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Variability of fluxes of particulate material in a submarine cave with chemolithoautotrophic inputs of organic carbon

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ABSTRACT: The composition and vertical fluxes of particulate material were studied in February, May and October 1994 and in February 1995 in a submarine cave (Grotta Azzurra, Capo Palinuro, southwestern coast of Italy) influenced by the presence in its innermost dark region (Snow Hall) of hot sulphurous springs supporting dense mats of chemolithoautotrophic bacteria. A multifactorial sampling design was used to specifically address whether there were differences in the quantity and quality of particles sedimenting at different sites within Snow Hall and in the outer non sulphurous region of the cave (Central Hall), and whether patterns were consistent over time. Material collected in sediment traps was analysed to quantify the content of coarse particles, total particulate material, particulate organic carbon, particulate organic nitrogen, chlorophyll *a*, phaeopigments, total carbohydrates, total proteins and total lipids. Microscopic analyses were also carried out in order to characterise coarse and particulate material. The most abundant recognisable particles in the traps were faecal pellets, *Posidonia* and algal debris and fragments of organisms living on the vault of the cave, while a great proportion of coarse material consisted of generally unidentifiable amorphous aggregates. Both the magnitude of flux and nature of the sedimented material were heterogeneous. Such variability was especially evident on a small spatial scale. Significant variation among sites sampled in each region was detected during each sampling period for the majority of the compounds that were analysed. Conversely, differences between the 2 regions were generally low and were not consistent through time. A clear spatial trend emerged only for chloropigments, whose sedimentation rates consistently decreased from Central Hall to Snow Hall. In contrast to the general paradigm of caves as simplified oligotrophic ecosystems driven by their proximity to an outside source of energy, the observed patterns suggest that vertical fluxes of particulate material in this peculiar environment are influenced by local processes acting on a small spatial scale within the cave. It is also indicated that bacterial chemosynthetic production supplies fresh organic material to the cave benthos in the form of sinking particles.

KEY WORDS: Spatial variability · Particulate material · Fluxes · Sources · Biochemical composition Sediment traps · Submarine caves · Chemosynthesis

INTRODUCTION

Knowledge of the composition and flux of sinking particulate material is central to identifying the origins, pathways and fates of constituent substances and provides insight into the ecological role of particles in marine environments (Smetaceck 1984, Valiela 1984, Lee & Wakeham 1988). In recent years, considerable improvement of sediment trap designs and techniques (Bloesh & Burns 1980, Blomqvist & Håkanson 1981) has facilitated quantification and characterisation of the fluxes of sedimenting particles in many oceanic (Honjo 1980, Deuser et al. 1981, Fellows et al. 1981, Fowler & Knauer 1986) and coastal areas (Peinert et al. 1982, Wassmann 1985, 1991, Bavestrello et al. 1991, Puskaric et al. 1992). Results from these studies have produced evidence that the quantity and quality of sinking particulate material reaching the sea floor are highly variable in space and time, reflecting the com-

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plex hydrographical and biological processes occurring in the water column and at the water-sediment interface. This variability is assumed to be one of the major factors influencing the distribution, biomass and metabolic activity of benthic communities in many different habitats (Mills 1975, Graf et al. 1982, Stewart 1983, Smetaceck 1984, Yap 1991, Pfannkuche 1993, Airoldi et al. 1996). Measuring spatial and temporal patterns in the flux of sinking particles contributes, therefore, to an understanding of the structure and functioning of marine ecosystems as well as of the supply of food and energy to the benthos.

Submarine caves are common along the coasts of the Mediterranean sea, especially where the predominating limestone rock undergoes erosion and karst formation, and may be considered a typical feature of this basin (Riedl 1966). Their distinctive geological, hydrodynamical and ecological characteristics, such as absence of light, limited water flows, low fluxes of organic material and occurrence of sharp physical, chemical and energy gradients, make them unique marine environments within coastal ecosystems (Laborel & Vacelet 1959, Ott & Svoboda 1976, Harmelin et al. 1985). Moreover, faunal and ecological similarities with deep sea habitats (Vacelet et al. 1994) contribute to the interest in submarine caves. This interest is reflected by an extensive and diverse body of literature (True 1970, Cinelli et al. 1977, Gili et al. 1986, Balduzzi et al. 1989, Bibiloni et al. 1989, Zabala et al. 1989, ISSD 1994). However few studies have examined the composition and cycling of particulate material in Mediterranean caves (Fichez 1990a, 1991a, b, c), and only one has included measurements of sedimentation rates (Fichez 1990b).

Dark caves are devoid of autochthonous phytoplanktonic production because of the absence of light, and the heterotrophs subsist on supplies of organic material advected from the open sea (Fichez 1990a, 1991b). Due to low levels of hydrodynamism and reduced mixing of the water masses, particles entering the caves via water exchanges rapidly sink to the surface of the sediments (Fichez 1990b, Garrabou & Flos 1995). Sedimentation, together with progressive filtering off and degradation of particulate organic material, typically results in a progressive impoverishment of trophic resources, which is thought to be responsible for severe reductions of organism biomass observed in the innermost parts of dark single-entrance caves (Pérès & Picard 1949, Laborel & Vacelet 1959, Gili et al. 1986, Balduzzi et al. 1989, Fichez 1990b, Palau et al. 1991, Garrabou & Flos 1995). However, recent multidisciplinary investigations on some caves with sulphide inputs from submarine hot springs have shown that in these unique environments sulphur-oxidizing bacteria act as primary producers fixing carbon through chemosynthesis (Mattison et al. 1996, Southward et al. 1996). Such autochthonous bacterial production may locally enrich invertebrate abundance, supplying fresh organic material in addition to the pelagic flux from outside primary production (Southward et al. 1996, L. Airoldi & F. Cinelli unpubl.).

The aim of the present work was to study the spatial variability in the composition and vertical fluxes of particulate material in a Mediterranean shallow-water submarine cave influenced by sulphur springs. The amount and the biochemical composition of sedimenting particles were studied by means of sediment-trap deployments. A multifactorial sampling design was used to specifically address whether there were differences in the quantity and quality of particles sedimenting in different areas of the cave and whether the observed patterns were consistent through time. The research was carried out in tandem with measurements of the concentration and composition of suspended particulate material (Airoldi & Cinelli unpubl.) and experimental investigations on factors affecting patterns of distribution of the biological communities (Benedetti-Cecchi et al. in press).

MATERIAL AND METHODS

Site description. The study was carried out from February 1994 to February 1995 in Grotta Azzurra cave, on the southwestern coast of Italy. The cave opens in the limestone massif of Capo Palinuro and may be separated into 2 topographically distinct regions with different characteristics (Fig. 1A). The first outer region (Central Hall) is a wide double-entrance chamber that reaches a maximum depth of about 30 m; here a faint light is still present, and currents create water exchanges with the open sea. A smaller, shallower (about 15 m), inner region (Snow Hall) opens on the south side of Central Hall with respect to the main entrance; this part of the cave is completely dark, has a reduced hydrodynamic regime (<10 cm s^{-1}; D. Stüben unpubl.) and is characterised by the presence of hot sulphur springs that arise from fissures in the floor and in the sides. The warm (23 to 24°C) sulphurous water stratifies above the ambient cooler (14 to 20°C) sea water just below the vault (Fig. 1B), forming a sharp boundary at about 9 m depth (a detailed description of the geochemical composition of the water masses of Grotta Azzurra cave is reported by Stüben et al. 1996 and Fitzsimons & Dando 1996). Dense mats of sulphur oxidising bacteria (including *Beggiatoa*-like filamentous colonies up to 100 µm in diameter) line the rocky walls and the vault above the chemocline and act as primary producers, fixing CO_2 by means of the autotrophic enzyme ribulosebisphosphate carboxylase

(Mattison & Dando 1994, Mattison et al. 1996, Southward et al. 1996). Below the chemocline, rich faunal assemblages occur on both the walls (sponges and cnidarians) and the sediment floor (bivalves, ophiurids, tubicolous polychaetes). Other information on the distribution of benthic fauna in Grotta Azzurra cave may be found in Akoumianaki & Huges (1996), Southward et al. (1996) and in L. Benedetti-Cecchi, L. Airoldi, M. Abbiati & F. Cinelli (unpubl.).

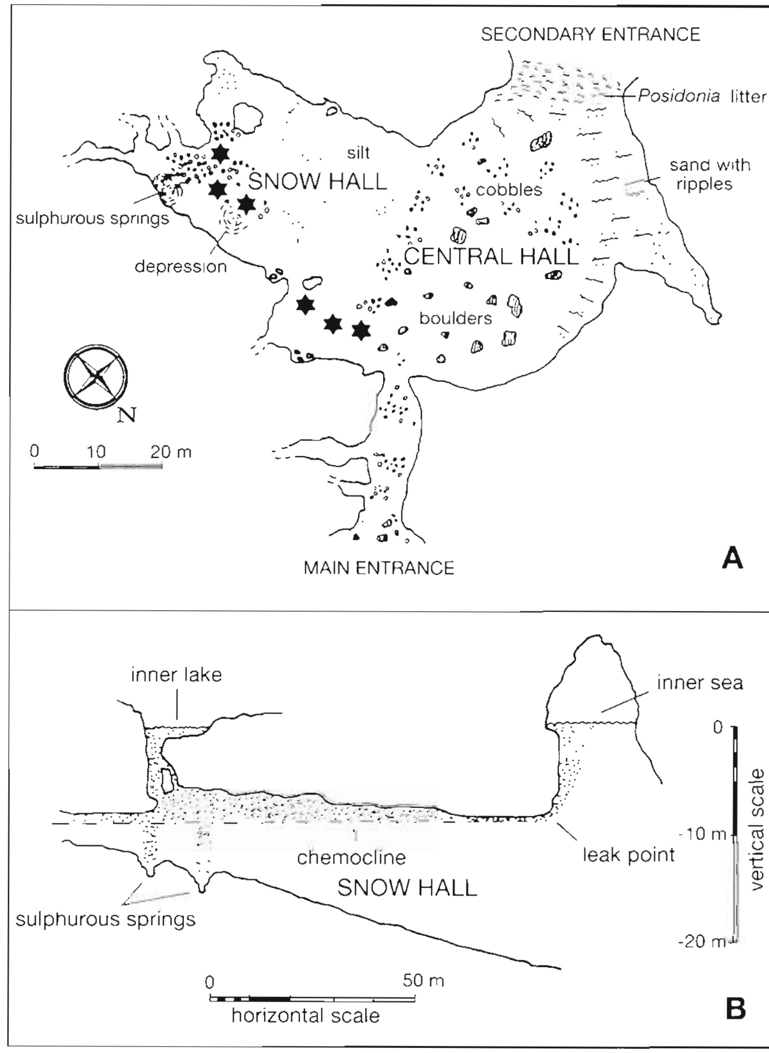


Fig. 1 (A) Sketch of the underwater portion of Grotta Azzurra cave showing location of the sampling sites (stars) in Central Hall and in Snow Hall and (B) cross section of Snow Hall (modified from Alvisi et al. 1994)

Sampling. The null hypothesis of no differences in the quantity and quality of particulate material sedimenting in Central Hall and in Snow Hall was experimentally investigated by comparing the fluxes measured at different sites in each of these 2 regions. Sedimentation rates of different compounds were measured using 6 trap systems, each consisting of 4 polypropylene cylindrical vessels positioned with their mouths at 1.5 m above the sea floor. Each vessel had a diameter of 51 mm and a height of 200 mm (aspect ratio: 3.9) and was fixed with rubber bands onto a cylindrical PVC tube (diameter 60 mm, height 150 mm) mounted at one of the 4 extremities of a stainless steel, cross shaped frame anchored to the bottom and made vertically stable in the water column by a buoyant float. The sediment traps were deployed at 6 sites (3 in Central Hall and 3 in Snow Hall; Fig. 1A) selected at random from 12 sites with similar topographic bottom characteristics, which in all cases consisted of rocky boulders covered by a thin layer of sediment and had a depth of about 15 m (location of sediment traps in depressions of the floor with accumulations of muddy sediment was deliberately avoided to prevent instability of traps and excessive resuspension of bottom sediments). Therefore, for each region (Central Hall vs Snow Hall) there were 3 replicated sampling sites, and for each site 4 replicated collection vessels.

The experiments were conducted in February, May and October 1994 and in February 1995 in order to verify whether patterns observed were consistent through different sampling periods. During these periods the traps were deployed for intervals of 7, 11, 9 and 7 d respectively. Deployment and retrieval of the vessels were carried out by SCUBA diving; vessels were closed with Parafilm and plastic stoppers before retrieval. In February and May 1994 during the periods of deployment of the traps some field activities were carried out in the cave by other divers involved in the same multidisciplinary research: on such occasions the vessels were closed with plastic stoppers for the entire length of the dives (about 70 min) in order to reduce possible perturbation induced by divers. No preservatives were added, since there is some debate about possible artifacts associated with their use (Knauer et al. 1984, Gundersen & Wassmann 1990, Lee et al. 1992, Hedges et al. 1993), and possible decay of organic carbon in non-poisoned traps generally affects measured fluxes only when traps are deployed in the field for intervals longer than those in present study (Gundersen & Wassmann 1990). The samples were immediately transported to the laboratory and stored in a cooler

(-4°C) until filtration, which was always completed within 20 to 30 h after retrieval.

Analysis. Material collected in each trap was passed through 200 µm mesh to separate the coarse particles retained on the mesh (hereafter coarse material, CM) from the finer ones (hereafter particulate material), and the abundance and composition of both components was then quantitatively assessed.

The CM from 1 trap from each site was picked up from the mesh and preserved with buffered formalin (5%) for microscopic analysis. A grid with 50 equally spaced dots was placed below the Petri dish where the material was being examined, and contacts with particles were counted under a stereomicroscope (Airoldi et al. 1996). The abundance of different kinds of particles was expressed as the percentage over the total number of contacts. The amount of CM from the remaining 3 traps at each site was determined gravimetrically on preweighed meshes (Krey 1964). The material was rinsed with distilled water to remove salts and dried at 60°C for 48 h before weighing

The smaller particles passing through the mesh were resuspended in 1 l of filtered cave seawater (Sartorius SM 113, 0.2 µm) and kept homogeneous by agitation on a magnetic stirrer. Aliquots were withdrawn by pipetting from the suspension and filtered through precombusted (450°C, 3 h) 25 mm Whatman GF/F glass microfibre filters for analysis of total (TPM) and inorganic (PIM) particulate material, particulate organic carbon (POC) and nitrogen (PON), chlorophyll *a* (chl *a*) and phaeopigments (phaeo), total carbohydrates (TCH), proteins (TPR) and lipids (TLI). Each measurement was replicated at least twice. Blank filters for all the analyses were prepared on each collection date and treated in the same manner as the samples, and corrections were made for values from these blanks. Filters were stored in darkness at -20°C until the analyses were done. A small aliquot (10 ml) was preserved with buffered formalin (5%) for qualitative microscopic analysis.

TPM was determined gravimetrically on preweighed filters (Krey 1964). Filters with retained material were rinsed with distilled water to remove salts, dried at 60°C for 24 h, allowed to cool in a dessicator and weighed on an Ohaus balance (mod. Galaxy TM100) to a precision of 10^{-4} g in the presence of silica gel. Filters were then ignited at 450°C for 3 h and reweighed after cooling in order to determine the content of PIM (Dean 1974).

POC and PON were analysed with a CHN analyser (Carlo Erba Model 1106). To remove any carbonates, filters were treated with fumes of HCl for 5 h and dried prior to analysis (Hedges & Stern 1984).

Chl *a* and phaeo were extracted with 90% acetone (24 h at 4°C in darkness) and determined spectrophotometrically before and after treatment with dilute HCl (Strickland & Parsons 1972). The total amount of chloropigments (pigm) was then calculated as their sum. In October 1994, fluxes of chloropigments were very low, and on 3 occasions the amount of chl *a* retained by the filters was below the limits of sensitivity of the analytical method. In such cases, in order to be able to calculate POC:chl *a* ratios (otherwise equal to ∞), the flux of chl *a* was arbitrarily assigned a value of 0.02 mg m^{-2} d^{-1}, a value slightly lower than the lowest measurement during the same period (0.03 mg m^{-2} d^{-1}).

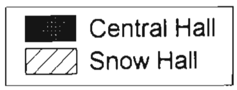
TCH, TPR and TLI were determined colorimetrically. Carbohydrates were titrated by the phenol-sulphuric acid method of Dubois et al. (1956) after extraction in distilled water (Moal et al. 1985) and expressed as glucose equivalents. Proteins were extracted with distilled water (Moal et al. 1985), titrated with the Folin phenol reagent method (Lowry et al. 1951) and expressed as albumin equivalents. Lipids were extracted with chloroform according to the method of Blight & Dyer (1959), titrated by the sulphuric acid method of Marsh & Weinstein (1966) and expressed as tripalmitic acid equivalents.

Variations in sedimentation rates of different compounds were analysed using a 3-way mixed model ANOVA, with time (February vs May vs October 1994 vs February 1995) and region (Central Hall vs Snow Hall) as fixed factors and sites as the random variable nested in region. Since vessels were attached in a regular pattern to the same frame, we may not exclude the possibility that fluxes measured by replicated traps within each site were non-independent. If some positive correlation occurred, then the outcome of the statistical tests for differences among sites and time × sites interactions might have been affected by an increased probability of Type I error (Underwood 1981). Before running the analyses, the homogeneity of variances was examined using Cochran's *C*-test (Winer 1971). CM and the ratios between different biochemical compounds were log transformed. Student-Newman-Keuls tests were used for *a posteriori* multiple comparisons of means.

RESULTS

Spatial and temporal variability

Mean vertical fluxes of compounds of sedimenting particulate material measured both in Central Hall and in Snow Hall displayed considerable small-scale spatial variability (Fig. 2). Significant differences among sites within regions were, in fact, detected for TPM, PIM, POC, PON, TPR and TLI for all the sampling



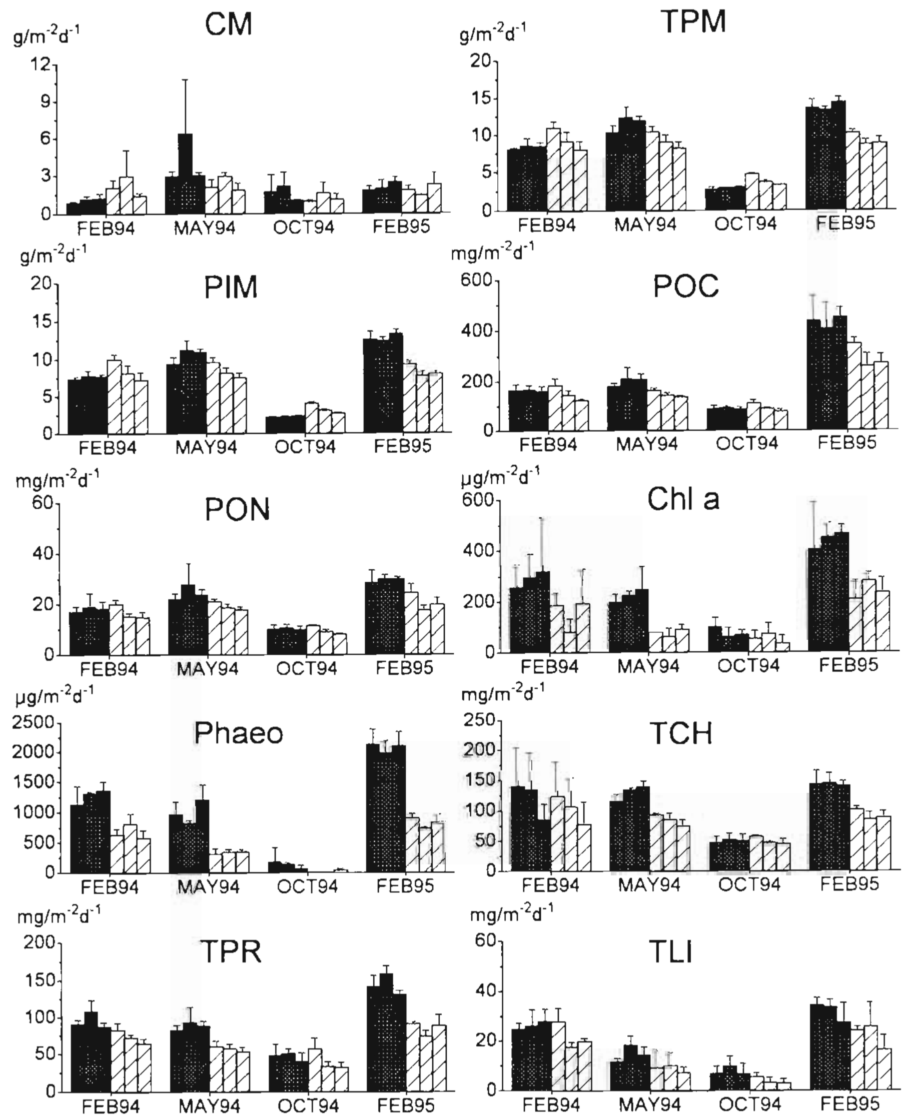


Fig. 2. Sedimentation rates of coarse material (CM), total particulate material (TPM), particulate inorganic material (PIM), particulate organic carbon (POC), particulate organic nitrogen (PON), chlorophyll *a* (Chl *a*), phaeopigments (Phaeo), total carbohydrates (TCH), total proteins (TPR) and total lipids (TLI) measured in different regions (Central Hall vs Snow Hall) of Grotta Azzurra cave during February, May and October 1994 and February 1995. Three random sites were replicated for each region. Data are means +1 SD (n = 3 for CM and 4 for all the other cases)

periods (Tables 1 & 2). Spatial variations among sites were also detected for phaeo, but these were not consistent through time, as indicated by the significant interaction time × site (region).

Variations between Central Hall and Snow Hall were highly dependent on the timing of sampling (Fig. 2): a significant region × time interaction was, in fact, observed for all the constituents that have been analysed with the exception of TLI (Tables 1 & 2). Overall (and especially in October 1994), the differences between the 2 regions of the cave were small, and/or no consistent spatial patterns were discernible. A clear trend was evident only for chl *a* and phaeo, whose vertical fluxes sharply decreased from Central Hall to Snow Hall during most of the research (Fig. 2, Table 1).

Nature and quality of sedimented particles

Microscopic analysis revealed that most of the CM found in the sediment traps from both Central Hall and Snow Hall consisted of amorphous aggregates, faecal pellets and inorganic detritus, such as spicules of sponges and fragments of the calcareous skeletons of cnidarians and other benthic organisms living on the vault and on the walls of Grotta Azzurra cave (Fig. 3). Sometimes large *Beggiatoa*-like bacterial filaments could be identified inside the aggregates, expecially in traps from Snow Hall. Eggs, larvae and a variety of juvenile benthic invertebrates such as crustaceans, clams, ophiurids and polychaetes were sporadically present, being more abundant in May 1994 in traps from Central Hall. Coarse particles clearly originating

Table 1. ANOVA table showing the effects of Time (Feb 94 vs May 94 vs Oct 94 vs Feb 95), Region (Snow Hall vs Central Hall) and Site on sedimentation rates of coarse material (CM), total particulate material (TPM), particulate inorganic material (PIM), particulate organic carbon (POC), particulate organic nitrogen (PON), chlorophyll *a* (chl *a*) and phaeopigments (phaeo) in Grotta Azzurra cave. Time and Region are fixed factors, while Site represents a random variable nested in Region. Log transformation was required for CM. Variances were homogeneous after Cochran's *C*-tests. Significant p values ($p < 0.05$) are shown in bold type

Source of variation		df	MS	*F*	p	SNK test	
CM						Time	Region
Time	(= T)	3	2.319	13.01	**0.0004**		
Region	(= R)	1	0.111	0.41	0.558	Feb 94	Snow Hall > Central Hall
T × R		3	0.989	5.54	**0.012**	May 94	Snow Hall < Central Hall
Site (R)	(= S)	4	0.273	2.02	0.106	Oct 94	Snow Hall = Central Hall
T × S (R)		12	0.178	1.32	0.239	Feb 95	Snow Hall = Central Hall
Error		48	0.135				
TPM						Time	Region
Time	(= T)	3	304.8	321.04	**0.0001**		
Region	(= R)	1	35.86	3.71	0.127	Feb 94	Snow Hall > Central Hall
T × R		3	43.5	45.82	**0.0001**	May 94	Snow Hall < Central Hall
Site (R)	(= S)	4	9.68	15.98	**0.0001**	Oct 94	Snow Hall > Central Hall
T × S (R)		12	0.95	1.57	0.121	Feb 95	Snow Hall < Central Hall
Error		72	0.61				
PIM						Time	Region
Time	(= T)	3	281.28	342.3	**0.0001**		
Region	(= R)	1	31.63	3.63	0.13	Feb 94	Snow Hall > Central Hall
T × R		3	40.22	48.94	**0.0001**	May 94	Snow Hall < Central Hall
Site (R)	(= S)	4	8.71	18.92	**0.0001**	Oct 94	Snow Hall > Central Hall
T × S (R)		12	0.82	1.78	0.067	Feb 95	Snow Hall < Central Hall
Error		72	0.46				
POC						Time	Region
Time	(= T)	3	327335	290.36	**0.0001**		
Region	(= R)	1	60357	10.04	**0.034**	Feb 94	Snow Hall = Central Hall
T × R		3	24561	21.79	**0.0001**	May 94	Snow Hall < Central Hall
Site (R)	(= S)	4	6015	3.81	**0.007**	Oct 94	Snow Hall = Central Hall
T × S (R)		12	1127	0.71	0.733	Feb 95	Snow Hall < Central Hall
Error		72	1580				
PON						Time	Region
Time	(= T)	3	1007	166.3	**0.0001**		
Region	(= R)	1	387	6.74	0.06	Feb 94	Snow Hall = Central Hall
T × R		3	87	14.37	**0.0003**	May 94	Snow Hall < Central Hall
Site (R)	(= S)	4	57.4	6.45	**0.0002**	Oct 94	Snow Hall = Central Hall
T × S (R)		12	6.05	0.68	0.765	Feb 95	Snow Hall < Central Hall
Error		72	8.9				
Chl *a*						Time	Region
Time	(= T)	3	0.327	65.56	**0.0001**		
Region	(= R)	1	0.387	128.03	**0.0003**	Feb 94	Snow Hall < Central Hall
T × R		3	0.033	6.62	**0.0069**	May 94	Snow Hall < Central Hall
Site (R)	(= S)	4	0.003	0.46	0.767	Oct 94	Snow Hall = Central Hall
T × S (R)		12	0.005	0.76	0.692	Feb 95	Snow Hall < Central Hall
Error		72	0.007				
Phaeo						Time	Region
Time	(= T)	3	7.88	169.21	**0.0001**		
Region	(= R)	1	10.17	308.35	**0.0001**	Feb 94	Snow Hall < Central Hall
T × R		3	1.3	27.99	**0.0001**	May 94	Snow Hall < Central Hall
Site (R)	(= S)	4	0.033	1.41	0.241	Oct 94	Snow Hall < Central Hall
T × S (R)		12	0.047	1.98	**0.038**	Feb 95	Snow Hall < Central Hall
Error		72	0.023				

from outside the cave were found in traps from both regions during all the sampling periods. These were mainly *Posidonia* and algal debris. Charcoal fragments, probably originating from coastal vegetation fires, were occasionally also found in October 1994 and February 1995.

The TPM also consisted mainly of small amorphous aggregates. Recognisable structures were chiefly

Table 2. ANOVA table showing the effects of Time (Feb 94 vs May 94 vs Oct 94 vs Feb 95), Region (Snow Hall vs Central Hall) and Site on sedimentation rates of total carbohydrates (TCH), total proteins (TPR), total lipids (TLI) and food material and on values of the food index and amount of food energy in Grotta Azzurra cave. Time and Region are fixed factors, while Site represents a random variable nested in Region. Food index and food energy were log transformed. Variances were homogeneous after Cochran's *C*-test. Significant p values ($p < 0.05$) are shown in bold type

Source of variation		df	MS	*F*	p	SNK test	
TCH						Time	Region
Time	(= T)	3	23131	29.92	**0.0001**		
Region	(= R)	1	19160	14.26	**0.02**	Feb 94	Snow Hall = Central Hall
T × R		3	3387	4.38	**0.027**	May 94	Snow Hall < Central Hall
Site (R)	(= S)	4	1344	1.71	0.157	Oct 94	Snow Hall = Central Hall
T × S (R)		12	773	0.98	0.471	Feb 95	Snow Hall < Central Hall
Error		72	785				
TPR						Time	Region
Time	(= T)	3	20348	131.31	**0.0001**		
Region	(= R)	1	20628	19.2	**0.012**	Feb 94	Snow Hall < Central Hall
T × R		3	3020	19.49	**0.0001**	May 94	Snow Hall < Central Hall
Site (R)	(= S)	4	1075	9.36	**0.0001**	Oct 94	Snow Hall = Central Hall
T × S (R)		12	155	1.35	0.21	Feb 95	Snow Hall < Central Hall
Error		72	115				
TLI						Time	
Time	(= T)	3	2407	65.04	**0.0001**		
Region	(= R)	1	896.3	12.64	**0.02**	Feb 95 > Feb 94 > May 94 > Oct 94	
T × R		3	40.34	1.09	0.39		
Site (R)	(= S)	4	70.89	3.26	**0.02**		
T × S (R)		12	37.02	1.7	0.08		
Error		72	21.72				
Food material						Time	Region
Time	(= T)	3	109320	103.7	**0.0001**		
Region	(= R)	1	97331	17.3	**0.014**	Feb 94	Snow Hall = Central Hall
T × R		3	13538	12.85	**0.0005**	May 94	Snow Hall < Central Hall
Site (R)	(= S)	4	5614	5.49	**0.0006**	Oct 94	Snow Hall = Central Hall
T × S (R)		12	1053	1.03	0.43	Feb 95	Snow Hall < Central Hall
Error		72	1022				
Food material:TPM						Time	Region
Time	(= T)	3	0.9207	69.63	**0.0001**		
Region	(= R)	1	1.4322	23.76	**0.0082**	Feb 94	Snow Hall < Central Hall
T × R		3	0.1116	8.44	**0.0028**	May 94	Snow Hall < Central Hall
Site (R)	(= S)	4	0.0602	1.84	0.13	Oct 94	Snow Hall < Central Hall
T × S (R)		12	0.0132	0.4	0.9575	Feb 95	Snow Hall = Central Hall
Error		72	0.0327				
Energy						Time	Region
Time	(= T)	3	4.6103	187	**0.0001**		
Region	(= R)	1	2.4372	11.42	**0.0278**	Feb 94	Snow Hall = Central Hall
T × R		3	0.1628	6.61	**0.0069**	May 94	Snow Hall < Central Hall
Site (R)	(= S)	4	0.2133	8.71	**0.0001**	Oct 94	Snow Hall = Central Hall
T × S (R)		12	0.0246	1.01	0.4522	Feb 95	Snow Hall < Central Hall
Error		72	0.0245				

small, oval or cylindrical faecal pellets and a few diatoms, such as *Nitzschia* sp., *Navicula* sp. and *Rhizosolenia* sp. Flagellate heterotrophs were also present, but they were not identified. Pollen grains were occasionally found in traps from both regions.

The major proportion (78 to 93%) of TPM collected by sediment traps in both regions was inorganic (Fig. 4). The fraction of POC was, consequently, quite low, varying between 1.6 and 3.4% (Fig. 4). The relative contents of both POC and PIM were rather similar among sites, and the extent and the direction of the differences observed between Central Hall and Snow Hall varied through time without any consistent trend (Fig. 4, Table 3). In contrast, the POC:chl *a* ratios were significantly lower in Central Hall than in Snow Hall throughout the investigation (Fig. 4, Table 3). This ratio estimates the relative content in plant pigments of organic detritus, and values lower than 100 indicate that the carbon originates primarily from phytoplankton (Zeitzschel 1970). The POC:chl *a* ratios of sedi-

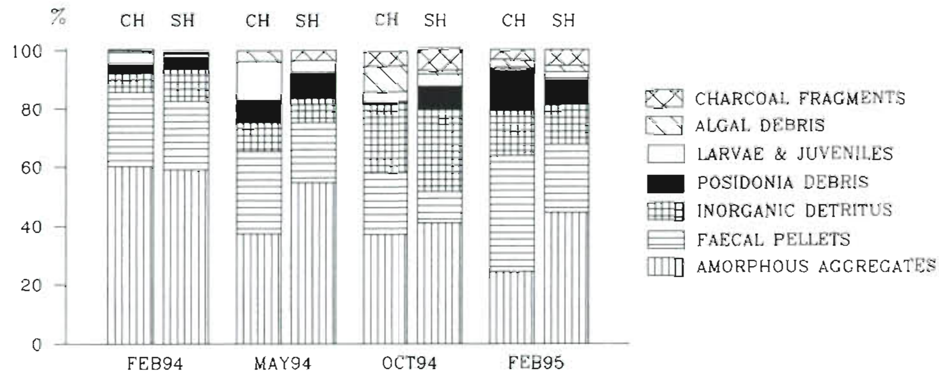


Fig. 3. Mean percentage composition of sedimented coarse material (CM) collected by sediment traps in Central Hall (CH) and in Snow Hall (SH) during February, May and October 1994 and February 1995. Data are means of 3 replicated sites

menting particulate material measured in Grotta Azzurra cave were always higher than 600 and reached values up to 3100 in Snow Hall (Fig. 4), suggesting a contribution from autochthonous sources of POC in addition to open sea phytoplanktonic production.

The total amount of food material sedimenting to the bottom of the cave was calculated as the sum of TCH, TPR and TLI (Fichez 1991b, Navarro et al. 1993) and converted into energy equivalents using the coefficients of 4.1, 5.65 and 9.45 kcal g^{-1} respectively for the above 3 components (a broad discussion of the utility and limits of such conversion factors may be found in Fichez 1991b). The inputs to benthic organisms of both food material and energy were highly variable among sites (Fig. 5, Table 2). Significant differences among regions were also detected in May 1994 and February 1995 (Table 2). Overall, the quantity of food material varied from 79 to 335 mg m^{-2} d^{-1} and represented from 1.6 to 3.9% of TPM (Fig. 4), probably due to heavy dilution with inorganic particles.

The quality of food material, i.e. the ratios between the different biochemical compounds of trapped organic material (POC, PON, TCH, TPR, TLI), was

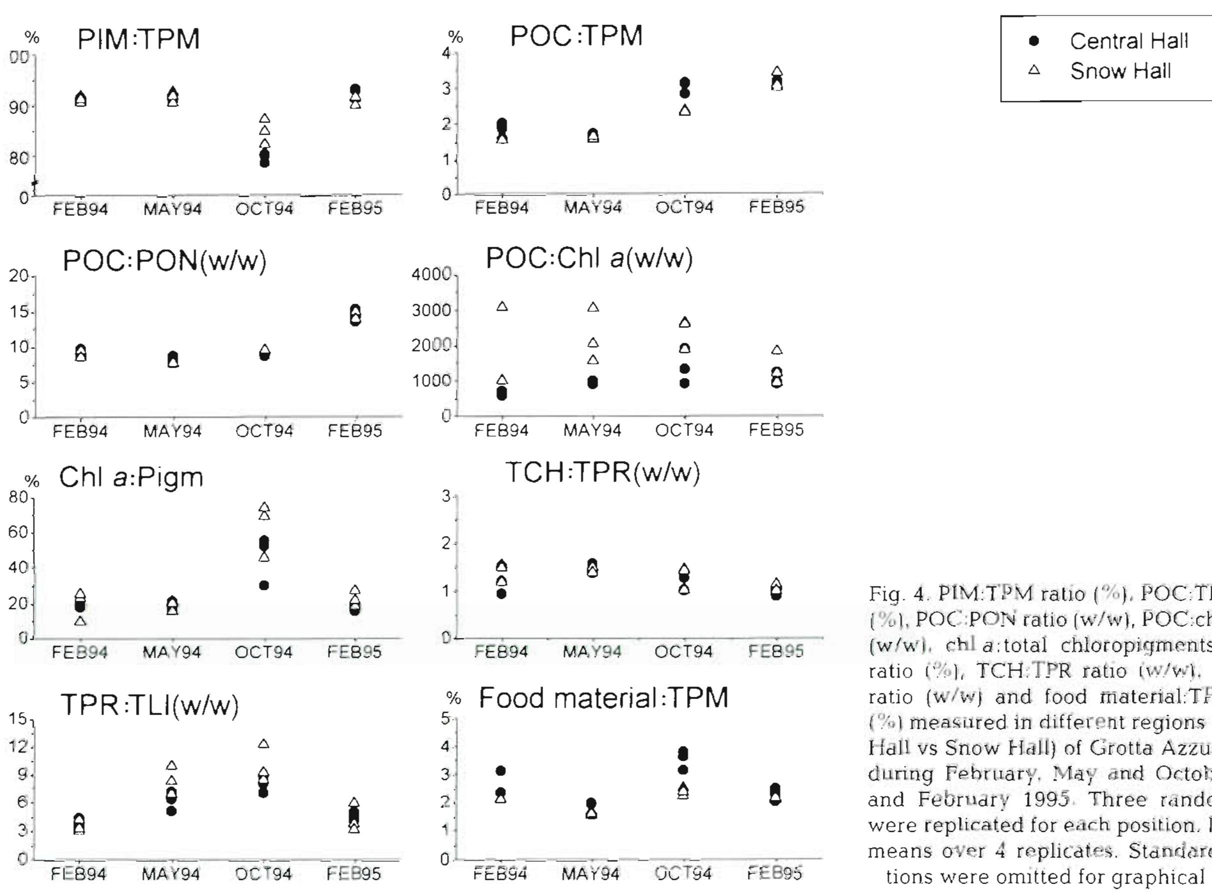


Fig. 4. PIM:TPM ratio (%), POC:TPM ratio (%), POC:PON ratio (w/w), POC:chl *a* ratio (w/w), chl *a*:total chloropigments (pigm) ratio (%), TCH:TPR ratio (w/w), TPR:TLI ratio (w/w) and food material:TPM ratio (%) measured in different regions (Central Hall vs Snow Hall) of Grotta Azzurra cave during February, May and October 1994 and February 1995. Three random sites were replicated for each position. Data are means over 4 replicates. Standard deviations were omitted for graphical clarity

rather constant at the spatial and temporal scales investigated (Fig. 4), although significant differences between regions were found for POC:PON ratios in May and October 1994 and for TPR:TLI ratios in October 1994 (Table 3). The POC:PON (w/w) ratios were low during February, May and October 1994, when they varied from a minimum value of 7.6 to a maximum of 9.8 (Fig. 4): this indicates the sedimentation of fresh

Table 3. ANOVA table showing the effects of Time (Feb 94 vs May 94 vs Oct 94 vs Feb 95), Region (Snow Hall vs Central Hall) and Site on the PIM:TPM ratio (%), POC:TPM ratio (%), POC:PON ratio (w/w), POC:chl *a* ratio (w/w), chl *a*:pigm ratio (%), TCH:TPR ratio (w/w) and TPR:TLI ratio (w/w) characterising sedimented particulate material in Grotta Azzurra cave. Time and Region are fixed factors while Site represents a random variable nested in Region. All data were log transformed. Variances were homogeneous after Cochran's *C*-test. Significant p values ($p < 0.05$) are shown in bold type

Source of variation		df	MS	*F*	p	SNK test	
PIM:TPM						Time	Region
Time	(= T)	3	0.07122	127.18	**0.0001**		
Region	(= R)	1	0.00294	2.69	0.1761	Feb 94	Snow Hall = Central Hall
T × R		3	0.00794	14.18	**0.0003**	May 94	Snow Hall = Central Hall
Site (R)	(= S)	4	0.00109	1.24	0.302	Oct 94	Snow Hall > Central Hall
T × S (R)		12	0.00056	0.64	0.801	Feb 95	Snow Hall < Central Hall
Error		72	0.00088				
POC:TPM						Time	Region
Time	(= T)	3	2.2714	335.06	**0.0001**		
Region	(= R)	1	0.3806	38.52	**0.0034**	Feb 94	Snow Hall < Central Hall
T × R		3	0.0924	13.64	**0.0004**	May 94	Snow Hall = Central Hall
Site (R)	(= S)	4	0.0098	0.44	0.777	Oct 94	Snow Hall < Central Hall
T × S (R)		12	0.0067	0.3	0.986	Feb 95	Snow Hall = Central Hall
Error		72	0.0223				
POC:PON						Time	Region
Time	(= T)	3	1.6415	236.82	**0.0001**		
Region	(= R)	1	0.0000	0.00	0.961	Feb 94	Snow Hall = Central Hall
T × R		3	0.0271	3.91	**0.037**	May 94	Snow Hall < Central Hall
Site (R)	(= S)	4	0.0156	1.21	0.313	Oct 94	Snow Hall > Central Hall
T × S (R)		12	0.0069	0.54	0.883	Feb 95	Snow Hall = Central Hall
Error		72	0.0129				
POC:chl *a*							
Time	(= T)	3	1.5891	4.17	**0.031**		
Region	(= R)	1	6.9011	56.05	**0.002**	No alternatives to H_0 could be specified	
T × R		3	0.3744	0.98	0.433		
Site (R)	(= S)	4	0.1231	0.5	0.738		
T × S (R)		12	0.3812	1.54	0.13		
Error		72	0.2477				
Chl *a*:pigm							
Time	(= T)	3	6.568	16.39	**0.0002**		
Region	(= R)	1	0.3218	2.39	0.197	No alternatives to H_0 could be specified	
T × R		3	0.3067	0.77	0.535		
Site (R)	(= S)	4	0.5378	0.7	0.594		
T × S (R)		12	0.4007	2.09	**0.028**		
Error		72	0.192				
TCH:TPR						Time	
Time	(= T)	3	0.4948	6.43	**0.008**		
Region	(= R)	1	0.1845	4.67	0.097	May 94 > Feb 94 = Oct 94 = Feb 95	
T × R		3	0.0276	0.36	0.784		
Site (R)	(= S)	4	0.0395	0.49	0.743		
T × S (R)		12	0.077	0.96	0.498		
Error		72	0.0806				
TPR:TLI						Time	Region
Time	(= T)	3	4.2734	32.66	**0.0001**		
Region	(= R)	1	0.4744	9.45	**0.0371**	Feb 94	Snow Hall = Central Hall
T × R		3	0.5604	4.28	**0.028**	May 94	Snow Hall = Central Hall
Site (R)	(= S)	4	0.0501	0.3	0.877	Oct 94	Snow Hall > Central Hall
T × S (R)		12	0.1308	0.78	0.669	Feb 95	Snow Hall = Central Hall
Error		72	0.1678				

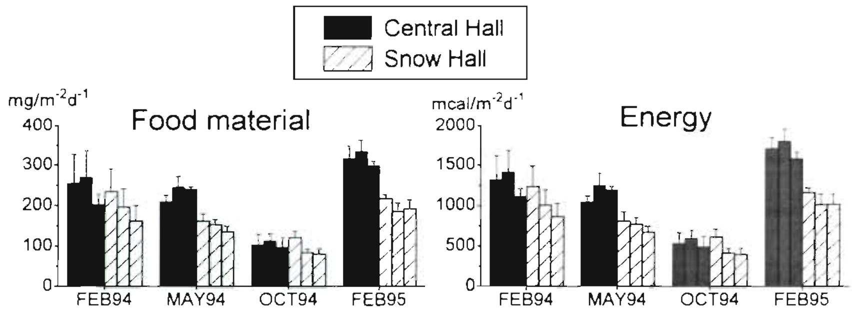


Fig. 5. Vertical fluxes of food material and energy measured in different regions (Central Hall vs Snow Hall) of Grotta Azzurra cave during February, May and October 1994 and February 1995. Three random sites were replicated for each region. Data are means +1 SD (n = 4)

detritus of good nutritional quality (Pocklington & Leonard 1979, Parsons et al. 1984, Mayzaud et al. 1989, Navarro et al. 1993) Higher values (13.5 to 15.4) were measured in February 1995, implying either low quality, older, nutrient-depleted material or inputs from terrestrial or resuspended particles. Confirmation of the good quality of organic particles sedimenting to the bottom came from the low values of the TCH:TPR ratios measured throughout the investigation (Poulet et al. 1986, Mayzaud et al. 1989), which were always lower than 1.5.

DISCUSSION

The composition and vertical fluxes of particulate material in Grotta Azzurra cave were highly heterogeneous. Such spatial variability was particularly evident on a small spatial scale. Significant differences among sites were detected during all the sampling periods for the majority of the compounds that were analysed. Conversely, variations between Central Hall and Snow Hall were not consistent through time; a clear spatial trend emerged only for chloropigments, whose sedimentation rates were consistently higher in Central Hall than in Snow Hall.

Field and laboratory experiments have shown that smooth cylindrical vessels with an inner diameter greater than 45 mm and an aspect ratio greater than 3, like those used in the present study, give reliable results both in calm and turbulent hydrodynamic conditions (Gardner 1980a, b, Butman 1986). The high spatial variability observed in Grotta Azzurra cave, therefore, is characteristic of this peculiar environment, and factors other than differences in trapping efficiency of the vessels must account for the observed patterns. The microscopic analysis of CM has shown that a large fraction of the material sinking to the bottom consists of particles produced by the organisms living on the vault and walls of the cave. Also the large amounts of PIM are probably a consequence of erosive processes of the limestone rock, enhanced by the aggressive action of the sulphurous water (Forti 1989). This suggests that the sedimentary characteristics of each site might be influenced by its location with respect to the vault and the walls of the cave. The role of erosion along rocky walls as a mechanism providing large amounts of detritus has been highlighted by Bavestrello et al. (1991). Moreover, during an investigation along a steep cliff in Balsfjorden, Gulliksen (1982) found that the amount of particulate material sedimenting at a distance of 5 m from the rocky wall was on average 64% less than that sedimenting at a distance of 1 m. The variability among fluxes measured at nearby sites might, therefore, reflect local differences of sedimentary environment, depending on the complex geomorphology of the cave.

The scattered accumulations of sediments observable both on the sides and the floor of Grotta Azzurra cave suggests that eddies of the water circulation caused by the irregular shape of the cave and local resuspension of bottom sediments might also contribute to the spatial heterogeneity observed in this system. Patterns of sediment deposition and resuspension, in fact, are dependent on the regime of water circulation, which in submarine caves is largely influenced by the degree of isolation from the open sea and consequently by the geomorphology of the cave. In Snow Hall, patterns of water circulation might be further complicated by the outflowing of sulphurous water from fissures in the floor, which could also produce a turbulent upward transport of particles. Unfortunately the degree of water circulation in Grotta Azzurra cave is still not well known, and further investigations are needed to clarify the potential role of this additional source of variability.

The analysis of the fluxes and the biochemical composition of sedimenting particulate material in Central Hall and in Snow Hall suggests that, in contrast to the heterogeneity observed on a small spatial scale, the overall quantity and quality of sinking particles in distinct regions of Grotta Azzurra cave are less variable than generally indicated for other submarine caves, where progressive impoverishment and degradation of POC have been observed with increasing distance from the entrance (Fichez 1990b, 1991b). With the

exception of chloropigments, in fact, the differences between Central Hall and Snow Hall were generally small, and no consistent spatial trends were discernible. This result essentially reproduces the patterns observed in the concentration and composition of suspended particulate material (Airoldi & Cinelli unpubl.), which have been explained as a consequence of autochthonous inputs of fresh POC from local bacterial production in addition to POC advected from outside via water exchanges. Using the POC:chl *a* ratio as an index of the relative amount of carbon of phytoplanktonic origin and stable isotope ratios as an index of autochthonous bacterial input, the fraction of chemosynthetically derived carbon over the total amount of suspended POC in Snow Hall has been estimated as about 31% (Southward et al. 1996, Airoldi & Cinelli unpubl.). In this study, lack of an external reference sediment trap system does not allow direct estimation of the relative contribution of chemosynthesis vs photosynthesis to the vertical fluxes of POC in Grotta Azzurra cave. However, the high values of POC:chl *a* ratios and the good nutritional quality of food material indicated by the low POC:PON and TCH:TPR ratios (Poulet et al. 1986, Mayzaud et al. 1989) suggest that fresh organic material produced by bacteria in the sulphurous region of the cave reaches the bottom in the form of fast sinking particles. Confirmation comes from the finding of large *Beggiatoa*-like bacterial filaments in the CM collected both in Snow Hall and in Central Hall.

Oxic-anoxic interfaces have great influence on the vertical fluxes of organic matter (Wassmann 1985). The high stratification and stability of the water column, in fact, may reduce losses of particles from the upper layers to underlying bottom sediments. Flocculation of bacterial material from the vault has often been observed as a consequence of disturbance of the water stratification by divers' bubbles, hence the name Snow Hall given to this inner, sulphur impacted region. Grotta Azzurra cave is of touristic importance and is commonly visited by amateur divers during most of the year Such diving activity presumably has important effects on the whole system and affects fluxes of particulate material. At the moment it is not possible to quantify the impact of diving activity on the overall cycling of carbon in this cave, and further research on this topic is worthwhile.

Fluctuation in the supply of food material is considered one of the major factors affecting the structure, the biomass and the metabolism of benthos (Mills 1975, Graf et al. 1982, Smetacek 1984, Yap 1991). The present results suggest that small-scale spatial variability of fluxes of particulate material is a constant feature of Grotta Azzurra cave, often overriding larger-scale patterns between distinct regions in the cave. This conclusion is consistent with modes of distribution and abundance of benthic organisms (Benedetti-Cecchi et al. unpubl.). Further research is needed to explore, in more detail, the causes and the ecological significance of this heterogeneity that previous studies on submarine caves have not addressed. Future work should also include investigations on temporal patterns. In the present study, in fact, significant variations of vertical fluxes through different sampling periods were detected, with possible important consequences for the benthic communities. However, no conclusions can be specifically drawn regarding these variations until replication at different temporal scales is included in the experimental design.

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