>Reniera</i> sp.				71	<i>Crassimarginatella maderensis</i> (Waters)		<i>Protolaeospora striata</i> (Quiévreux)
39	<i>Reniera valliculata</i> Griessinger				72	<i>Cribrilaria innominata</i> (Couch)		<i>Protula</i> sp.
40	<i>Rhabderemia minutula</i> (Carter)				73	<i>Cribrilaria pedunculata</i> (Gautier)	125	<i>Semivermlia crenata</i> (O.G. Costa)
41	<i>Rhaphisia spelea</i> Pulitzer-Finali				74	<i>Cribrilaria radiata</i> (Moll)	126	<i>Semivermlia cribrata</i> (O.G. Costa)
	<i>Spirastrella cunctatrix</i> Schmidt				75	<i>Cribrilaria venusta</i> (Canu & Bassler)		<i>Semivermlia pomatostegoides</i> (Zibrowius)
42	<i>Spirastrella minax</i> (Topsent)				76	<i>Cribrilaria sp.</i>	127	<i>Serpula massiliensis</i> Zibrowius
	<i>Spirastrella</i> sp.				77	<i>Crisia</i> sp.	128	<i>Serpula vermicularis</i> L.
43	<i>Spiroxya heteroclitia</i> Topsent				78	<i>Diaperoclella indistincta</i> Canu & Bassler	129	<i>Spirobranchus polytrema</i> (Philippi)
44	<i>Spongia virgulosa</i> (Schmidt)				79	<i>Diplosolen obelia</i> (Johnston)	130	<i>Spirorbis cuneatus</i> Gee
45	<i>Spongisorites intricatus</i> (Topsent)				80	<i>Entalophoroecia</i> sp.	131	<i>Vermiliopsis infundibulum</i> (Philippi)
46	<i>Stelletta</i> sp.				81	<i>Escharella</i> sp.	132	<i>Vermiliopsis labiata</i> (O.G. Costa)
47	<i>Sivostichon dives</i> (Topsent)					<i>Escharella vulgaris</i> (Moll)	133	<i>Vermiliopsis monodiscus</i> Zibrowius
48	<i>Suberites</i> sp.						134	<i>Vermiliopsis striaticeps</i> (Grübe)
	<i>Sycon</i> sp.							
	<i>Tethya sarantium</i> (Pallas)							
49	<i>Thoosa</i> sp.							
50	<i>Timea antistellata</i> (Topsent)							

(the sponges *A. millari*, *Cliona levispira*, *C. schmidii*, *Thoosa* sp., and the mollusc *Lithophaga lithophaga*) are excluded. Boring species sharply modify also the indexes of species diversity and evenness (Fig. 4 b, c), which are more regular when these forms are excluded. The diversity index slightly increases in correspondence of sharp decreases in cover, when no diminution in the number of species occurs. Excluding boring species, the evenness index has his minimal values at the entrance, owing to the sharp dominance of *Spongia virgultosa*, and has rather high values inside the cave, so that dominances are not evidenced, by the standard samplings, in any station.

The evaluation of the euclidean distances between neighbouring stations could individuate discontinuities or ecotones along ecological gradients (LUDWIG & CORNELIUS, 1987). The use of this index on presence/absence data (Fig. 5 a) indicates that the differences between neighbouring stations are relatively low, slightly decreasing from the entrance to the end of the cave. Species substitution, then, results as gradual and no evident qualitative discontinuity occurs. On the other hand, the use of cover values, omitting boring species (Fig. 5 b), individuates a sharp discontinuity between station 1 and station 2, whereas the pattern shows gradual differences between station 2 and 6. Stations 6 to 9 are quite homogeneous.

The factorial analyses of the correspondences were carried out on different sets of data: presence/absence, cover of the substrate (boring forms excluded), classes of abundance (Fig. 6 a, b, c); but the obtained results were not clearly interpretable, possibly due to the high stochasticity of cave assemblages. The pool of species typical of caves is considerably reduced, many of the recorded species being simply troglaxene. The dispersion of both species-points and station-points is high, the percentage of explained variance is always low (15.9 to 21.9 %), sometimes below the level of significance. The separation of station 1 from station 2, and of these two stations from all the others, is however clear. A further distinction between an intermediate zone (stations 3, 4, 5) and an inner one (stations 6, 7, 8, 9) is not so sharp, espe-

cially if cover values are considered. The points corresponding to the most typical species of dark caves (*Petrobiona massiliana*, *Rhaphisia spelea*, *Cras-simarginatella crassimarginata*, *Cribrilaria pedunculata*, *C. venusta*, *Diaperoecia indistincta*, *Filogramula annulata*, *F. calyculata*, *Janita fimbriata*, *Metaver-milia multicristata*, *Semivermilia pomatostegoides*, *Serpula massiliensis*, *Vermiliopsis labiata*, *V. monodiscus*) have been included in figures 6 a and 6 b with the numbers indicated in Table I. These species-points are scattered in the whole factorial plan, but not in the area around station 1:

The combined analysis of cover values with those of light and water movement, both resolved into classes of abundance (Fig. 6 c), shows that the fall in light intensity (which is almost parallel to axis 2) could be important in discriminating station 1 from station 2. On the contrary, the gradual decrease of water movement (which superimposes on axis 1) could play a major role in the distribution of the inner assemblages.

DISCUSSION

The comparison between our findings in the Miti-gliano cave and the literature data leads to some considerations of general interest.

1. The biocoenosis of semi-dark caves (GSO)

This biocoenosis has a limited extension in our cave, if compared to that schematized by HARMELIN *et al.* (1985). The biological cover sharply decreases at less than ten metres from the entrance. From there on, the features of the faunal assemblage are typical of the GO biocoenosis. The bryozoan facies (at Miti-gliano *Celleporina caminata* and *Diaperoecia in-distincta*), considered by HARMELIN *et al.* (1985) as an ecotone between GSO and GO biocoenoses, has been found within the biocoenosis of dark caves, linked to particular microhabitats determined by the morphology of the cave. The same is valid for the facies of the sponge *Aaptos aaptos*.

PÉRÈS & PICARD (1964) stated that the biocoeno-sis of semi-dark caves can be found also in protected or concealed microhabitats within the coralligenous bio-coenosis, when light is feeble. In our opinion this point of view could be reversed. The typical species of GSO listed by PÉRÈS & PICARD (1964) can be commoly found, in the Mediterranean, on cliffs, overhangs and, also, at the entrance of caves. It is probable that the typical species of the semi-dark caves biocoenosis have acquired their adaptations during the coloni-zation of cliffs and overhangs (abundant and wide-spread in rocky shores) and not in that of caves (which are relatively rare and localized features).

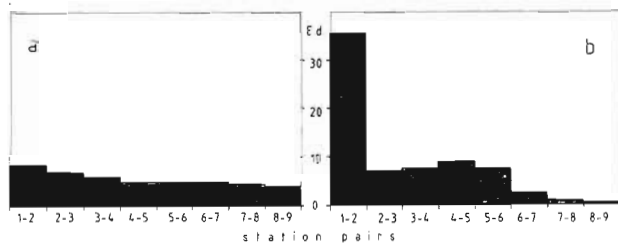


FIG. 5. — Euclidean distances (E.d.) between neighbouring stations, calculated: a) on presence/absence data; b) on cover data (boring species excluded).

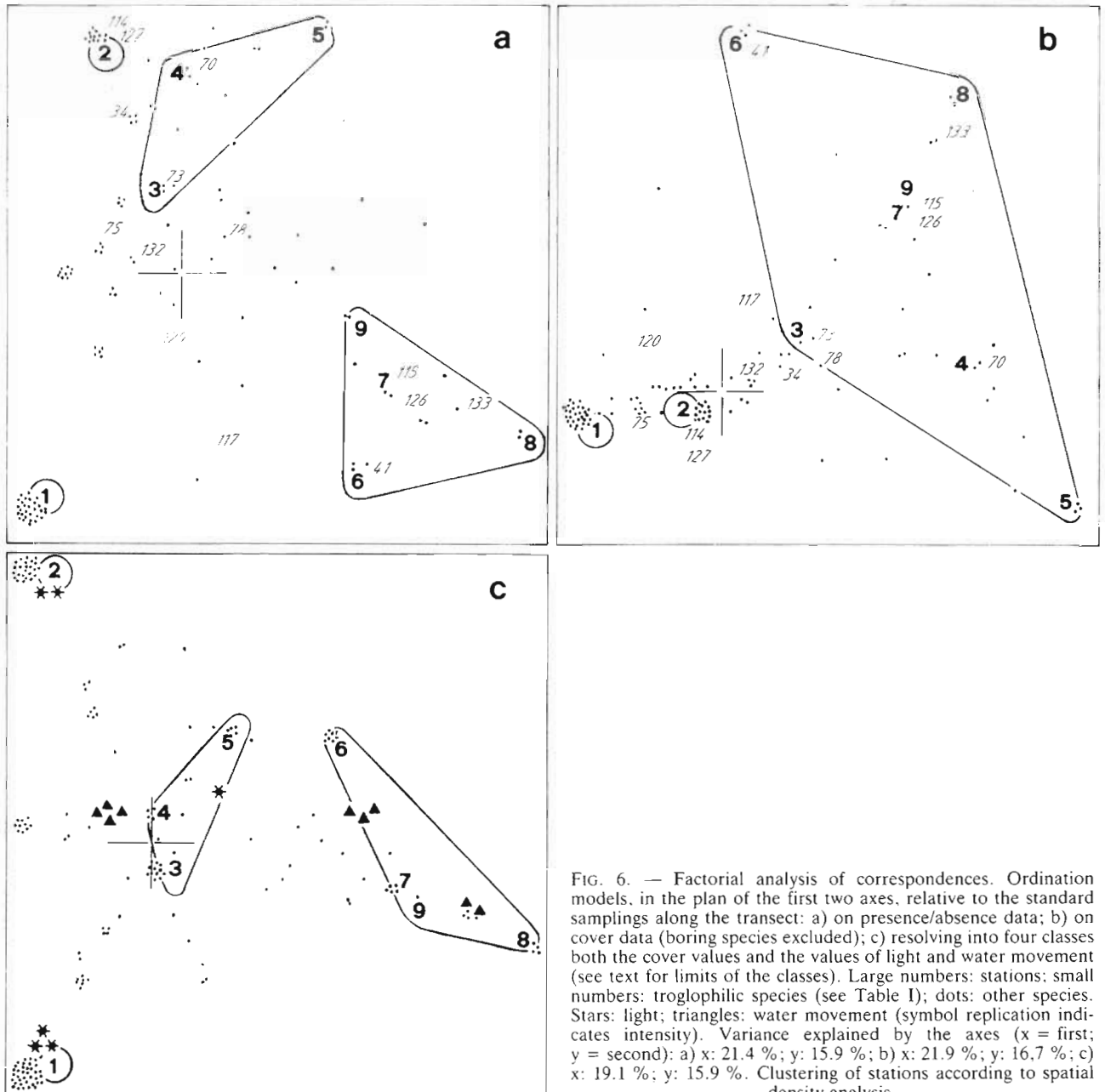


FIG. 6. — Factorial analysis of correspondences. Ordination models, in the plan of the first two axes, relative to the standard samplings along the transect: a) on presence/absence data; b) on cover data (boring species excluded); c) resolving into four classes both the cover values and the values of light and water movement (see text for limits of the classes). Large numbers: stations; small numbers: troglomorphic species (see Table I); dots: other species. Stars: light; triangles: water movement (symbol replication indicates intensity). Variance explained by the axes (x = first; y = second): a) x: 21.4 %; y: 15.9 %; b) x: 21.9 %; y: 16.7 %; c) x: 19.1 %; y: 15.9 %. Clustering of stations according to spatial density analysis.

2. The biocoenosis of dark caves (GO)

The organismal cover and the species composition indicate that, at Mitigliano, the biocoenosis of dark caves is already present at about ten metres from the entrance of the cave, where a sharp decrease of light occurs. This would confirm the importance of light in the distinction between the GSO and the GO biocoenosis as suggested by PÉRÈS & PICARD (1964). The rest of the cave is characterized by a gradual decrease of the biological cover, if the high cover of the facies of bryozoans or sponges in some locations is neglected. The measures of water movement indicate a

continuous decrease of this factor, which turned out to be related more than light to the changes in the community structure and composition. This agrees with the views of HARMELIN *et al.* (1985) and GILI *et al.* (1986), which tend to individuate in the availability of food (directly linked to water movement) the conditioning factor of the biocoenosis of dark caves. A confirmation of this view comes also from the different penetration of the trophic groups in the Mitigliano cave. Passive filter feeders (the hydroids) are limited to the first half of the cave and no hydroid species has been found after the gully.

The presence of passive filter feeders could then

divide the dark-cave biotope in two zones, which could correspond to those described by LABOREL & VACELET (1959): an outer zone, where water renewal is sufficient to support passive filter feeders; an inner zone, where trophic conditions are too severe for them and where only a few species of active filter feeders, mainly sponges and serpuloids, remain.

The already mentioned bryozoan facies is at the end of the first zone, and could indicate the transition between these two zones. However, this seems to be valid only when water circulation is restricted by the topography of the cave, otherwise the fall in the biological cover (HARMELIN, 1969) and the exclusion of passive filter feeders (BIANCHI *et al.*, 1986) do not occur.

The nycthemeral migration of mysidaceans towards the end of caves (PASSELAIGÜE & BOURDILLON, 1985) has been observed also at Mitigliano and it could account for a certain energy input even when water renewal is scarce (BIANCHI *et al.*, 1986).

3. Stochasticity of cave assemblages and adequacy of sampling methods

As stressed by SARÀ (1974), cave environments show a high degree of individuality, being mainly characterized by the manifold microhabitats due to the topography of the cavities. A general feature, with the exception of the caves with high water circulation, is the decrease of the biological cover, but the occurrence of facies and the patchiness of the organisms seem not to follow a single pattern. Owing to this situation, the samplings from standard surfaces not always provided data describing the real distribution of the population inhabiting the Mitigliano cave, mainly in the inner part. Only visually oriented samplings and photographic surveys allowed the individuation of some of the features of the filter-feeder assemblages. For instance, *Petrobiona massiliana*, a species typical of dark caves, was found only in the outer stations of the cave by using samplings from standard surfaces, whereas its presence in the inner part of the cave was detected only by direct observation. The same happened for the facies of sponges and bryozoans. The integration of different sampling methods, then, is very important for the study of a scattered fauna such as that of caves.

4. Evolutionary aspects of cave fauna

The species inhabiting dark cave environments can be divided into four different groups: a) accidental species; b) cryptobiotic species, living in crevices and microcavities; c) bathyphilic species; d) relict species (cryptobiotic or bathyphilic), such as *Petrobiona massiliana*, referable to archaic groups. The existence of a group of species exclusive of the

cave environment is an open question which will be possibly solved by the study of other caves, taking into account the individuality of the single cavities (SARÀ, 1974). As HARMELIN *et al.* (1985) did, it is possible to hypothesize that there are no exclusive species of marine caves. The species "typical" of caves should be cryptobiotic or bathyphilic species which colonize *also* cave environments: this phenomenon can be defined as "secondary troglobiosis", widening the meaning of a term already introduced by CATTANEO & PASTORINO (1974). Thus the colonization of cave environments and the formation of the resident communities could have hypothetically followed two different patterns:

- a) colonization by generalist species: this could have led to specialization and speciation;
- b) colonization by preadapted species, living in environments with features comparable to those of caves. In this case specialization and speciation should not necessarily occur, unless when isolation from the outer environment is complete (ILIFFE *et al.*, 1983).

The second pattern seems to fit better the case of the species "typical" of Mediterranean marine caves in shallow water which, in fact, can be found also in other environments. Thus caves should be, as stressed by HARMELIN *et al.* (1985), a refuge environment or, better, a replica of other habitats.

Neoendemisms in marine caves, at least in shallow waters, do not seem to exist. This should be due to the recent geological origin of shallow Mediterranean caves, which did not allow speciation, but also to the continuity of the marine environment and the biological features of marine organisms. Some of the species colonizing cave and cryptic environments of the Mediterranean may have autochthonous origin, but others could have evolved outside the Mediterranean and have then migrated into it during glaciations. They could be considered as glacial relicts living in cryptic, bathyal and cave environments of the Mediterranean, as indicated, for instance, by some data on the sponges of shallow water caves (SARÀ, 1958).

CONCLUSION

The schematization of cave biocoenoses proposed by HARMELIN *et al.* (1985) fits only partly with our findings in the Mitigliano cave (Fig. 7). The main differences are: a) the biocoenosis of semi-dark caves has a very limited extension; b) the bryozoan facies cannot be considered as an ecotone between semi-dark and dark cave biocoenoses.

In the Mitigliano cave light turned out to be the main factor characterizing the passage from a semi-dark to a dark cave biocoenosis. Water movement

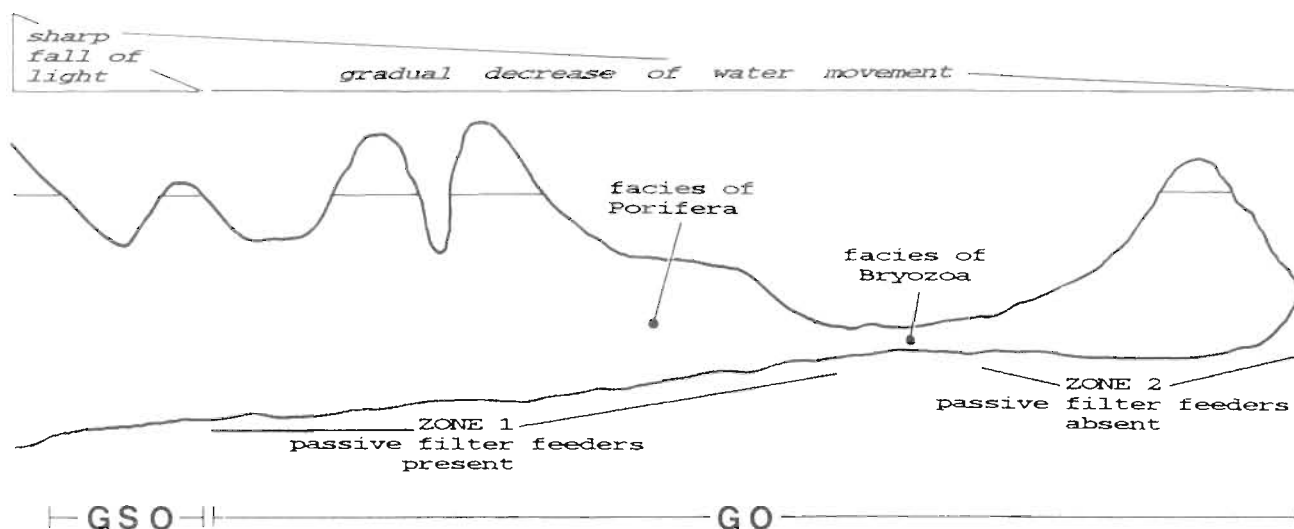


FIG. 7. — Diagram summarizing the main ecological features of the Mitigliano cave.

seems a "landscaping" factor of the dark cave biocoenosis which, at Mitigliano, can be divided into two parts affected by different amounts of water movement and thus characterized by different trophic inputs to the suspension-feeder assemblage. In the outer part the food supply is apparently sufficient for the maintenance of passive filter feeders (hydroids), whereas in the inner part only active filter feeders survive and the organismal cover is very low. The bryozoan facies marks the transition between these two zones.

The pool of species inhabiting the Mitigliano cave, and the Mediterranean shallow water caves in general, could be considered as characteristic of other habitats, being composed mainly by cryptobiotic and, to a lesser extent, bathyphilic species. Cryptic environments are very widespread and it is more probable that a set of species evolved during the colonization of such habitats, rather than during the colonization of caves which are, after all, rather exceptional geological events. Cryptic environments should be, then, the biocoenotic reservoir from which cave environments draw their populations.

Therefore, the biocoenoses of semi-dark caves (GSO) and of dark caves (GO) are not restricted to marine caves because, as already stressed, they are also widespread on vertical walls, overhangs, in microcavities and cryptic habitats in general. The word "cave", with which they are named, only partially reflects their actual features and then their denomination should be re-formulated.

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