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Suspended particulate organic matter in a Mediterranean submarine cave

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Abstract. Submarine caves display a paucity of benthic density and biomass that may be related to low trophic resources. Analysis of organic carbon, organic nitrogen, carbohydrate, protein and lipid content of suspended particulate matter was made during the period July 1985–July 1987 in a Mediterranean cave (Marseille, France) in order to determine any differences in the particulate organic matter composition along an horizontal transect. Particulate organic matter content clearly declined from the entrance of the cave to the dark inner area. This impoverishment could not be explained by a simple decrease in a few organic compounds, but appeared to be related to the combination of a decrease in both the amount and the composition of the suspended particles. Three progressive levels of impoverishment were identified towards the dark inner area of the cave: (i) decreasing amounts of seston; (ii) decreasing organic content of particles; (iii) increasing proportions of the geopolymeric (i.e., humic) components in the remaining organic matter, indicating increased degradation. The cave appeared to be sharply divided into two distinct sections – a twilight outer section whose waters contained slightly lower amounts of particulate organic matter than the open sea, and a dark inner section, 8 to 10 m higher, separated from the outer section by a steep rise and with waters of low organic matter content. The water in the twilight section appeared to be in thermal equilibrium with the open sea, and that in the dark inner section displayed thermal stratification. These differences indicated the presence of two distinct water bodies with contrasting average residence times, estimated as 1 d in the outer twilight section and 8 d in the dark inner section. The joint action of sedimentation and degradation resulted in an abrupt depletion of particulate organic matter in the dark inner section accompanied by a decrease in the benthic fauna. The decline in benthic heterotroph populations is probably related to the abrupt transition to oligotrophic conditions.

Introduction

Biological communities in submarine caves of the Mediterranean Sea are characterized by a general decrease in the benthic population from the open ocean to the dark inner parts. These inner parts have been separated on the basis of light level into twilight and dark communities (Pérès 1982). Illumination levels (visible spectrum) recorded in the *Corallium rubrum* facies located in the twilight section range between 0.02 and 0.03 E m^{-2} d^{-1}, corresponding to 0.04 to 0.06% of surface values (Marinopoulos 1988). Light is well below 0.01% of surface values in dark inner caves in temperate (Weinberg 1975) and tropical (Logan 1981) areas. The twilight community is rich in animal species, which cover the whole available hard substratum, whereas the dark inner community displays a striking decrease in biomass (Gili et al. 1986, Fichez 1989), and sessile animals may cover less than 10 to 20% of the available substratum (Pérès 1982, Harmelin et al. 1985). Similar decreases in abundance and biomass have been observed in communities of soft-bottom caves (Monteiro-Marques 1981, Fichez 1989). This type of faunal zonation has also been reported for submarine caves in tropical areas (Garret 1969, Hartman and Goreau 1970, Vasseur 1974, Logan 1981). Submarine caves are considered to represent habitats intermediate between those of the open-sea and anchialine caves, the latter consisting of very long underground systems invaded by ultra-oligotrophic sea water and mostly devoid of any sessile fauna (Sket 1981, Iliffe et al. 1984).

The decreases in population density and biomass towards the dark inner parts of caves are generally supposed to be related to limiting trophic resources (Harmelin et al. 1985). This hypothesis has been confirmed for suspended chloropigments (Fichez 1990 a) and sedimentation rates (Fichez 1990 b); the present study investigated changes in the composition of suspended particulate organic matter across a transect from the entrance to the dark inner section of a Mediterranean submarine cave over a 2 yr period.

The biological importance of suspended particulate matter (SPM) in heterotroph food webs is well established (Mayzaud et al. 1989), and determination of its biochemical composition (organic carbon and nitrogen, carbohydrates, proteins and lipids) is necessary to enable quantitative and qualitative assessments of the nutritional value of such particles (Chervin et al. 1981, Mayzaud et al. 1984, 1989, Khripounoff et al. 1985, Poulet et al. 1986, Claustre et al. 1989). Nevertheless, there is a lack of such information (Cauwet 1978, 1981). New techniques (e.g. gas and high-performance liquid chromatography associated with mass spectrometry) for the detailed analysis of organic compounds have recently considerably improved our knowledge of their precise composition; paradoxically, few studies on the global composition of organic matter are available. New information on the biochemical composition of naturally occurring particles is necessary for a better understanding of the biological influence of SPM (Poulet et al. 1986), and could provide an index for estimating the trophic potential of suspended food webs and the nutritional value of detritus (Heral et al. 1983, Etcheber et al. 1985).

Dark single-entrance caves (Riedl 1966), devoid of significant autochthonous production because of the absence of light, constitute ecosystems exclusively dependent on supplies of organic matter from the open sea (except for insignificant chemiotrophic processes indicated by black iron-manganese oxide deposits on the rocky substrates). Furthermore, the geomorphological structure of the caves largely influences the nature of the inputs of trophic resources from the open sea to the inner most parts of the caves. Sequentially decreasing water exchange towards the inner cave could effect a concomitant decrease in the amount of particulate matter (Harmelin et al. 1985). An analysis of the composition and fate of SPM could thus provide information on the degree of isolation of the inner-cave waters and on the effect of a consequent decrease in trophic resources on the benthic populations.

Site description

The Trémies cave is located on a limestone shore, 20 km east of Marseille (France). It is 60 m long; at the entrance the floor is at 15 m depth and covered with fallen rocks which form a 3 m high barrier partially separating the cave from the open sea (Fig. 1). Inside the cave, two sections are separated topographically by an abrupt 8 to 10 m rocky ramp, located 30 m from the entrance. The first outer section is 6600 m^3 wide, with its floor at 17 m depth; the second inner section is smaller (2800 m^3), its floor lying between 8 and 5 m depth. The biological communities in these two sections closely resemble the biological community sub-assemblies described by Pérès (1982): the outer section of the cave is occupied by a "semi-dark" (twilight) community, the inner part by a "dark" community. In the Trémies cave, five sampling sections were selected – TR1 (entrance), TR2 (twilight section) and TR3, TR4, TR5 (dark section).

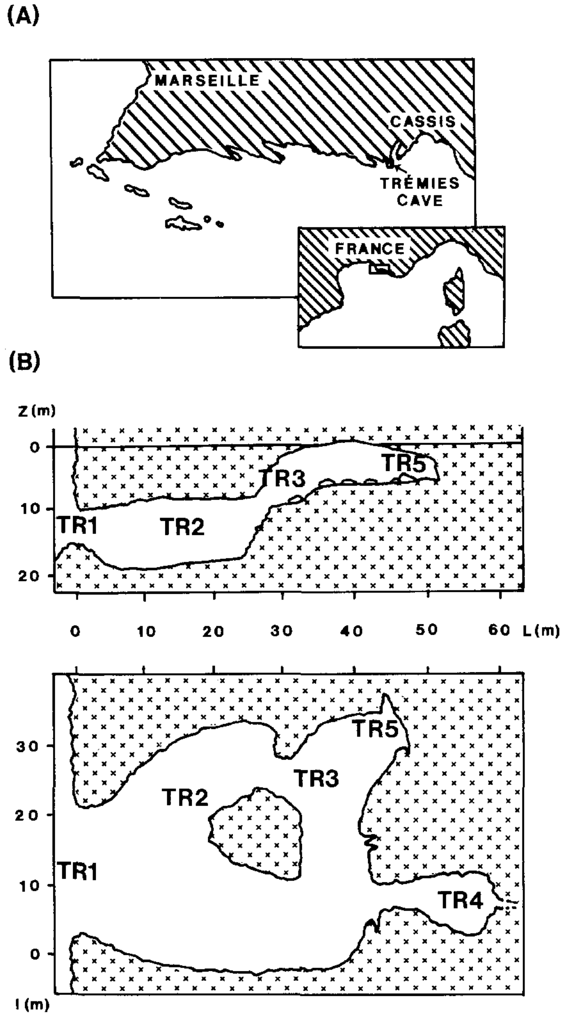

Fig. 1. Location of Trémies cave near Marseille, France (A), and sketches (B) of cave in longitudinal (top sketch) and horizontal (bottom sketch) cross-sections, showing sampling stations at entrance (TR1), in twilight area (TR2) and in dark inner area (TR3, TR4, TR5). Ordinates show depth (z), abscissas length (L)

Biomass values recorded in this cave (Fichez 1989) revealed a clear decrease in the faunal benthic population from the entrance to the dark innermost part of the cave. The values (ash-free dry wt) recorded for the hard substrate of the cave walls was 360 g m^{-2} at the entrance (TR1), decreasing slightly to 250 g m^{-2} in the twilight section (TR2) and strongly to 26 g m^{-2} in the innermost section (TR4 and TR5). The benthic fauna of the sediment displayed a similar pattern: 3.4 g m^{-2} at TR2, decreasing steeply to homogeneous values of ~0.3 g m^{-2} in the dark innermost section, with the macrofauna (>250 μm) accounting for 80% and the meiofauna (>40 μm) for 20% of the total weight in all sections.

Materials and methods

Using 3- to 5-litre PVC bottles, water samples were collected monthly by SCUBA at each sampling point from July 1985 to July 1987 for seston, organic carbon and nitrogen, and from July 1986 to July 1987 for carbohydrate, protein and lipid. These opaque sampling bottles were fitted with screw stoppers to avoid light stimulus and bubble formation which can modify the composition of the organic matter content of the particles during transport (Riley et al. 1965, Cauwet 1978). Each water sample was transferred from the sampling bottle to the measuring cylinder immediately before filtration.

Suspended matter was retained on precombusted (500 C°) and preweighed Whatman GF/C glass-fibre filters. The filters were weighed on a Mettler balance to a precision of 10^{-5} g, and particle concentrations were calculated as a function of the volume filtered (Krey 1964). Dried loaded filters and blank filters that had been subjected to identical treatment were stored deep-frozen prior to analysis.

Particulate organic carbon (POC) and nitrogen (PON) were analysed using a Perkin-Elmer Model 240 CHN-analyser. The filters were first treated with HCl vapour for 2 h and then dried for 12 h at 50 °C. The HCl-treatment removed carbonates, enabling remaining organic carbon and nitrogen to be measured directly (Dame et al. 1986). Carbohydrates (CH), proteins (PR) and lipids (LI) were determined by colorimetric reactions measured on a spectrophotometer. Carbohydrates were titrated following Dubois et al. (1956), and expressed as glucose equivalents. Proteins were titrated following Lowry et al. (1951), and expressed as albumin equivalents. Lipids were extracted by chloroform, titrated following Marsh and Weinstein (1966), and expressed as tripalmitic acid equivalents.

Techniques for organic compound analysis have been widely discussed. The method from Dubois et al. (1956) is that most widely used for carbohydrate titration (Chevolot et al. 1985); another method has been reported to be more precise (Johnson and Sieburth 1977), but is not usually used due to the length of time it requires (Dawson et al. 1983). Various methods (Krey 1951, Lowry et al. 1951, Bradford 1976) have proved efficient for titration of total protein, and the advantages of each have been discussed by Moal et al. (1985); the Lowry titration was chosen for its ease and sensitivity. Various techniques are also applicable for lipid analysis (Barnes and Blackstock 1973, Moal et al. 1985), the most effective for titration of total lipid being those of Amenta (1964) and Marsh and Weinstein (1966); the method of the latter authors was selected because of its sensitivity and ability to detect a large range of lipid species.

The organic carbon compounds were converted to energy using the energetic equivalents of biochemical compounds. Conversion factors were 11 kcal g^{-1} for carbon, 4.1 kcal g^{-1} for carbohydrates, 5.65 kcal g^{-1} for proteins and 9.45 kcal g^{-1} for lipids (Brody 1945, Salonen et al. 1976, Brett and Groves 1979, Henken et al. 1986, Horn et al. 1986). Caution must be exercised when using general energetic conversion factors, as they may vary widely for a single biochemical category (Lieth 1975, Craig et al. 1978, From and Rasmussen 1984). Such conversions should be considered as useful but rough approximations of the energetic content of organic matter.

Results

There were wide temporal variations in the concentrations of suspended particulate matter (Fig. 2A), but a regular decreasing trend was discernible from July 1985 (4200 to 2700 $\mu g\,l^{-1}$) to December 1986 (500 to

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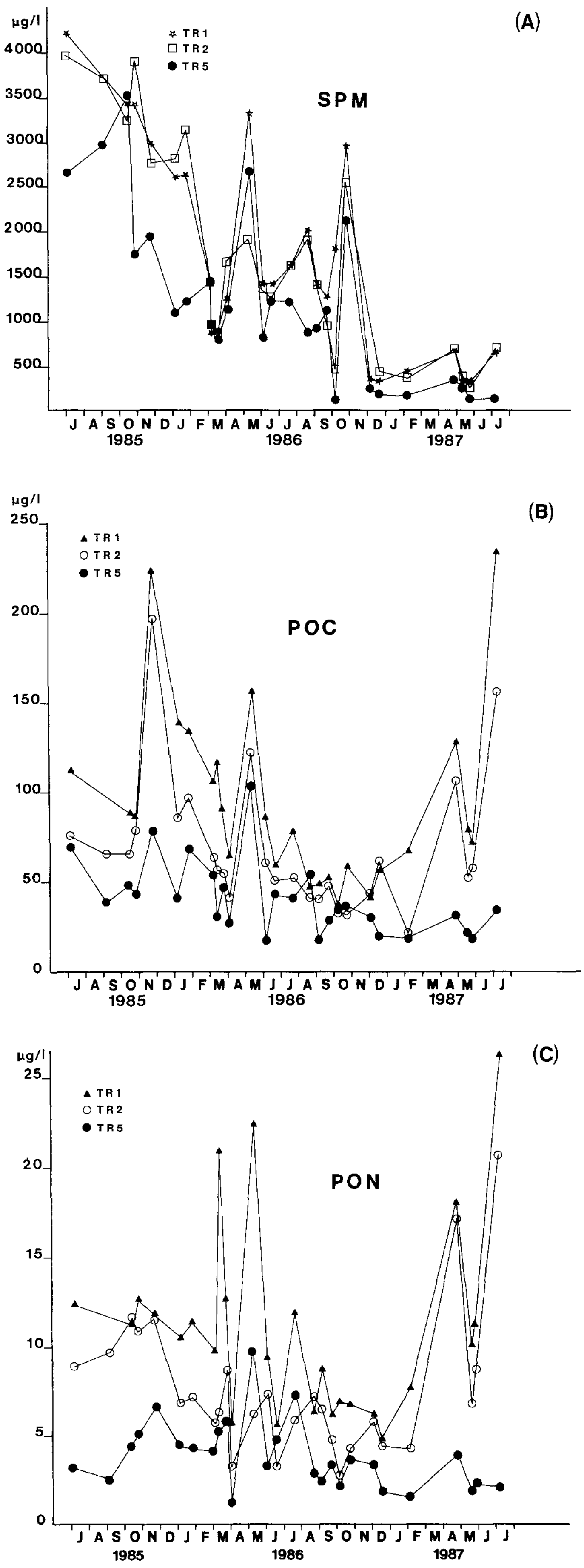

Fig. 2. Temporal variations in concentrations of suspended particulate matter (A), particulate organic carbon (B), and particulate organic nitrogen (C) during 1985–1987 at entrance (TR1), in twilight section (TR2), and in dark inner section (TR5) of cave. Variations were similar at all three dark inner-section stations (TR3, TR4, TR5), so data for TR5 only are presented, to preserve clarity. (No. of sampling occasions = 27)

Table 1. Mean (±SD) concentrations ($\mu g\ l^{-1}$) of suspended particulate matter (SPM), particulate organic carbon (POC) and nitrogen (PON), and C:N ratio (POC:PON) during 1985–1987 in five stations of Trémies cave: TR1, entrance; TR2, twilight section; TR3, TR4, TR5, dark section. ($n=27$ determinations in each case)

Particle constituent	TR1		TR2		TR3		TR4		TR5	
	Mean	(SD)	Mean	(SD)	Mean	(SD)	Mean	(SD)	Mean	(SD)
SPM	1 757	(1 191)	1 665	(1 186)	1 379	(1 021)	1 228	(866)	1 183	(945)
POC	94.51	(50.89)	69.14	(38.82)	50.80	(30.86)	42.32	(16.93)	40.83	(20.55)
PON	11.08	(5.48)	7.63	(4.09)	5.04	(2.67)	4.08	(1.86)	3.82	(1.97)
C:N	8.53		9.06		10.08		10.37		10.69	

Table 2. Mean (±SD) salinity and temperature recorded, and mean (±SD) concentrations ($\mu g\ l^{-1}$) of SPM, POC, PON, carbohydrate (CH), protein (PR) and lipid (LI) during 1986–1987. Further details as in legend to Table 1 ($n=13$)

	TR1		TR2		TR3		TR4		TR5	
	Mean	(SD)	Mean	(SD)	Mean	(SD)	Mean	(SD)	Mean	(SD)
Salinity (‰)	38.08	(0.13)	38.05	(0.30	37.99	(0.26)	38.09	(0.19)	37.87	(0.34)
T (°C)	15.58	(3.51)	15.58	(3.49)	16.92	(3.80)	16.89	(3.81)	17.17	(3.90)
(SPM)	1 081	(824)	925	(722)	729	(716)	736	(671)	600	(606)
(POC)	77.04	(52.89)	57.63	(35.96)	39.53	(20.06)	35.01	(8.00)	29.84	(10.56)
(PON)	10.10	(6.05)	7.63	(5.32)	3.72	(1.51)	3.20	(1.18)	2.94	(1.53)
(CH)	29.96	(17.91)	15.99	(8.93)	12.91	(10.87)	11.49	(8.30)	7.09	(4.43)
(PR)	37.18	(22.95)	29.04	(16.54)	17.63	(6.70)	16.17	(8.50)	13.70	(7.06)
(LI)	39.11	(32.93)	26.87	(18.69)	16.60	(7.95)	14.34	(8.75)	11.85	(6.98)

200 $\mu g\ l^{-1}$), and values remained below 1 000 $\mu g\ l^{-1}$ over the following 7 mo. Despite strong temporal variability, seston concentrations were always lower in the dark inner stations (TR3, TR4, TR5) than at the entrance (TR1) and in the twilight (TR2) stations, as indicated by the mean values over the two years (Table 1), which decreased from the entrance (1 757 $\mu g\ l^{-1}$) to the dark inner sections (1 228 $\mu g\ l^{-1}$ at TR4 and 1 183 $\mu g\ l^{-1}$ at TR5).

Organic carbon (Fig. 2 B) did not show any clear temporal tendency such as that seen for the seston; marked maximum peaks appeared in November 1985, March and May 1986 and April and July 1987. TR2 contained somewhat less POC than TR1, but the temporal pattern was quite similar. TR5 contained less POC than the other stations, and its temporal pattern differed slightly from that of TR1 and TR2. The mean values (Table 1) revealed a steady decrease in POC from TR1 (94.51 $\mu g\ l^{-1}$) to TR3 (50.80 $\mu g\ l^{-1}$). Concentrations in both dark inner stations were homogeneous (42.32 $\mu g\ l^{-1}$ at TR4, 40.83 $\mu g\ l^{-1}$ at TR5).

Organic nitrogen (Fig. 2 C) displayed no long-term trend. There were large peaks in March and May 1986 and in April and July 1987. A decrease was apparent along the transect TR1 to TR5; the mean values over the two years clearly declined from TR1 (11.1 $\mu g\ l^{-1}$) through to TR4/TR5 (4.0 $\mu g\ l^{-1}$) (Table 1). The C:N ratio increased from 8.5 at TR1 to values above 10 in the dark inner cave (TR3, TR4, TR5); TR2 displayed an intermediate mean value of 9.

During the year in which carbohydrate concentrations were measured, they exhibited low values from the end of July until February, peaking in spring and at the beginning of summer (Fig. 3 A). Values decreased on a transect from TR1 to TR5, except on 19 February 1987, when concentrations at the outermost stations (TR1 and TR2) suddenly dropped at the same time as concentrations in the dark inner stations (TR3–TR5) reached their maximum. The average concentrations over one year (Table 2) decreased strongly from TR1 to TR2 and slightly from TR2 to TR3. Carbohydrate concentrations were similar at TR4 and TR3 but lower at TR5.

Protein concentrations over the same period were initially high in July; they decreased markedly in August, remained low until February and then steadily increased until July (Fig. 3 B). Maximum concentrations were recorded in July for TR1 and TR2 and in May for TR3, TR4 and TR5. The average concentrations over the year (Table 2) revealed a strong and steady decrease from TR1 to TR3, but there was little difference between stations TR3, TR4, TR5 in the inner dark area.

Lipid concentrations decreased from July to August in all stations and remained low until December, when a small increase occurred (Fig. 3 C). There were marked increases from February to April–May, when maximum values were recorded; concentrations then decreased or remained at the same level until the beginning of July. Average annual concentrations displayed a strong and steady decrease from TR1 to TR3, and further decreases were slight in the dark area (TR4, TR5) (Table 2).

SPM, POC and PON concentrations during the CH, PR and LI sampling period (July 1986 to July 1987) were smaller than the corresponding average amounts for the overall 1985–1987 recording period (cf. Tables 1 and 2). Concurrent with an increase in the C:N ratios, the organic matter:SPM ratios and the carbon-compounds:POC ratios clearly decreased from the entrance towards the dark inner section (Table 3).

The energetic contents of carbon and its biochemical compounds are shown in Table 4. If it is assumed that the sum of energy from carbohydrate, protein and lipid compounds represents the biopolymeric fraction of the organic carbon (i.e., simple molecules), then the remaining amount of energy represents the geopolymeric fraction (i.e., complex molecules, heteropolycondensates or humic substances) (Cauwet 1981, Saliot et al. 1984, Khripounoff et al. 1985). Table 4 shows that the proportional importance of the geopolymers increased from 17% at TR1 to 34% at TR5. Proteins were quite stable, accounting for 23 to 26% of the total energetic content of the organic matter. By contrast, carbohydrates decreased from 14% at TR1 to 9% at TR5 and lipids from 44% at TR1 to 34% at TR5.

Average salinities (Table 2) remained at ~38.0 ± 0.1‰ at every station. Average temperatures were similar at TR1 and TR2 but higher in the dark inner section, with a maximum difference of 1.59 C° between TR5 and the open ocean.

Table 3. Ratios (conc.: conc.) of constituents of particulate organic matter in Trémies cave–organic constituent: SPM (%), C:N (POC:PON), and organic compounds:COP. Based on data in Table 2; further details as in Tables 1 and 2

Ratios	TR1	TR2	TR3	TR4	TR5
POC:SPM (%)	7.13	6.23	5.43	4.76	4.97
PON:SPM (%)	0.93	0.82	0.51	0.43	0.49
CH:SPM (%)	2.77	1.73	1.77	1.56	1.18
PR:SPM (%)	3.44	3.14	2.42	2.20	2.28
LI:SPM (%)	3.62	2.90	2.28	1.95	1.98
C:N	7.63	7.55	10.63	10.94	10.15
CH:POC	0.39	0.28	0.33	0.33	0.24
PR:POC	0.48	0.50	0.45	0.46	0.46
LI:POC	0.51	0.47	0.42	0.41	0.40

Table 4. Energetic composition of particulate organic matter (converted from organic compound concentrations in Table 2) for POC, CH, PR and LI in Trémies cave. Biopolymeric and geopolymeric fractions expressed as energetic units (mcal l^{-1}) and as percentage of total amount of POC energy (% POC) (see "Materials and methods" for energetic conversion factors used)

Particle constituent	TR1	TR2	TR3	TR4	TR5
POC (mcal l^{-1})	847	634	435	385	328
CH (mcal l^{-1})	123	66	53	47	29
PR (mcal l^{-1})	210	164	100	91	77
LI (mcal l^{-1})	370	254	157	136	112
Biopolymeric fraction = (CH + PR + LI)					
(mcal l^{-1})	703	484	310	274	218
(% POC)	(83)	(76)	(71)	(71)	(66)
Geopolymeric fraction = (POC) − (CH + PR + LI)					
(mcal l^{-1})	144	150	125	111	110
(% POC)	(17)	(24)	(24)	(29)	(34)

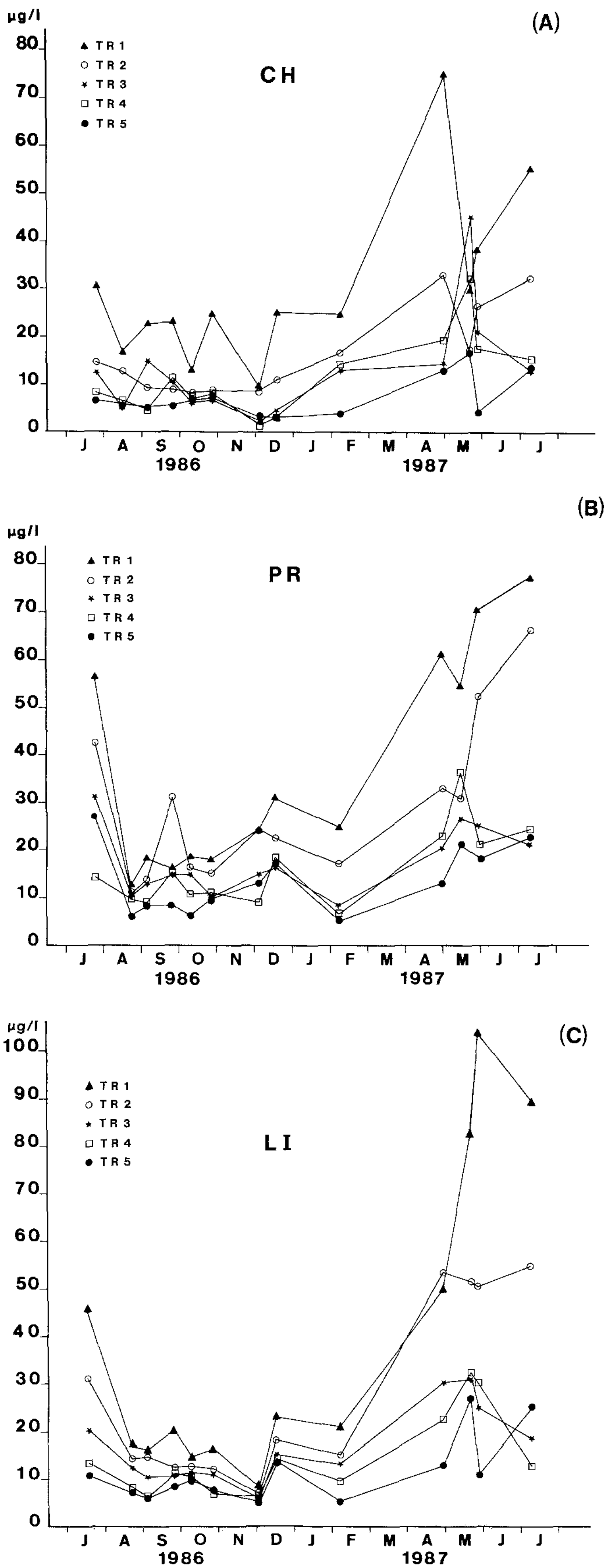

Fig. 3. Temporal variations in particulate carbohydrates (A), particulate proteins (B), and particulate lipids (C) during 1986–1987 at entrance (TR1), in twilight section (TR2), and in dark section (TR3, TR4, TR5) of cave. (No. of sampling occasions = 13)

Discussion and conclusions

The long-term decrease in seston at all stations from 1985 to 1987 appears to have resulted from the large decrease in the inorganic fraction of the SPM, since neither organic carbon nor nitrogen followed this trend. The wide variation in the inorganic fraction content may be related to the irregular inputs of inorganic particles from the continent to coastal waters. This is supported by the climatic conditions during the study period, with heavier rainfall during 1985 and 1986 than during 1987 (rainfall periods result in high inputs of inorganic particles due to increased erosion and transport of continental material to the sea). The organic carbon and nitrogen concentrations were much less affected by variations in continental inputs of particles, indicating the organic matter to be mainly marine in origin.

The organic matter concentrations in Trémies cave were low throughout most of the year, with maximum concentrations at the end of spring and the beginning of summer. This general trend approximately corresponds to the annual cycle of chlorophyll *a* in the cave (Fichez 1990a).

All components of the particulate matter decreased distinctly from the entrance to the dark inner part of the cave. This decrease was reflected by decreased SPM content along the transect from the entrance to the dark inner sections of the cave, and was also related to changes in the composition of the particulate organic matter. Three progressive levels of particulate matter impoverishment were discernible: (1) SPM concentrations decreased from the entrance to the dark inner sections of the cave; sedimentation results in a loss of >30% of the suspended particulate matter in the water, directly through deposition of suspended particles, but also by particle compaction by filter-feeders (as faeces, pseudofaeces). (2) The organic matter content of the particles decreased from the cave entrance to the innermost stations; this was demonstrated by the decreasing ratios of organic compounds : SPM (Table 3), which revealed that particles inside the cave contained proportionately less organic and more inorganic material than particles fresh from the open sea. (3) The composition of the organic matter changed; complex geopolymers became increasingly important, as biopolymers proportionately decreased from the entrance to the dark inner stations (Table 4). The biopolymeric fraction is assumed to represent the labile and easily degradable fraction of organic matter, and the heavy heteropolycondensates, which form the geopolymeric fraction, are more difficult to degrade (Saliot et al. 1984, Khripounoff et al. 1985).

Estimations of bio- and geopolymeric fractions based on energetic equivalents must be viewed with caution; biases produced by analytical procedure or conversion factors are possible. CH, PR and LI analyses involve acid treatment of samples that partially hydrolyses complexed organic compounds, and complex geopolymers may comprise several different functional groups that react with different reagents, thus increasing the apparent amount of simple compounds (Cauwet 1981). Furthermore, analytical identification of bio- and geopolymers (on the basis of molecular weights, fluorimetric responses, reaction to reagents, extraction sequences, or non-reaction to analytical protocols) is arbitrary; it does not take into account the natural continuity of the condensation spectrum of organic matter (from free molecules to humic acids), and the resulting categories of compounds are not clearly related to the metabolism (Etcheber et al. 1985). At present it is not possible to determine, in a simple way, that fraction of the particulate organic matter which supports heterotrophic requirements.

Nevertheless, the results achieved using energetic equivalents demonstrate increasing degradation of particulate matter in the dark inner section of the cave, as reflected by increasing C:N ratios. Lipid contents decreased markedly towards the interior of the cave; this high-energy compound provides a large amount of the energetic requirements of heterotrophs feeding on particulate matter. Carbohydrate and protein contents also decreased from the cave entrance to the dark inner stations. Protein was the only organic compound to display a constant ratio in relation to total organic carbon concentrations throughout the length of the cave.

Compared to both carbohydrate and protein, the lipid concentrations were very high; the reason for this is not clear. Other studies of the composition of particulate matter inside and outside other caves situated on this coast, using the same techniques, have revealed low lipid concentrations (PR:CH:LI around 3:2:1) (Fichez 1989), demonstrating that the extraction and titration techniques used cannot be responsible for the anomaly. The high values may be associated with the nearby (1 km) presence of a leisure port, with concurrent boat and human wastes.

In the dark inner section of the cave, variation in organic compound amounts was low, perhaps because of the undegradability of the organic matter and the homogeneous hydrologic conditions in this section. The thermal data show the dark inner area to be generally 1 to 2 C° warmer than the entrance (Station TR1), and temperature was proved to be the main varying factor affecting water density (salinities were always close to 38‰: Table 2). The thermal stratification revealed the water of the inner section of the cave (Stations TR3, TR4, TR5) to be isolated. In the twilight section (TR2), despite an obvious decline in organic matter, the waters are of the same temperature as the open sea. Both the thermal structure and organic composition of the seston demonstrate that the topographic rise in the floor of Trémies cave divides the water body into two sections (twilight and dark), exhibiting different characteristics (Fichez 1990a). In a previous study (Fichez 1989), the water-residence time in the two sections was estimated using two approaches – the relationship between vertical flux and total SPM, and the assessment of the degradation time of particles determined by the changes in chloropigment concentrations inside the cave. The average residence time was estimated to be 1 d in the twilight section and 8 d in the dark inner section. The water mass in the twilight section is very similar to the outside, productive, waters and is rapidly renewed; this area supports a dense benthic population of hard substrate filter-feeders which are partly responsible for the decreased organic-matter content of the suspended detritus. Conversely, little of the water entering the cave reaches the dark, inner, upper section, resulting in a section of warmed water, depleted in organic matter, with a long average residence time (ca. 8 d). The remaining organic matter is highly degraded and the particles provide insufficient energy to support a dense benthic fauna. This general stratification pattern is disturbed during spring by the warming of the open sea, resulting in rapid renewal of the waters in the innermost parts of the cave and concomitant fresh inputs of organic matter (Fichez 1989, 1990 b), which explain the maximum concentrations of organic compounds recorded in the dark innermost section in May. These spring incursions occur during the period of phytoplankton bloom, and the inputs of fresh organic matter influence the annual cycle of the benthic fauna.

The benthic zonation correlates well with the decrease in the particulate organic matter associated with isolation of the inner water-body. Although particulate composition and quantity are the main factors affecting the benthic populations in Trémies cave, other fine-scale processes, such as wall effects (thin layers of water deplete in organic matter in contact with hard substrata communities: Harmelin et al. 1985, Gili et al. 1986), may also be partly responsible for the benthic decrease in the inner cave.

Depletion of organic matter would seem to provide some explanation for the decrease in benthic fauna in dark caves. Dark inner areas of caves constitute aphotic-oligotrophic enclosures in the coastal system. Caves could, then, be considered a natural compact transect from productive photic systems to oligotrophic aphotic systems characterized by limiting trophic conditions.

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