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The distribution of macroinfauna along a Mediterranean submarine cave with sulphur springs

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Abstract: The distribution of macroinfauna and Total Organic Carbon (TOC) were investigated in the muddy substrates along a transect at 14 m depth in the Grotta Azzurra (Capo Palinuro, Tyrrhenian Sea, Italy), a submarine cave with warm (18-24°C) sulphur-water springs in its innermost, aphotic chamber. Due to thermal stratification, sulphidic compounds remain trapped above the cooler sea-water in the anoxic upper sulphidic layer supporting dense sulphur-oxidizing bacterial mats that detach and disperse when disturbed. The macroinfauna of Grotta Azzurra comprised 97 species. The assemblage bore similarities to those previously described from non-cave Mediterranean oligotrophic regions, and also indicated environmental instability. Unlike in other caves, where benthic zonation is prominent, no inward decrease of macroinfaunal abundance or diversity was observed. It is assumed that the chemosynthetic inputs in the inner region provide an additional source of food that has a positive effect on the colonization and survival of macroinfauna inside the resource limited cave environment.

Résumé : *La distribution de la macrofaune endogée le long d'une grotte sous-marine méditerranéenne soumise à des resurgences d'eau sulfureuse*. La distribution de la macrofaune endogée et le Carbone Organique Total (COT) ont été étudiés dans les substrats vaseux le long d'un transect à 14 m de profondeur dans la Grotta Azzurra (Capo Palinuro, Mer Tyrrhénienne, Italie), une grotte sous-marine recevant des sources d'eau chaude (18-24°C) sulfureuse dans sa partie la plus sombre. En raison de la stratification thermique, les composés sulfureux restent emprisonnés au-dessus de l'eau de mer plus froide dans la couche anoxique supérieure, où se développent des nappes bactériennes oxydant le soufre, qui se détachent et se dispersent une fois dérangées. La macrofaune endogée de la Grotta Azzurra est constituée de 97 espèces. Cet assemblage présente des similitudes avec des communautés méditerranéennes oligotrophes ne se développant pas dans des grottes, et indique aussi une instabilité environnementale. A la différence d'autres grottes où la zonation benthique est manifeste, aucune diminution vers l'intérieur de la grotte de l'abondance, de la diversité ou des niveaux de COT, n'a été observée dans la Grotta Azzurra. L'hypothèse est émise que les apports chimiosynthétiques dans la partie profonde de la grotte représentent une source supplémentaire de nourriture, qui a un effet positif sur la colonisation et la survie de la macrofaune à l'intérieur de cet environnement cavernicole limité en ressources.

Keywords: Macrofauna, Submarine caves, Mediterranean, Sulphur.

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Introduction

Marine caves have been characterized as simplified, oligotrophic systems, depending solely on energy inputs from the surrounding productive coastal areas, with a worldwide homogeneity in their community structure and organization (Ott & Svoboda, 1976; Harmelin et al., 1985). Sharp outside–inside ecological gradients concerning current regime and light as well as epifaunal cover are the most common features of submarine caves (Harmelin et al., 1985), while progressive losses of imported organic material, are considered to be the main causal factors in the zonation of hard substrate communities in dark caves (Riedl, 1966; Cinelli et al., 1977; Harmelin et al., 1985; Gili et al., 1986; Balduzzi et al., 1989; Zabala et al., 1989). Preliminary investigations on the infaunal component, also highlighted the influence of limited food supply on the soft bottom communities of cave ecosystems (Monteiro-Marques, 1981; Bianchi, 1985).

The existing experimental evidence that cave communities rely on the flux of phytodetrital material produced in the surrounding coastal areas and the successful colonization by larvae of deep-water species (Fichez, 1991; Harmelin, 1997), offer striking similarities to deep-sea ecosystems. An exception to this rule has been reported from the Calabrian Volcanic Arc in Italy, where unusually rich epifaunal assemblages have been found in submarine caves with sulphur-water springs at Capo Palinuro (Cinelli et al., 1994). There is evidence (Southward et al., 1996) that the fauna inhabiting these cave habitats is supported, to a certain extent, by fresh organic material supplied by bacteria fixing carbon through chemosynthesis in association with the sulphide rich vent fluids.

The present study was carried out as part of a multidisciplinary research in Grotta Azzurra, one of the submarine caves with thermal sulphidic springs at Capo Palinuro. Dense colonies of filamentous sulphur-oxidizing bacteria similar to *Beggiatoa* and *Thiothrix* species in association with endolithic Cyanobacteria (Mattison et al., 1998) cover the walls and the ceiling in contact with the sulphidic water. Small-scale spatial and temporal variability in the amount, composition and origin of food inputs within the cave (Airoldi & Cinelli, 1997) in conjunction with variations in the flow and geochemistry of the venting fluids (Stuben et al., 1996), make Grotta Azzurra a highly complex cave habitat. In the present study, the distribution of soft-bottom macroinfaunal community was investigated with respect to organic carbon budget in the sediments and the distance from the entrance of the cave. The abundance, species composition and biomass of macroinfauna were examined by means of quantitative sampling, in tandem with organic carbon and microbial biomass in the sediment and granulometry along a transect spanning both the inner and the outer part of the cave. This study is the first quantitative attempt to explore soft-bottom communities in Mediterranean submarine cave habitats.

Material and Methods

Detailed information concerning the individual physical and geomorphological characteristics of the numerous karst-type caves which extend below the sea level at Capo Palinuro (40°02'N, 15°17'E), is given by Alvisi et al. (1994). Grotta Azzurra, a large cavity of about 120,000 m^3 and depth range from 10 to 30 m, opens to the carbonate rock of Palinuro peninsula by means of two major channels (Fig. 1). In the outer and main region of the cave, called the "Central Hall", light although reduced is still present and there is considerable water exchange with the open sea via the two entrances. A rich and diverse encrusting and soft bottom epifauna was found there, succeeded by a completely dark transitional area (hereafter called the "Transition

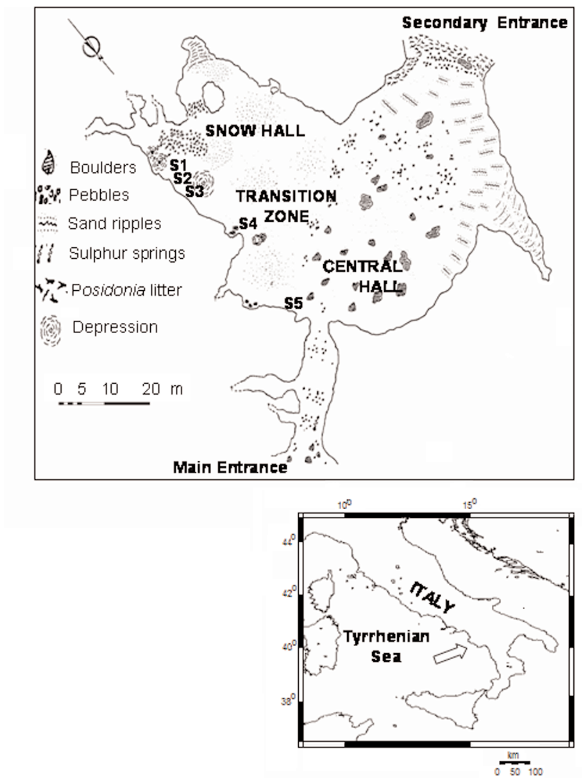

Figure 1. Plan of the underwater part of Grotta Azzurra, based on the survey by Alvisi et al. (1994), showing the sampling stations. In the inset, the arrow shows the position of Palinuro peninsula in the Tyrrhenian Sea.

Figure 1. Plan de la partie sous-marine de la Grotta Azzurra, d'après Alvisi et al. (1994), présentant les stations échantillonnées. La flèche représente la position de la péninsule Palinuro en Mer Tyrrhénienne.

Zone") where epifauna was gradually impoverished. A smaller, completely dark, inner chamber with reduced hydrodynamic regime and the main sulphur springs of the cave, known as the "Snow Hall", expands approximately 40 m south-east of the Central Hall. The discharge fluids are warm (< 25°C), mildly acidic, depleted in Cl^-, Na^+ and Mg^{2+}, and enriched in Si, alkalinity, Ca^{2+}, Sr^{2+}, Mn, NH_4^+, PO_4^{3-} and H_2S, relative to surrounding seawater (Stuben et al., 1996). The venting fluids form a warm sulphide rich water layer (23 to 24°C) above the cooler (17 to 18°C) and denser seawater setting up a thermocline and chemocline at 9.5 m seawater depth. The dense white microbial mats covering the walls and the roof in contact with the sulphidic water, slough when disturbed, and form flakes that disperse within and even outside the cave. A rich epifaunal community was observed on both the walls and the rocky floor of the "Snow Hall" (Cinelli et al., 1994) contrasting with the impoverished faunal cover in the "Transition Zone".

The soft-bottom macroinfaunal assemblages in the three sites, the "Snow Hall", the "Transition Zone" and the "Central Hall" (Fig. 1) were sampled in October, 1993. The three sampling sites were aligned in a transect from the innermost to the outermost area of the cave so that all samples were collected at 14 m water depth at soft-bottom substrate flat areas close to the cave walls. Three stations were sampled in the "Snow Hall" (S1, S2 and S3), one in the "Transition Zone" (S4) and one in the "Central Hall" (S5) (Fig. 1). Stations S1, S2 and S3 were 3.5 m apart, S1 being located only 0.5 m away from the main sulphur spring in the Snow Hall (Fig. 1). Hand-held acrylic tubes of 9.4 cm internal diameter (69.4 cm^2) were used by SCUBA divers to sample all stations. Three replicate core samples were taken at each station, less than 30 cm apart and down to a maximum sediment depth of 10 cm. *A posteriori* tests showed that the precision of the mean total infaunal abundance at each station obtained with this size of core was generally acceptable (SE/mean ≤ 0.25, Elliott, 1977). Samples were sieved through a 0.5 mm mesh and the residue was preserved in 10% buffered formalin with seawater. The organisms retained were sorted, weighed to the nearest 0.0001g, after blotting dry on filter paper and identified to species level. Their numbers per core sample were converted to numbers per 100 cm^2. Ash Free Dry Weight biomass was calculated based on conversion factors according to Ricciardi & Bourget (1998). The patterns of larval development of the dominant species were identified based on published information. The feeding types of taxa were determined according to information in the literature for families or genera such as Fauchald & Jumars (1979), Stephen & Edmonds (1972) and Rupert & Barnes (1994) as well as in systematic keys. Species were divided to Carnivores (C), Omnivores (O), Subsurface deposit feeders (S) and Interface feeders (I). The latter category includes detritivorous species that utilize food particles in the sediment water interface, irrespective of their being suspended or settled in the sediment surface, because resuspension of fine material is a probable phenomenon.

In conjunction with macrofauna sampling, duplicate undisturbed 50 ml cut-off syringe sediment cores were taken for the estimation of biochemical parameters, that is Total Organic Carbon (TOC) and Adenosine Triphosphate (ATP), as a measure of microbial and meiofaunal biomass. The sediment surface layer corresponding to the top 1 cm and the subsurface layer, from 1 to 2 cm sediment depth, were taken. A core (internal diametre 9.4 cm) sample was also collected at each station for granulometry. All samples were immediately stored frozen at -22°C for subsequent laboratory analyses. TOC was analysed by the wet oxidation method of Walkley & Black (1934). ATP was extracted from 0.5 ml homogenized sediment portions with boiling phosphate buffer using a modification of the method described by Holm-Hansen & Booth (1966). Particle size analysis was carried out according to Buchanan (1984), without the addition of hydrogen peroxide, and grain size was given according to the Wentworth grade classification.

Species diversity for each sample and the associated evenness component J' (Pielou, 1966) were calculated applying the (log_2) Shannon-Wiener diversity index (H') (Shannon & Weaver, 1963). One-way ANOVA was used to detect differences among stations by means of Systat statistical package version 5.0 (1992).

Results

Silty sediments invariably dominated the soft-bottom substrates of Grotta Azzurra. However, Silt-Clay percentage gradually increased from 52% at the Central Hall station to 81% at S3 in the "Snow Hall" (Table 1). In general, the coarser fractions of the sediment included a considerable amount of biogenic material originating from sponge spicules, fragments of the calcareous skeletons of cnidarians living on the vault and the walls of Grotta Azzurra as well as mollusk shells and larger non-biogenic fragments. Sorting coefficient declined from 3.281 (very poorly sorted) at S5 to 1.913 (poorly sorted) at S1, indicating a seaward increase of sediment heterogeneity. Skewness gradually decreased from S5 (0.027) to S1 (-0.07), showing a seaward increase in resuspension and hydrodynamic regime.

TOC concentrations in the surface layer varied from 0.49% (S4) to 0.86% (S2), while in the 1-2 cm sediment layer these ranged from 0.47% (S4) to 0.84% (S3) (Table 1). Organic carbon may come from the settlement of fractions of chemosynthetic mats or epifaunal organisms but also from material advected from outside the cave.

Table 1. Range of results from granulometric analysis, biochemical analyses and macrofaunal community analyses along the transect in Grotta Azzurra.

Tableau 1. Gamme des résultats des analyses granulométriques, biochimiques et de la macrofaune benthique le long du transect dans la Grotta Azzurra.

Parameter	Stations	S1	S2	S3	S4	S5
Granulometry	Median Grain Size (μm)	0.022	0.022	0.014	0.024	0.056
	% Silt-Clay	71.14	76.83	81.43	74.67	52.31
	Sorting	1.913	1.974	2.000	2.161	3.281
	Skewness	-0.078	0.066	-0.091	0.152	0.027
Biochemistry	% TOC (0-1) cm	0.68-0.74	0.64-0.86	0.78	0.49-0.71	0.52-0.67
	% TOC (1-2) cm	0.66-0.68	0.65-0.72	0.84	0.47-0.67	0.53-0.61
	ATP (ng g^{-1}) (0-1) cm	220-230	150-170	40-500	30-200	300-500
	ATP (ng g^{-1}) (1-2) cm	40-70	0-50	40-100	10-50	80
Macrofauna	Density (inds. $100cm^{-2}$)	111-120	21-48	26-56	13-76	109-125
	AFDW (mg $100cm^{-2}$)	17-21	63-82	110-115	70-72	240-265
	Number of species (sample)	24-29	12-14	9-18	9-21	28-37
	Shannon-Wiener, H'	3.7–4.1	3.2-3.5	2.8-3.3	3.0-3.4	3.6-4.4
	Eveness, J'	0.8-0.9	0.8-0.9	0.8-0.9	0.7-0.9	0.7-0.8

However, despite the occurrence of rich microbial and epifaunal communities in the "Snow Hall", there were not detected significant differences in sedimentary TOC levels among the stations ($F = 1.183$, $p > 0.05$).

ATP concentrations were consistently about four times lower in the subsurface (1-2 cm sediment depth) than the surface layer (Table 1), providing evidence for more abundant microbial populations and subsequently higher organic matter quality in the sediment surface.

A total of 97 species was recorded from the five stations at the three topographic zones within Grotta Azzurra. These comprised 55 Polychaeta species, 17 Mollusca species, 12 Crustacea species, 4 Sipuncula, 2 Echinodermata and 7 miscellaneous species belonging to Anthozoa, Oligochaeta, Nemertea, Pycnogonida, Enteropneusta, Brachiopoda and Ascidiacea, collectively (Table 2). It should be noted that 28 % of the total number of species found in Grotta Azzurra were exclusively present at the "Snow Hall", 7 % exclusively present at the Transition Zone (S4) and 29 % were found only in the "Central Hall" (S5) while 20 % of the species were common between the innermost (S1) and the outermost station (S5).

The ranges of species richness, species diversity, density and biomass values of the infauna at each station are presented at Table 1. Mean number of species was significantly different among stations ($F_{4,10} = 80.21$, $p < 0.05$) and displayed a parabolic trend along the transect with highest values at the endmost stations (S1 and S5) and lowest at one of the intermediate stations (S2, S3, S4). Polychaetes largely contributed to species composition of the cave (Fig. 2). Mean macroinfaunal density and ash-free dry weight (AFDW) showed a similar trend and were invariably dominated by Polychaeta followed by miscellanea and mainly Sipuncula (Fig. 2). Echinoderms considerably contributed to the high densities measured at the "Snow Hall" (Fig. 2). Densities were significantly different along the cave ($F_{4,10} = 15.46$, $p < 0.05$) and the post-hoc Tukey tests revealed two groups of stations, one with the intermediate (S2, S3, S4) and the second with the endmost stations (S1, S5) of the transect. Correspondingly, the comparison among AFDW levels along the stations demonstrated significant differences ($F_{4,10} = 12.89$, $p < 0.05$) and showed that stations S1 and S5 differ from S2, S3 and S4.

Seven species accounted for 62 % of the total numbers of individuals found in Grotta Azzurra, namely *Levinsenia gracilis* (24.5 %), *Onchnesoma steenstrupi* (14.6 %), *Paradoneis lyra* (7.2 %), *Amphiura chiajei* (4.9 %), *Cossura soyeri* (3.9 %), *Pseudofabriciola analis* (3.5 %) and *Myriochele oculata* (3 %). Their percentage contributions to mean density at each station along the transect are shown in Table 3. The mean density of *L. gracilis* ranged from a maximum of 40 individuals 100 cm^{-2} (S1) to 7 individuals 100 cm^{-2} (S2). *O. steenstrupi* reached highest density at S5 (32 individuals 100 cm^{-2}), *Cossura soyeri* at S4 (10 individuals 100 cm^{-2}) whereas *Paradoneis lyra* exhibited higher density at S5 (20 individuals 100 cm^{-2}). The species *A. chiajei* and *M. oculata* were numerically impor-

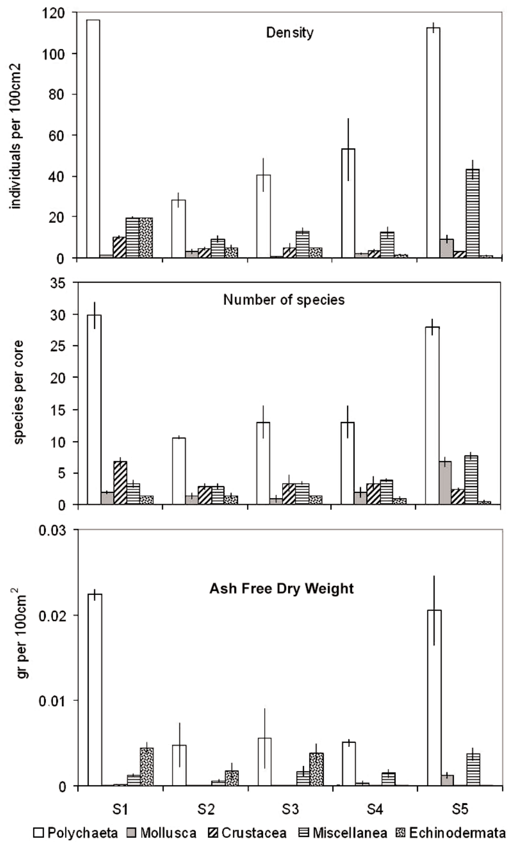

Figure 2. Mean density, numbers of species per core sample and Ash Free Dry Weight (AFDW) of macroinfauna at all stations. Bars indicate standard error.

Figure 2. Valeur moyenne de la densité, du nombre d'espèces et du poids sec libre de cendres (AFDW) de la macrofaune endogée dans les différentes stations. Les barres représentent l'erreur standard.

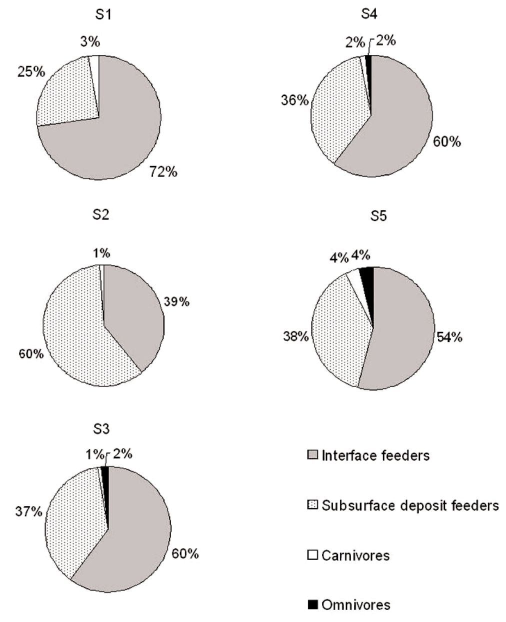

Figure 3. Relative contribution (%) of feeding types to mean abundance at all stations. I: Interface feeders. S: Surface deposit feeders. C: Carnivores. O: Omnivores.

Figure 3. Contribution (%) de chaque type d'alimentation à l'abondance moyenne à chaque station. I : Alimentation à l'interface. S : Alimentation à la subsurface. C : Carnivores. O : Omnivores.

tant at the "Snow Hall" stations yet were completely absent at S4 and S5. It should be also noted that the species *Notomastus latericeus, Aricidea catherinae*, *Prionospio multibranchiata* and *Terebellides stroemi* were ranked among the 10 most dominant species in at least one of the stations.

Interface feeding is the prevailing trophic mode along Grotta Azzurra (Fig. 3). The dominant infaunal species of the cave mainly comprise surface or subsurface deposit feeders, with planktotrophic or direct development, known from littoral waters down to abyssal depths (Table 3). Moreover, these are species with worldwide distribution, from the Arctic to the Mediterranean and from the Atlantic to the Pacific ocean (see references cited in Table 3).

Discussion

The gradual inward increase in the Silt-Clay percentage content provides a measure of the gradual decline in current regime from the outer to the inner section of the cave. Furthermore, it indicates that sedimentation rate, due to the chemosynthetic microbial mats and the rich epifaunal cover, is higher in the "Snow Hall".

TOC levels in Grotta Azzurra felt within the range of values reported by Fichez (1991) for the oligotrophic Trémies cave in the NW Mediterranean (0.65-0.70%). They were also comparable with those reported by Fredj & Laubier (1985) for the deep seafloor in the Mediterranean Sea (0.2-1.6%) and those provided by Delille et al. (1990) for the NW Mediterranean slope (0.60-0.68%). The lower ATP concentrations in the subsurface sediment layer provide evidence for lower activity and hence lower quality of buried organic material, most likely because of the degradation activities of sediment surface microbes and fauna.

The prevalence of surface deposit feeders among the species found in Grotta Azzurra can thus be explained, to a great extent, from the higher quality of fresh recently settled organic material. The insignificant contribution of carnivorous predators and scavengers among macroinfauna,

Table 2. List of the macroinfaunal species collected in Grotta Azzurra.
Tableau 2. Liste des espèces de macrofaune endogée collectées dans la Grotta Azzurra.

TAXA	S1	S2	S3	S4	S5
POLYCHAETA					
Scoloplos sp.	+		+		
Levinsenia gracilis Tauber, 1879	+	+	+	+	+
Paradoneis lyra Southern, 1914	+	+	+		+
Aricidea catherinae Laubier, 1967	+	+	+	+	+
Paraonidae sp. indet.		+			
Aonides oxycephala Sars, 1862	+				+
Prionospio multibranchiata Berkeley, 1927	+	+	+	+	+
Tharyx heterochaeta Laubier, 1961	+				
Chaetozone setosa Malmgren, 1867					+
Caulleriella alata Southern, 1914					+
Notomastus latericeus Sars, 1851	+	+	+		
Notomastus aberans Day, 1957				+	+
Notomastus sp.			+		
Notomastus profundus Eisig, 1887	+			+	+
Pseudoleiocapitella fauveli Fauvel, 1913			+		+
Decamastus gracilis Hartman, 1963			+		+
Leiochrides sp.					+
Leiocapitella sp.					+
Heteromastus filiformis Claparede, 1864					+
Capitella capitata Fabricius, 1780					+
Capitelethus dispar Ehlers, 1907					+
Capitomastus minimus Langerhans, 1880					+
Maldane sarsi Malmgren, 1865	+		+	+	+
Euclymene sp.	+	+	+	+	+
Myriochele sp.					+
Myriochele oculata Zaks, 1922	+	+	+		
Cossura soyeri Laubier, 1979	+	+	+	+	+
Pherusa eruca Claparede, 1868	+	+	+	+	
Brada villosa Rathke, 1843	+				+
Sternaspis scutata Renier, 1807				+	
Micronephtys maryae San Martin, 1982			+	+	+
Terebellides stroemi Sars, 1835	+			+	+
Polycirrus sp.			+		
Jasmineira caudata Langerhans, 1880			+		
Sabellidae sp. juv			+		
Chone duneri Malmgren, 1867	+				
Chone collaris Langerhans, 1880				+	
Pseudofabriciola analis Fitzhugh et al., 1994	+	+	+	+	+
Salmacina incrustans Claparede, 1868	+				+
Josephella marenzelleri Caullery & Mesnil, 1897	+				+
Glycera tesselata Grube, 1863			+	+	+
Harmothoe longisetis Grube, 1863		+			
Aphrodite aculeata Linneaus, 1758	+				
Pholoe minuta Fabricius, 1780				+	
Chrysopetalum debile Grube, 1855					+
Syllis cornuta Rathke, 1843	+				
Exogone verrugera Claparede, 1868					+
Kefersteinia cirrata Keferstein, 1863	+				+
Ophiodromus flexuosus Delle chiaje, 1825	+				
Fauveliopsis sp.	+	+			
Ophelina acuminata Orsted, 1843					+
Eunice vittata Delle chiaje, 1825					+
Hyalinoecia bilineata Baird, 1870					+
Protodorvillea kefersteini McIntosh, 1869					+
Schistomeringos rudolphi Delle chiaje, 1828					+

ANTHOZOA	+		+		+
OLIGOCHAETA				+	
NEMERTEA		+	+	+	+
GASTROPODA					
Caecum sp.	+				
Pyramidellidae	+				
Gastropoda sp. juv.	+				
Rissoidae			+		
BIVALVIA					
Arca noae Linneo, 1758			+		+
Loripes lucinalis Lamarck, 1818		+		+	+
Thracia pubescens Pulteney, 1799					+
Thracia sp. juv.				+	
Tellinacea		+			+
Gouldia minima Montagu, 1803				+	+
Thyasira flexuosa Montagu, 1803				+	
Tellina serrata Brocchi, 1814					+
Parvicardium sp.					+
Acanthocardia sp. juv.					+
Ctena decussata Costa, 1829					+
Solemya togata Poli, 1795					+
Corbula gibba Olivi, 1792					+
CAUDOFAUVEATA					
Solenogaster sp.					+
CUMACEA					
Iphinoe elisae Bacescu, 1950		+			
Iphinoe trispinosa Goodsir, 1843		+	+		
Iphinoe inermis Sars, 1878				+	+
ISOPODA					
Isopoda sp. Indet.				+	
Cyathura sp.	+	+			
OSTRACODA	+	+	+		+
MYSIDACEA			+		
TANAIDACEA					
Leptochelia savignyi Kroyer, 1842	+	+	+	+	+
AMPHIPODA					
Harpinia crenulata Boeck, 1871	+				
Atylus swammerdami Milne-Edwarda, 1830	+			+	
Monoculodes griseus Della Valle, 1893	+		+	+	+
Liropus minimus Mayer, 1890			+		
PYCNOGONIDA					+
SIPUNCULA					
Onchnesoma steenstrupi Koren & Danielsen,1875	+	+	+	+	+
Aspidosiphon muelleri Diesing, 1851			+	+	+
Sipunculus nudus Metalnikoff , 1900					+
Phascolion strombi Montagu, 1804					+
ECHINODERMATA					
Amphiura chiajei Forbes,1843	+	+	+		+
Labidoplax buski McIntosh, 1866		+		+	
BRACHIOPODA	+				
ASCIDIACEA					+
ENTEROPNEUSTA					

Table 3. Relative contribution (%) to the abundance at each station, bathymetric distribution, feeding type (FT) and larval development patterns (LD) of the most dominant macroinfaunal species recorded in the present study. I: Interface feeder, S: Subsurface feeder, DI: Direct development, PL: Planktonotrophic development, LE: Lecithotrophic development. References: 1. Fauchald & Jumars, 1979, 2. Giangrande, 1997, 3. Laubier & Ramos, 1973, 4. Stephen & Edmonds, 1972, 5. Buchanan, 1964, 6. Reyss, 1971, 7. Fitzhugh et al., 1994, 8. Nilsen & Holte, 1985.

Tableau 3. Abondance relative (%) à chaque station, distribution bathymétrique, type d'alimentation (FT) et de développement larvaire (LD) des espèces de macrofaune endogée les plus dominantes enregistrées dans la présente étude. I : Alimentation à l'interface, S : Alimentation à la subsurface, DI : Développement direct, PL : Développement planctotrophe, LE : Développement lécithotrophe. Références : 1. Fauchald & Jumars, 1979, 2. Giangrande, 1997, 3. Laubier & Ramos, 1973, 4. Stephen & Edmonds, 1972, 5. Buchanan, 1964, 6. Reyss, 1971, 7. Fitzhugh et al., 1994, 8. Nilsen & Holte, 1985.

	% Contribution to Abundance along Grotta Azzurra								
Species	**S1**	**S2**	**S3**	**S4**	**S5**	**Depth range**	**FT**	**LD**	**References**
Levinsenia gracilis	25	9	31	35	20	10 – 2,700	I	DI	1; 2; 3
Onchnesoma steenstrupi	10	15	16	10	19	40 – 3,000	I	LE	4
Paradoneis lyra	7	2	8	0	12	10 – 700	I	DI	1; 2; 3
Amphiura chiajei	12	8	8	0	0	10 – 1,200	I	PL	5
Cossura soyeri	2	3	1	13	3	10 – 1,000	S		1; 6
Pseudofabriciola analis	6	1	1	5	3	10 – 20	I	DI	1; 2; 7
Myriochele oculata	3	18	2	0	0	10 – 2,500	S	PL	1; 8

for example small size species from the polychaete families Phyllodocidae, Syllidae, Onuphidae and Nephtyidae, signifies striking differences from other oligotrophic environments, such as the deep areas of the Eastern Mediterranean (Kröncke et al., 2003) and other dark non-hydrothermal caves adjacent to Capo Palinuro (Bianchi, 1985).

The dominance of small-size, non or discretely motile interface feeders, suggests that the infauna within the cave is adapted to respond to recently settled, apparently labile, organic material (Fauchald & Jumars, 1979). This contention, however, raises the question whether infaunal trophic structure in Grotta Azzurra, is better explained as a response to chemolithoautotrophic inputs (i.e. the "hydrothermal effect") or to outside – inside gradients in the amount of phytodetrital inputs from the coastal system (i.e. the "cave effect"). The relative contributions of chemosynthesis versus photosynthesis in supplying food to benthic heterotrophs were estimated to be 31 and 69%, respectively (Airoldi & Cinelli, 1997). This has been considered as the main reason for the homomogeneity of particulate material fluxes, excluding chloropigments, along the outside-inside transect in Grotta Azzurra (Airoldi & Cinelli, 1997). This finding is also supported by the consistent sedimentary TOC values along the cave. Consequently, the "hydrothermal effect" corresponds to an additional food source for macrofauna as it is mainly related to organic inputs derived by the fallout of the dense microbial mats that is caused by "unpredictable", natural or manmade, perturbations of the water masses.

Regarding density trends, the present study reveals higher variability among stations rather than within stations indicating that differences are prominent in the scale of a few meters inside the cave. An other important feature is that there is no inward decline of abundance and biomass, as it was generally believed for cave macroepibenthos (Riedl, 1966; Harmelin et al., 1985; Gili et al., 1986). The fact that 28% of the species found in this survey are exclusively present in the "Snow Hall", indicates that there is sufficient water exchange for the transportation of invertebrate larvae so that colonization is not confined to the outer parts of the cave. Moreover, those that are numerically important, such as *A. chiajei* and *M. oculata,* display dispersive apparently planktotrophic larval development.

Harmelin et al. (1985) hypothesized that the formation of soft-bottom cave communities takes place through colonization of pre-adapted species, living in environments with features comparable to those of caves, such as the deep-sea. However, the species composition of the Grotta Azzurra macrobenthos suggests coexistence of species from different Mediterranean infralittoral and circalittoral soft-bottom biocoenoses as described by Pérès (1967). The eurybathic and extra-Mediterranean distribution of the dominant infaunal species in Grotta Azzurra, suggest analogies with the deep-sea Mediterranean soft-bottom biocoenoses (Fredj & Laubier, 1985). Finally, endemic "cave fauna" or "vent species" were not detected.

Special attention should be given to the relatively high density of *P. lyra*, *L. gracilis*, *P. multibranchiata* but also to the presence of *C. gibba*, *T. flexuosa*, *P. kefersteini*, *S. rudolphi*, and 12 Capitellid species including *Capitella capitata*, *Capitomastus minimus* and *Heteromastus filiformis*. These species have been considered indicators of environmental instability in coastal areas as they are tolerant to excess organic matter enrichment (Borja et al., 2000). Similarly, in a qualitative study of macrofauna in three oligotrophic caves in the Marseilles region, only twelve infaunal species were found (Monteiro-Marques, 1981) including *Spio multioculata* Rioja, 1918 and *Scolelepis ciliata* Keferstein, 1862 that are also known to form sizeable populations under organic enrichment.

The comparable results from the qualitative study in Marseilles region and the present quantitative study in Grotta Azzurra, despite their relaltively low number of stations, provide evidence that cave macroinfauna is preadapted to respond not only to oligotrophy but also to environmental instability. It is suggested that the unpredictable, apparently not seasonal, variations in the supply of sediment and food particles as well as larvae, induce physical stress on community structure thus favouring the successful colonization of caves from tolerant species to unbalanced conditions.

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