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Decrease in allochthonous organic inputs in dark submarine caves, connection with lowering in benthic community richness

Renaud Fichez
Centre d'Océanologie de Marseille, Station Marine d'Endoume, rue de la Batterie des Lions, 13007 Marseille, France; Present address: School of Environmental Sciences, University of East Anglia, NR4 7TJ, Norwich, England

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Abstract

Ten sediment trap arrays were deployed over two years for periods of 3 to 40 days in three different sampling points along a 50 m long Mediterranean submarine cave. Mean total particulate matter flux decreased strongly from the semi-dark area ($3.3\ \mathrm{g\,m^{-2}\,d^{-1}}$) to the dark area (0.8 and $0.6\ \mathrm{g\,m^{-2}\,d^{-1}}$). Carbon represented 3.3% to 3.5% and nitrogen 0.34% to 0.38% of settling dry matter. The decrease in organic input from the entrance to the terminal part of the cave results in increasingly oligotrophic conditions with distance from the cave entrance. Horizontal resource limitation can be connected with a strong zonal decrease in fauna richness. Biomass declines both in hard substrate and soft bottom communities. Despite major differences, some similarities are noticed between oligotrophic conditions that may occur in the dark cave and those in around 1000 m depth ecosystems. Dark oligotrophic submarine caves can be considered to be good scale models for the study of some aspects of general trophic pathways.

Introduction

Decrease of fauna richness has been noticed in early studies of Mediterranean cave communities, both in hard substrata communities (Pérès & Picard, 1949; Laborel & Vacelet, 1958; 1959) and in soft bottom communities (Monteiro-Marques, 1981) when compared to communities outside the cave. More recently a biomass study gave new evidence of a strong decrease in benthic populations in a Mediterranean dark cave (Gili *et al.*, 1986) which is presumed to be related to a decrease in trophic resources inside the cave (Harmelin *et al.*, 1985).

In an attempt to examine the validity of this hypothesis, vertical flux studies were performed for two years (10 sampling operations) in a Mediterranean sea cave close to Marseille (France). Vertical flux provides information on particulate flows to the benthic boundary layer. Since under aphotic conditions in submarine caves photosynthetic production does not occur, the supply of dissolved and particulate organic material to the cave sediment emanates from outside sources. It enters the cave through water exchange and subsequent sedimentation of particles to the water-sediment interface.

Direct measurement of the particulate flux to sediments is commonly carried out using sediment traps (Hargrave & Phillips, 1986; Noriki & Tsunogai, 1986). Comparative studies between sediment trapping and other methods of measuring sedimentation rates have been made (Spencer *et al.*, 1978; Lorenzen *et al.*, 1981). Other studies focus on the effect of trap geometry and current velocity on the amount of collected particles (Hargrave & Burns, 1979; Gardner, 1980a; 1980b; Blomqvist & Kofoed, 1981; Butman, 1986). The main results from these studies have demonstrated that cylinders should be used as sediment traps (Hargrave & Burns, 1979; Gardner, 1980b) both in turbulent and calm hydrodynamic conditions (Blomqvist & Hakanson, 1981). The aspect ratio, h/d (h = trap height, d = trap diameter), is considered to be the main geometrical parameter for traps. Its minimum values is estimated at 2.3 (Gardner, 1980a), 3 (Butman, 1986) or more than 3 (Blomqvist & Kofoed, 1981). Results obtained with sediment traps provide valuable information about vertical fluxes; nevertheless, they should be treated with caution (Smetacek, 1984).

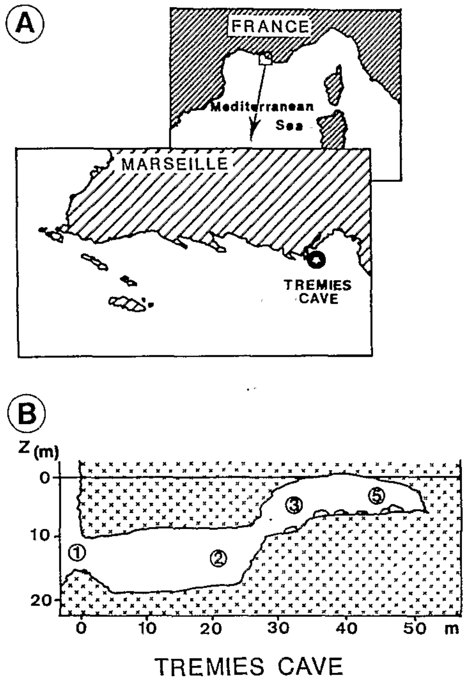

Fig. 1. Trêmies submarine cave location (A) and cross section (B). Numbers indicate corresponding sampling points. Point 1 (TR1) at the entrance, point 2 (TR2) in the semi-dark area, points 3 (TR3) and 5 (TR5) in the dark area.

Description of site studied

The submarine cave studies is located on the calcareous coastline close to Marseille (France) (Fig. 1). Abundant karst formations in this area have been transformed into submarine caves by the last marine transgression.

Trêmies cave is 60 long, 35 m wide and up to 9 m high. A 8 to 10 m high step 30 m from the entrance separates two topographic areas. The first area extending from the entrance to the step, is a wide chamber (6600 m^3) where the light level quickly decreases (semi-dark area). About 15 m from the entrance close to a *Corallium rubrum* population, light is expected to range from 0.04% to 0.06% of surface illumination (Marinopoulos, 1989). The second area is smaller (2800 m^3) and sinuous and includes two distinctive terminal parts. The very poor benthic fauna covering the hard substrata in full darkness is termed the dark cave community, the corresponding area being the dark area. It should be noted that, in Trêmies cave, the dark cave community is more extensive than in any of the surrounding caves (Harmelin, 1969).

Sampling stations were numbered TR1, TR2, TR3, TR5. TR1 was located at the entrance where the bottom is covered with fallen rocks. No vertical flux measurements were performed at this point exposed to various perturbations (slumping, current effects, human activities). TR2 was located 22 m from the entrance in the semi-dark area over a muddy grey sediment layer. TR3 was located at the beginning of the dark area 35 m from the entrance over a muddy brown sediment layer close to the rocky vertical wall. TR5 was in the terminal part of the cave 45 m from the entrance over a muddy brown sediment layer.

Materials and methods

Sediment trapping

Each sediment trap (Fig. 2) consisted of three to four cylindrical glass collectors set on a central axis holder terminated by a cylindrical guiding

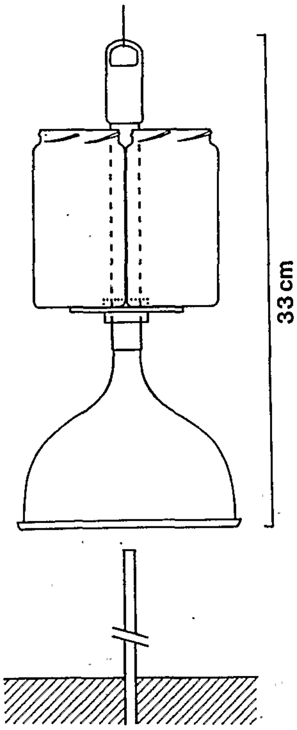

Fig. 2. Sediment trap design used in this study. Trap carrier stick permanently anchored in the sediment (1), guiding cone (2), collector holder (3), collectors (4) (three to four for each sediment trap), handling rope and float (5).

cone. Each collector was 5.5 cm in diameter (24 cm^2 collecting area) and 12.5 cm high ($h/d = 2.3$). No poison was added to these collectors.

Sediment trap handling was performed using SCUBA diving. The traps were brought underwater upside down to the sampling point. The collecting apparatus was released close to the sampling point and held by a 2.5 m rope equipped with a terminal float. With the cone acting as a guide, it was then carefully lowered and placed onto a stick permanently anchored in the sediment. Sediment traps were then held 30 cm above the bottom sediment. Collectors remained in place for 3 to 40 days. During retrieval, each collector was directly closed with a 'twist off' cover and the sediment trap was carried on board and brought back to the laboratory in the dark.

Treatment

After sedimentation under calm conditions, the supernatant was poured into a vessel and the residue was rinsed twice using an isotonic ammonium formiate (NH_4 COOH) solution. Ammonium formiate was proved to be a volatile rinsing solution well suited to the necessary low temperature drying. Rinsed material was then centrifuged at 5000 rev./min for 20 minutes and the new supernatant was added to the previous supernatant. The residue was then dried at 40 °C for 40 hours. The whole supernatant collected was filtered through a preweighed Whatman GF/C filter. Residue and filter retained dry weights were added and were then correlated with collection time and surface and expressed in $g\,m^{-2}\,d^{-1}$.

Analysis

Carbon and nitrogen were measured using a CHN autoanalyzer (Perkin Elmer 240). To remove carbonate, the filters were treated with concentrated HCl vapour for 2 hours and then redried at 40 °C for 12 hours. This treatment could not be applied to sediment which had undergone a direct acid attack, as the autoanalyzer was not equipped with an HCl vapour trap and would have been severely damaged. Therefore the difference on ignition (DOI) method (Hirota & Szyper, 1975; Byers *et al.*, 1978) was used to measure organic carbon (OC) and organic nitrogen (ON) in the sediment. Comparison of these two methods showed that the DOI method is recommended for routine measurements of OC in sediments (Kristensen & Andersen, 1987).

Sediment from sediment traps was homogenized in a mortar and three subsamples were analyzed to check reproducibility. OC and ON concentrations expressed as percentage of dry matter were then associated with the correpondingvertical particle fluxes and converted into sedimentation rate units (mgC or $mgN\,m^{-2}\,d^{-1}$). Despite the great interest of CHN analysis, it should be pointed out that the detection limits of

Table 1. Sedimentation rate measurements for each sediment trap array and each sampling point. Values are expressed in mg m^{-2} d^{-1} of dry matter. Mean and standard deviation (SD) of point/array couple values are listed in the table. Mean and standard deviation over the two years survey for each sampling point appear in the last part of the table.

Start	End	Sampling point TR2		Sampling point TR3		Sampling point TR5	
		Flux/collector	Mean (SD)	Flux/collector	Mean (SD)	Flux/collector	Mean (SD)
28/06/85	08/07/85	3583.5		1122.3		1070.5	
		3032.1	3303.2	1238.7	1128.0	1083.8	1088.4
		3447.3	(255.8)	1009.7	(93.9)	1051.3	(41.8)
		3149.8		1141.2		1147.8	
12/09/85	24/09/85	2509.2		571.3		483.1	
		2425.1	2382.8	537.2	569.2	510.4	505.2
		2214.0	(152.1)	599.0	(31.0)	522.0	(20.0)
24/09/85	15/10/85	2555.2		987.3		987.2	
		2318.5	2648.8	1122.6	1096.0	883.5	923.6
		2729.0	(284.2)	1145.3	(73.1)	930.3	(46.9)
		2992.4		1128.8		893.5	
15/10/85	13/11/85	6840.5		1941.0		939.7	
		6703.2	6720.0	1635.8	1600.8	1090.5	1463.6
		6639.7	(85.2)	1455.3	(252.3)	1854.0	(523.7)
		6696.6		1371.0		1970.2	
29/11/85	08/01/86	834.3		121.2		103.9	
		1512.0	1296.8	137.3	130.0	112.4	116.8
		1122.5	(395.1)	142.3	(11.5)	121.5	(11.1)
		1718.3		119.2		129.4	
04/03/86	01/04/86	6922.9		1005.6		831.7	
		7220.4	7227.2	1533.4	1307.2	1332.4	1015.2
		7342.7	(219.2)	1312.1	(221.5)	1188.4	(226.3)
		7422.6		1377.7		808.2	
06/06/86	09/06/86	3859.7		875.2		482.3	
		3677.2	4320.0	930.3	920.0	567.0	543.2
		4803.5	(643.6)	938.1	(30.1)	550.6	(41.7)
		4939.6		936.4		572.8	
30/09/86	07/10/86	2540.5		493.2		559.4	
		2374.3	2580.4	685.7	648.0	511.3	519.2
		2896.0	(222.5)	763.9	(113.8)	497.2	(27.5)
		2510.8		649.2		508.9	
05/02/87	17/02/87	1283.2		259.4	99.5		
		1307.6	1361.3	310.2	250.7	110.7	106.4
		1399.4	(80.0)	248.6	(51.6)	103.3	(6.0)
		1455,0		184.6		112.1	
19/05/87	25/05/87	925.6		155.6		70.2	
		946.8	912.4	250.4	234.0	54.8	68.0
		847.8	(44.0)	239.2	(56.9)	90.0	(16.2)
		929.2		291.2		56.8	
Mean			3275.3		788.4		635.0
Standard deviation			2196.2		500.5		474.7

Table 2. Vertical organic carbon and nitrogen flux values for the two years survey in Trémies cave (mg m^{-2} d^{-1}). Sampling points are numbered TR 2, TR 3, TR 5. Mean and standard deviation of survey (n = 10) appear at the end of the table.

Start	End	Organic carbon			Organic nitrogen		
		TR 2	TR 3	TR 5	TR 2	TR 3	TR 5
28/06/85	08/07/85	102.72	35.20	29.00	11.58	4.22	2.67
12/09/85	24/09/85	122.96	42.80	22.64	10.18	3.65	2.14
24/09/85	15/10/85	61.98	44.83	41.10	13.69	4.99	5.79
15/10/85	13/11/85	176.06	37.14	52.40	13.89	3.16	3.95
29/11/85	08/01/86	43.36	5.00	3.96	6.08	0.84	0.62
04/03/86	01/04/86	136.35	28.50	19.39	9.40	1.70	0.91
06/06/86	09/06/86	160.52	20.32	18.36	16.54	2.86	1.80
30/09/86	07/10/86	150.56	32.52	23.20	13.38	5.45	2.85
05/02/87	17/02/87	72.21	10.80	6.72	9.31	0.98	0.66
19/05/87	25/05/87	49.12	11.24	4.68	8.46	2.04	0.45
Mean		107.58	26.84	22.15	11.25	2.99	2.19
Standard deviation		108.12	25.91	21.38	11.21	2.85	2.13

available industrial autoanalysers are poorly suited to sediments with low contents of organic matter.

Results

Sedimentation rate evolution over time and in space and the corresponding mean values over 2

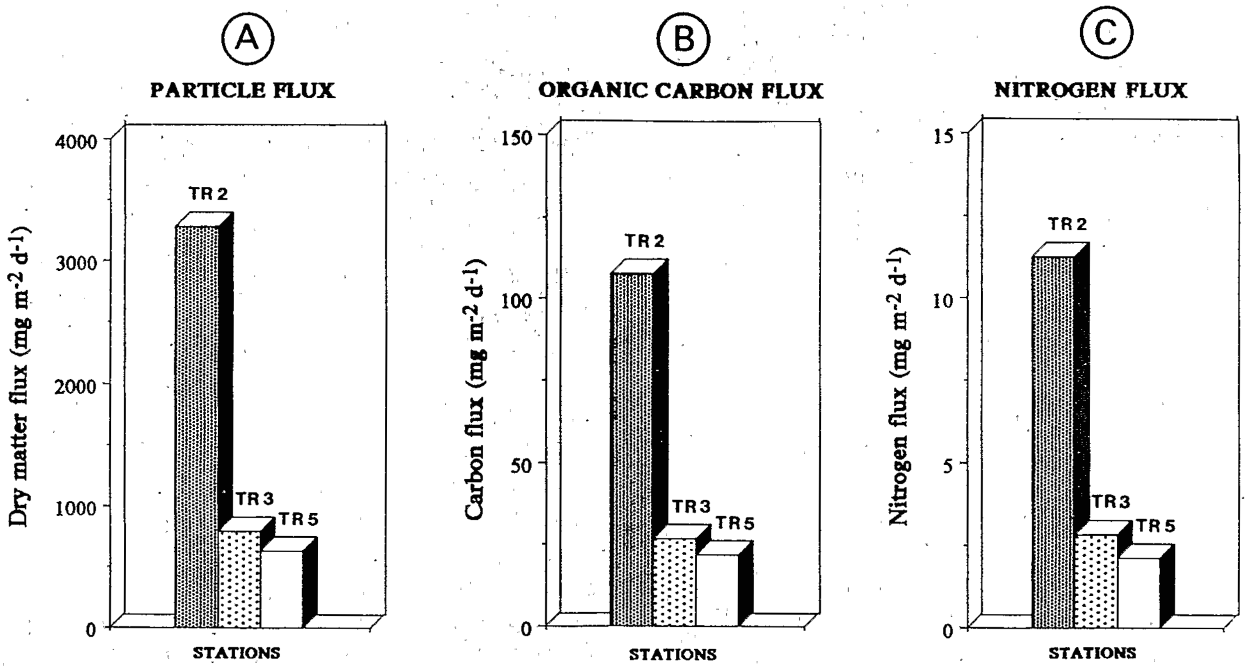

Fig. 3. Mean vertical fluxes (n = 10) over two years at sampling stations TR2, TR3 and TR5 in Trémies cave. Total particle flux (A), organic carbon flux (B), organic nitrogen flux (C).

Table 3. Comparison of the organic carbon (OC) and organic nitrogen (ON) content of suspended and sedimented particles. Suspended particle carbon and nitrogen content values are means of a two years survey (n = 27 for each sampling station) from Fichez (1989). Theoretical fluxes are calculated by multiplying total dry particulate flux with suspended particulate carbon or nitrogen content and are compared with calculated fluxes.

		TR2	TR3	TR5
Measured flux	(g m^{-2} y^{-1})	1195	288	232
Suspended particle OC	(% dry matter)	4.07	3.68	3.45
Sedimented particle ON	(% dry matter)	3.30	3.40	3.49
Suspended particle ON	(% dry matter)	0.46	0.37	0.32
Sedimented particle ON	(% dry matter)	0.34	0.38	0.34
OC theoretical flux	(g m^{-2} y^{-1})	48.6	10.6	8.0
OC measured flux	(g m^{-2} y^{-1})	39.3	9.8	8.1
ON theoretical flux	(g m^{-2} y^{-1})	5.5	1.1	0.7
ON measured flux	(g m^{-2} y^{-1})	4.1	1.1	0.8

years ($n = 10$) are listed in Table 1. At each sampling point spatial variation of fluxes is moderate; however temporal variation is high with strong variations in particulate input into the sediment. The mean values over two years was 3275 mg m^{-2} d^{-1} at station TR2 in the proximal part of the cave 25 m from the entrance. In the distal part, mean values strongly decreased to 788 mg m^{-2} d^{-1} at station TR3 35 m from the entrance and 635 mg m^{-2} d^{-1} at station TR5 55 m from the entrance.

Organic carbon and organic nitrogen sedimentation values (mean for 3 or 4 collectors) and corresponding mean values over 2 years ($n = 10$) confirmed the importance of temporal variation (Table 2). Comparison of mean values over 2 years (Fig. 3) showed that organic carbon flux was 108 mg m^{-2} d^{-1} at TR2 and decreased strongly to respectively 26 and 22 mg m^{-2} d^{-1} at TR3 and TR5. Organic nitrogen flux values had a similar evolution and decreased from 11 mg m^{-2} d^{-1} at TR2 to 3 mg m^{-2} d^{-1} at TR3 and 2 mg m^{-2} d^{-1} at TR5.

Mean decrease remained constant for each parameter (particles, OC, ON). Flux at TR3 represented 25% of flux at TR2 and flux at TR5 represented 20% of flux at TR2. This constancy between different component fluxes demonstrates a stability in particulate material composition. Organic carbon content ranges from 3.3% to 3.5% of dry particulate matter with an average C/N values close to 10. Organic carbon, measured using ignition loss technic, accounted for 13% to 24% of total dry matter.

Discussion

The results demonstrate the general decrease in vertical particulate matter flux from the entrance to the inner dark parts of the cave. Similarity in settling particle and organic matter amounts at TR3 and TR5 attests homogeneous environment conditions in the dark area. Settling particles exhibit low organic matter contents that may be mainly related to the continental origin of the coastal particulate matter entering the cave.

Sediment traps placed 30 cm over the sediment may be affected by resuspension but, due to its size, the whole cave system is certainly affected too. On the other hand degradative processes occur on organic material in unpoisoned traps. Both phenomena are responsible for a decrease in the organic content of trapped particles, thus their importance could be estimated by the difference between the suspended and the sedimented particle organic matter composition (Table 3). Few differences were observed in the dark parts of the cave (TR3 and TR5) indicating insignificant resuspension and degradative processes. It further demonstrates that the suspended organic matter is resistant to decomposition processes. In contrast, at TR2, sedimented particles showed lower organic carbon and nitrogen content than suspended particles and the measured flow is less than the theoretical flow. This indicates the influence of both resuspension and degradation, but these processes cannot be separated in this study.

There is no apparent seasonal cycle in vertical flows, because of the irregular sampling and collecting times and the variability of vertical fluxes. Temporal variability can be explained by temporal variations in both suspended matter and hydrodynamic conditions. The scale of water exchanges between the inner water mass and the open sea directly influences the amount of suspended matter reaching the water sediment interface. High vertical fluxes at TR2 show the importance of water exchange between the productive open sea and the anterior part of the cave. This area is characterized by a dense hard substrate community mainly composed of active filter feeders; passive filter feeders (Gorgonians) are present only near the entrance (Harmelin *et al.*, 1985). The hard substrata biomass is about 250 g m^{-2} and soft bottom community biomass is about 3.4 g m^{-2} 22% of which are meiofauna and 78% are macrofauna (>250 μg) (Fichez, 1989). In the dark area (TR3 and TR5) considerably lower vertical fluxes were observed with very similar sedimentation values at both sampling points. Benthic communities are known to be poor in dark areas (Monteiro-Marques, 1981; Harmelin *et al.*, 1985; Gili *et al.*, 1986) the cover being always much less than 100% of rocky substrata. Recorded biomass for sessile fauna was 36 g m^{-2} at TR3 and 25 g m^{-2} at TR5 and sediment fauna was 0.3 g m^{-2} at each sampling point. Repartition ratio between meiofauna and macrofauna was the same as in TR2 (Fichez, 1989).

Along with these results a strong decrease in suspended chloropigment amount was observed in water between TR2 and TR3, with similar concentrations in TR3 and TR5 (Fichez, 1990). On the other hand, the sediments from the dark area (TR3 and TR5) were characterized by the absence of any redox potential discontinuity layer. This suggests a very low flow of organic material to the sediment, implying low degradative processes and thus low oxygen consumption (Fichez, 1989).

The cave studied can therefore be separated into two subunits with different hydrodynamic features. The proximal part (semi-dark area) has a rich benthic population related to efficient water exchange and high organic inputs. Nevertheless, a general hydrodynamic slowdown can already be seen in the disappearance of passive filter feeders a few meters away from the entrance. In the distal part (dark area) the overall decrease in benthic population density and biomass can be related to an oligotrophic water mass with low organic inputs. Cave topography (the dark area being separated from the semi dark area by a 9 m high step) made such a specific water mass system possible. This structure allowed for heat stratification and isolation of a slowed hydrodynamic system with a long renewal time (several days). This general feature of water mass confinement may be broken by high hydrodynamic activity or by heat counterbalancing currents (Fichez, 1989). In fact, storms, mainly occurring during winter, may affect the whole cave and cause a rapid renewal of the inner waters. On the other hand, spring warming of the surface layer outside the cave results in a density differences between open sea and inside trapped waters. Because of the topography and because water salinity always stays close to 38‰, colder inner waters will be replaced by warmer waters. This second feature, occurring during the spring bloom period when particulate organic matter reaches high values, increases water exchange and influences benthic metabolism (Fichez, 1989).

The general oligotrophic conditions suggest that dark cave heterotrophs are drastically food-limited. On the basis of this feature, submarine cave ecosystems can be compared with ecosystems in the aphotic deep sea. Some values of organic carbon and nitrogen fluxes in the deep ocean, near the benthic boundary, come close to those obtained in the present study, particularly at depths ranging from 1000 to 2000 m all over the world (Hinga *et al.*, 1979; Knauer *et al.*, 1979; Lorenzen *et al.*, 1983; Karl & Knauer, 1984; Tsunogai & Noriki, 1987) or in the north-western Mediterranean (Cauwet, 1985; Buscail *et al.*, 1987). Of course, environmental conditions are extremely diverse in the deep sea and divergent results can also be found in numerous works. Comparing different oceanic regions is difficult and no general vertical flux value may correspond with a precise depth in the whole ocean. On the other hand large differences, e.g. of temperature, pressure, residence time of particles or transport processes characterize deep sea and littoral caves. Accordingly, these two ecosystems should be compared with great caution in view of a simple parallel between two oligotrophic systems having some comparable features.

However, the decrease in vertical flux from the entrance to the dark terminal area in Trémies submarine cave indicates an input lowering. Trophic resource limitation has produced an oligotrophic ecosystem where degradative processes are extremely low. Submarine caves thus appear to be very interesting environments for trophic pathway studies. The energetic flow is clearly channelled from the entrance to the innermost part of the cave with a strong decrease in resources. This simplified oligotrophic ecosystem may constitute a good model for the general study of benthic trophic transfers and particularly for organic carbon fluxes.

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