Benthic oxygen uptake and carbon cycling under aphotic and resource-limiting conditions in a submarine cave

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Abstract. To establish relationships between organic input to the benthos and decreases in benthic population biomass and density, benthic oxygen uptake was measured in an oligotrophic submarine cave in the northwestern Mediterranean Sea (Marseille, France), on seven separate occasions in 1987, using an in situ bell-jar respirometer. Oxygen uptake was measured in both the outer twilight section and the dark inner section of the cave during an annual survey (seven recording periods from February 1987 to November 1988). The mean annual benthic oxygen uptake was 80.9 litres O_2 m^{-2} yr^{-1} for the twilight outer section and 15.5 litres O_2 m^{-2} yr^{-1} for the dark inner section. The results are discussed and the biogeochemical budget for particulate organic carbon at the sediment-water interface calculated. Respiration rates (expressed as carbon equivalents), together with previously published data on vertical fluxes and burial of organic carbon, revealed that anaerobic pathways accounted for 14% and aerobic pathways for 86% of the total benthic metabolism in the outer part of the cave. In the inner section of the cave, degradation of organic carbon occurred only through aerobic degradation, indicating a strongly carbon-limited ecosystem. The low respiration rates recorded in the dark section were similar to values recorded for some oligotrophic deep-sea environments (1 000 to 2 000 m). Such budgets are essential preliminary steps in order to accurately model benthic metabolic pathways. The determination of annual fluxes linked to the acquisition of long-term data will yield better knowledge of the recycling processes at the water-sediment interface.

Introduction

Single-entrance cave systems are commonly characterized by an outer twilight section supporting a high benthic population, and an inner dark section with low benthic biomass and density (Pérès 1982, Harmelin et al. 1985, Gili et al. 1986). The decreasing population biomass and density towards the dark inner parts of such caves have been related to limited trophic resources (Harmelin et al. 1985, Fichez 1989). Topographical surveys of most caves have revealed the inner sections to be generally higher than the entrance. Under these conditions, temperature stratification occurs as a result of decreased hydrodynamic exchange, and oligotrophic conditions develop. Suspended chloropigments (Fichez 1990a), suspended particulate matter and the organic carbon, organic nitrogen, carbohydrate, protein, and lipid content of particles (Fichez 1991) all clearly decrease from the entrance to the dark inner section of the cave. Strong decreases in vertical inputs of particulate material to the sediment have been recorded (Fichez 1990b). Well-oxygenated conditions were observed down to 15 cm in the top sediment layer (Fichez 1990c), suggesting low degradation rates of organic material.

In order to determine the relationships between decreasing organic input to the benthos and decreasing benthic populations, benthic oxygen uptake was studied in a submarine cave. Oxygen uptake was measured to quantify the aerobic benthic metabolism under increasingly oligotrophic conditions. The oxygen uptake was then compared with previous data on both the vertical flux and burial rates of particulate organic carbon (POC) to yield a biogeochemical budget for POC in the top sediment layer (15 cm). However, anaerobic metabolism, which cannot be measured by means of oxygen uptake, may account for a large part of the total metabolism (Famme et al. 1981, Crisp 1984, Packard et al. 1984, Kepkay and Andersen 1985).

Various methods have been used to measure the metabolism of benthic communities (Pamatmat 1977, 1982, 1983, Christensen and Packard 1979, Packard 1979, Bowman and Delfino 1980, Smith and Hinga 1983), but in situ measurement of oxygen production or consumption is the most frequently used technique in both littoral (Nowicki and Nixon 1985, Griffith et al. 1987) and deep-sea (Pamatmat 1973, Smith 1978, 1987) environments. However, while oxygen uptake by a benthic community depends on temperature (Pamatmat

1977), current velocity and turbulence in the overlying water (Boynton et al. 1981), and bioturbation (Aller 1980, Hylleberg and Henriksen 1980), the flux of organic matter reaching the benthic boundary layer is the main factor regulating benthic community structure, biomass, and metabolism (Graf et al. 1982, 1983, Jørgensen 1983, Smetacek 1984, Wassmann 1984, Smith 1987, Grebmeier and McRoy 1989).

Metabolic activity of marine benthic communities is measured either by shipboard incubation of bottom cores or by in situ measurements using bell-jar respirometers. Both methods disturb the sediment and its benthic community. Oxygen uptake measured in shipboard incubations is known to diverge from that measured in situ (Edberg and Hofsten 1973, James 1974, De Wilde et al. 1986); the latter measurements reflect benthic-community uptake closer to natural conditions (Patching et al. 1986). However, while stratification and microgradients (which sometimes occur) can be controlled by artificial agitation (Smith 1974), a community enclosed in a bell-jar is isolated from both continuous food supplies and significant water-exchange (Boynton et al. 1981, Kautsky 1984). Given the need for measuring in situ respiration rate, a bell-jar system was used in this study.

Description of site

The Trémies cave, situated on the limestone coast of Marseille (France), has been described earlier (Fichez 1991). It is a 50 to 60 m long, single-entrance cave. The floor rises from 15 to 17 m depth at the entrance to 5 m depth in the dark inner section (Fig. 1).

Oxygen uptake was measured at two sampling points: Station TR2 in the twilight outer section, 25 m from the entrance at 17 m depth; and Station TR5 in the dark inner section, 50 m from the entrance at 6 m depth. The sediment was mud, grey in colour at TR2 and brown in colour at TR5 (Fichez 1990c). During 1987, data were recorded on seven separate occasions at each sampling point.

Materials and methods

The oxygen-uptake system, comprised of a bell-jar, a water-circuit and an oxygen-measurement unit (Fig. 2), was set up in the sediment by SCUBA divers. The PVC cylindrical corer (0.189 m², 25 cm high) was first pushed into the sediment. After a period of about 1 h to allow resuspended sediment to settle and the water to clear, a 31-litre Plexiglas hemispherical bell-jar was fixed onto the corer, and the water-circuit connected to the stirring pump was activated. Oxygen concentrations were measured using a Ponselle oxygen sensor (platinum probe) inserted into the circuit between the bell-jar and the stirring pump and connected to a Safare-Crouzet (Nice, France) autonomous measurement unit. This unit is one of the rare, completely submersible and surface-independent oxygen recorders commercially available (Svoboda and Ott 1983), which gives continuous in situ records of oxygen concentration. Data were collected over 20 to 51 h periods with a 10 min sampling interval.

The oxygen probe was calibrated before the experiments and the validity of the calibration was checked by comparison of the probe measurements with Winkler titration of dissolved oxygen (Aminot 1983) on samples taken at the end of each experiment.
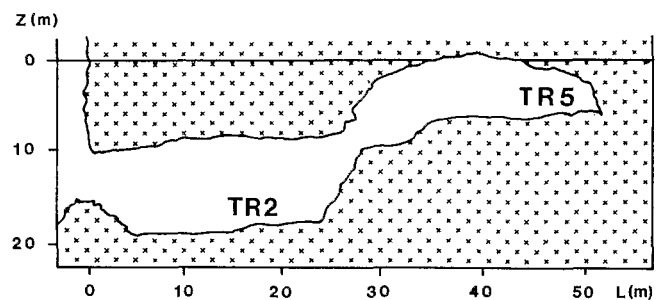

Fig. 1. Trémies cave (Mediterranean Sea, France) (cross-section). TR2, TR5: twilight outer section and dark inner section, respectively. L: cave length; Z: water depth
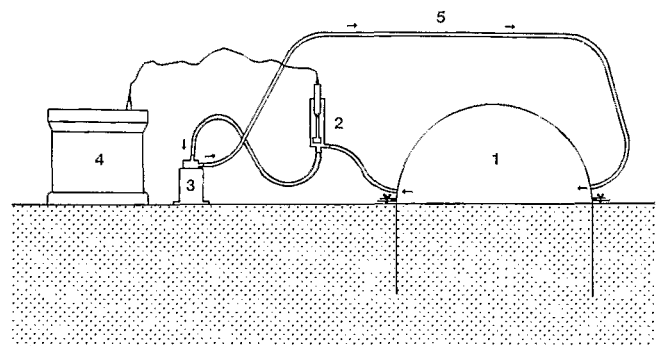

Fig. 2. Bell-jar system used for continuous in situ recordings: 1: Plexiglas bell-jar fixed on PVC corer; 2: oxygen sensor attached to water circuit; 3: pump; 4: continous data recorder (Safare-Crouzet); 5: water circuit

Measurements of the chemical oxygen demand (COD) were achieved by poisoning the sediment community with Formalin (5% final concentration inside the bell-jar). The oxygen demand (recorded as in non-poisoned experiments) represents chemical oxidation (Smith 1974).

A blank chamber, measuring respiration in the water column, showed no significant variation in oxygen concentration over periods up to 48 h. A more sensitive analysis of water-oxygen uptake was performed using the biological oxygen demand (BOD) technique. Darkened BOD bottles (125 ml) were incubated for 1 d (BOD 1) and 5 d (BOD 5) at 24 °C ± 1 C° and 17 °C ± 1 C°. The decrease in oxygen concentration related to bottle volume and incubation time yielded the values for oxygen uptake in the water. However, the BOD technique has mainly been used in pollution studies of organic-rich waters, and is certainly not very accurate when applied to the determination of low oxygen-uptake rates.

Water temperature was recorded concurrently to oxygen measurement. Since the first continuous recordings over 24 h periods showed no noticeable change in temperature (± 0.1 C°), continuous monitoring was not carried out during the following experiments. The temperature was measured at the beginning and the end of bell-jar deployments as a check of hydrologic stability during the oxygen-uptake surveys.

Oxygen-uptake rate was then calculated using a linear relationship between oxygen concentration and time:

$$[O_2] = Ut + b, \tag{1}$$

where $[O_2]$ is the oxygen concentration (ml l^{-1}), U the oxygen uptake rate (ml l^{-1} h^{-1}), t the time in h, and b the linear regression constant. The uptake-rate associated with the bell-jar volume (31 litres) and the enclosed sediment surface (0.189 m²) yielded the benthic oxygen uptake (ml m^{-2} h^{-1}).

Respiration can be expressed as oxidised carbon equivalents, assuming a respiratory quotient (RQ) of 0.85 (Smith 1974, De Wilde et al. 1986). This yields the conversion factor of 0.46 g of oxidised organic carbon for one litre of respired oxygen (0.46 g l^{-1}) used in this study. It must be emphasized that the absolute amounts of carbon oxidized depend on the choice of the RQ value; values usually range between 1.0 and 0.7, which would cause a variation in the calculated result of 17% (Hargrave 1973, Parsons et al. 1984).

Results

No significant chemical oxygen demand was recorded at either cave station (TR2, TR5), and COD thus seems to be a negligible parameter compared to the benthic oxygen uptake.

Table 1. Biological oxygen demand (μl l^{-1} h^{-1}) of twilight outer (TR2) and dark inner (TR5) stations in Trémies cave after 1 d (BOD 1) and 5 d (BOD 5) at two incubation temperatures (17 and 24°C)

Experimental conditions	TR2	TR5
17°C±1 C°		
BOD 1	1.21	1.18
BOD 5	1.13	1.10
24°C±1 C°		
BOD 1	1.46	1.54
BOD 5	1.60	1.45

The biological oxygen demand (BOD) rates in the water ranged from 1.1 to 1.6 μl l^{-1} h^{-1} (Table 1). For each incubation temperature (17 and 24°C), oxygen demands over periods of 1 d (BOD1) and 5 d (BOD5) at both stations were similar. BOD was only influenced by changes in the water temperature, as reported by Pamatmat (1977). Oxygen uptake in the water was below the detection limit of the oxygen sensor (70 μl l^{-1}), as confirmed by the results of the blank chamber. Water oxygen demand was thus not included in the calculation of the benthic oxygen uptake.

The continuously recorded data showed linear decreases in oxygen concentration over time (Fig. 3). Variations within the first few hours of recording may have been due to disturbances related to the settlement of the bell-jar (i.e., enclosed water heterogeneity, disruption of benthic metabolism); after 2 or 3 h stabilization, oxygen concentrations decreased steadily. The oxygen-uptake rate was low and the oxygen concentration was high; thus in the present experiments, the enclosed water never reached oxygen-limiting conditions (Hall et al. 1989). The correlation coefficient r for the linear regression from 14 surveys ranged between 0.85 and 0.99.

Ambient oxygen concentrations, expressed as percentage of saturation (Table 2), were always lower in the dark inner section of the cave (TR5) than in the twilight outer section (TR2). The water was occasionally over-saturated with oxygen, especially at TR2 (up to 108%), or slightly under-saturated (never far below 80%), indicating no strong oxygen depletion, even at TR5.

Table 2. Benthic oxygen uptake at outer and inner cave stations (TR2 and TR5, respectively) in 1987. Duration of continuous recording, water temperature, oxygen concentration and oxygen-uptake measurements are shown. Seasonal average was first calculated, and annual values are averages of seasonal values in ml m^{-2} h^{-1} and 1 m^{-2} yr^{-1}, and in organic carbon equivalents (conversion factor = 0.46 g C l^{-1} O$_2$)

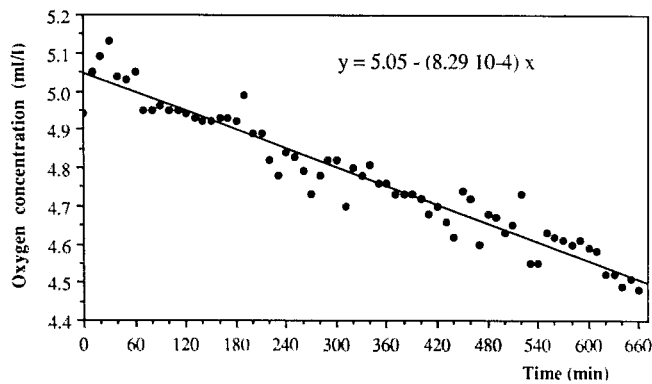| Date	Rec. time (h:min)	Water T (°C)	O$_2$ conc (% saturation)	Benthic O$_2$ uptake (ml m^{-2} h^{-1})	Seasonal average (ml m^{-2} h^{-1})	Mean annual benthic respiration (ml m^{-2} h^{-2})	(1 m^{-2} yr^{-1})	(g C m^{-2} yr^{-1})
Station TR2								
Winter								
24 Feb.	21:40	13.0	85	8.12	8.12			
Spring								
14 May	23:10	13.5	108	7.55	7.55			
Summer								
24 June	22:40	21.3	106	20.52		9.24	80.9	37.2
30 June	21:10	19.4	87	10.56	12.42			
28 July	19:50	17.0	103	6.19				
Fall								
30 Sep.	19:50	20.5	89	9.98				
3 Nov.	51:20	17.5	97	7.79	8.88			
Station TR5								
Winter								
25 Feb.	20:30	13.5	78	1.08	1.08			
Spring								
15 May	22:20	15.0	103	1.62	1.62			
Summer								
25 June	20:50	22.5	98	2.18		1.77	15.5	7.1
1 July	24:10	22.8	82	4.17	2.57			
29 July	21:00	23.0	95	1.37				
Fall								
28 Sep.	47:10	21.1	85	1.32				
5 Nov.	22:30	21.0	87	2.25	1.79			

Fig. 3. Continuously-recorded data profile of oxygen concentration over first 11 h of TR2 experiment on 24 February 1987. Linear regression equation and correlation coefficient ($r=0.97$) cover whole 21 h 40 min of experiment (oxygen uptake$=8.12$ ml m^{-2} h^{-1})

The benthic oxygen uptake ranged between 6.19 and 20.52 ml l^{-1} h^{-1} in the twilight section (TR2) and between 1.08 and 4.17 ml l^{-1} h^{-1} in the dark section (TR5) (Table 2). During the annual survey, maximum oxygen uptake was recorded on 24 June 1987 at TR2 (20.52 ml l^{-1} h^{-1}), and 7 d later at TR5 (4.17 ml l^{-1} h^{-1}). The annual benthic respiration rate, calculated as an average of the four seasonal values, was 80.9 litres O_2 m^{-2} yr^{-1} in the twilight section (TR2) and 15.5 litres O_2 m^{-2} yr^{-1} in the dark section (TR5). Respiration, expressed as oxidized carbon equivalents and yielding the annual amount of organic carbon oxidized through aerobic processes, decreased from 37.2 g C m^{-2} yr^{-1} at TR2 to 7.1 g C m^{-2} yr^{-1} at TR5.

Discussion and conclusions

Oxygen uptake was over five times lower in the dark inner section than in the twilight outer section. This decrease was not related to temperature which was always slightly higher at the inner station because of water stratification (Fichez 1991).

Respiration rates in the dark part of Trémies cave were far below values found in shallow coastal ecosystems throughout the world (Nowicki and Nixon 1985, De Wilde et al. 1986, Hall et al. 1989), but were similar to respiration rates recorded in deep-sea environments between 1 000 and 2 000 m depth (Smith 1974, 1978, 1987, Wiebe et al. 1976, Hinga et al. 1979, Smith et al. 1979, Patching and Raine 1986). This similarity between environments that differ widely in physical conditions (temperature and pressure) suggests that trophic resources have a strong influence on the metabolic activity of benthic communities.

These results were combined with simultaneous measurements of vertical carbon fluxes at the benthic boundary layer in the same environment and at the same sampling stations to establish budgets for the biogeochemical processes. Those fluxes measured in association with respired carbon were the vertical flux of POC to the water-sediment interface and the flux of POC buried in the sediment.

Table 3. Benthic cycling of organic carbon at outer and inner stations (TR2 and TR5, respectively). Suspended particulate organic carbon (Fichez 1991) and sediment POC (Fichez 1989) are expressed as percentages of dry matter. Vertical flux values are from Fichez (1990b). Fluxes in g m^{-2} yr^{-1} organic carbon or in percentage of reported ratios. DM: dry matter. (Steps used to calculate the fluxes are detailed in Paragraph 4 of "Discussion and conclusions")

Parameter and (ref. no.) used in calculations		Calculation	TR2	TR5
Data				
Respiration (g m^{-2} yr^{-1})	(1)		37.2	7.1
Vertical POC flux (g m^{-2} yr^{-1})	(2)		48.6	8.0
Suspended POC (% DM)	(3)		6.23	4.97
Sediment POC (% DM)	(4)		0.70	0.65
Output				
POC buried (%)	(5)	[(4)÷(3)]·100	11	13
POC degraded (%)	(6)	[((4)−(3))÷(1)]·100	89	87
Output rate				
Burial rate (g m^{-2} yr^{-1})	(7)	(5)·(2)	5.4	1.0
Degradation rate (g m^{-2} yr^{-1})	(8)	(6)·(2)	43.2	7.0
Respiration÷degradation (%)			86	101

Vertical fluxes of POC were measured in ten sediment-trap experiments between 28 June 1985 and 19 May 1987 (Fichez 1990b). The suspended POC values are means of 27 measurements at each station over a 25 mo survey (Fichez 1991) and the sediment organic carbon was measured at 15 cm depth (Fichez 1989). Mean values were taken from the present and from previous studies to calculate benthic fluxes (see Table 3 for calculations and literature references). The budget for organic carbon cycling was calculated using the data for input flux (sedimentation), output flux (burial), and benthic metabolism (oxygen consumption) in the top 15 cm of the sediment, as follows: The fraction of POC buried below 15 cm depth (numbered 5 in Table 3) was calculated as the POC content of the sediment at 15 cm depth (4 in Table 3) divided by the POC content of the suspended particles (3). The fraction of POC degraded in the top 15 cm layer of sediment (6) was calculated as the POC oxidized in this layer [POC content of suspended particles (3) minus POC content remaining at 15 cm depth (4)] divided by the POC content of the suspended particles (3). The flux of sedimenting POC (2) multiplied by the fraction of POC buried (5) or degraded (6), respectively, gave the burial and degradation rates (7 and 8). The annual average values for vertical organic carbon inputs, benthic respiration and burial, yielded an evaluation of the organic carbon pathways at the benthic boundary layer (Fig. 4). Fluxes were much lower in the dark section (TR5) than in the twilight section (TR2). However, burial and consumption accounted for similar relative fractions of vertical fluxes at both stations: burial represented slightly > 10%, while ~90% of the remaining vertical carbon flux was
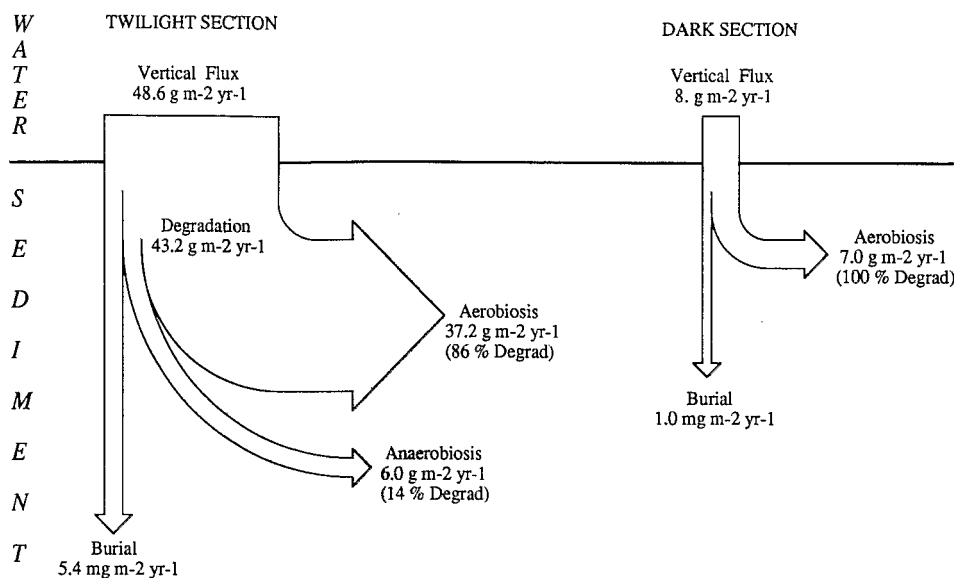
Fig. 4. Organic carbon cycle at water-sediment interface of twilight (TR2) and dark station (TR5). Fluxes are organic carbon flux $(g\ m^{-2}\ yr^{-1})$ and percentage of total organic carbon degradation in top 15 cm layer of sediment (in parentheses). Width of arrows is proportionate to amount of carbon flux

degraded at the water-sediment interface, demonstrating that most of the input was oxidized by the benthic communities. It proves that benthic communities are highly efficient in degrading sedimenting organic matter under limited resource conditions.

The relative importance of aerobic degradation in the two sections of the cave differed greatly. At TR2 it accounted for 77% of the vertical organic carbon input and 86% of the overall degradative processes in the upper 15 cm of sediment. The organic carbon degraded through non-oxygen consuming processes (e.g. anaerobiosis) was assessed as the difference between degraded and respired organic carbon. At TR2, anaerobiosis accounted for 12% of the vertical flux of organic carbon to the sediment, or 14% of the organic carbon degraded in the upper 15 cm of sediment (Fig. 4). At TR5, aerobic carbon degradation reached 89% of the vertical flux of organic carbon and corresponded to 100% of the carbon degraded by the sediment community, demonstrating that the entire degradation processes were due to aerobiosis. Organic input was very low, due to oligotrophic conditions, and most of the degradation of organic carbon $(7\ g\ m^{-2}\ yr^{-1})$ occurred at the water-sediment interface. The amount of oxygen was never limiting. Oxygen diffusion was sufficient to allow aerobic oxidation of organic matter down to 15 cm depth. This is a feature of environments which may be defined as highly carbon-limited ecosystems (Emerson et al. 1985); before the present study, such ecosystems had only been described from the deep-sea.

It must be emphasized that, for the dark section of the cave, the entire benthic oxygen uptake could be explained by the input of particulate organic carbon to the sediment, suggesting that, for this benthic community, dissolved organic carbon (DOC) accounts for an insignificant trophic resource. This conclusion may be premature, as there is evidence of uptake of DOC by benthic microorganisms and invertebrates (Stephens 1982, Siebers and Winkler 1984, Wright and Secomb 1984). While POM seems to be the main trophic resource for benthic communities, uptake of dissolved organic matter (DOM) may represent a complementary energetic resource, especially under oligotrophic conditions where amounts and fluxes of POM are low, and the assessment of POC flow values may not be precise enough to identify such processes. Unfortunately, DOM has not yet been studied in these submarine caves, and its importance at the water-sediment interface is therefore unknown.

Uncertainties in the carbon-budget calculations are related to the use of a conversion factor linking oxygen uptake to carbon respiration. In order to estimate these uncertainties, maximum and minimum values of respired carbon together with the corresponding percentage ratios of respired:degraded carbon were calculated. Assuming an RQ range of 0.7 to 1, carbon respiration ranged from 30.3 to 43.7 g C m^{-2} yr^{-1} at TR2, and from 5.8 to 8.4 g C m^{-2} yr^{-1} at TR5, corresponding to respired:degraded carbon ratios of 70 to 101% and 83 to 120%, respectively. Moreover, the accuracy of the calculated annual average values for POC, vertical flux, and oxygen uptake is uncertain, and the uncertainties are difficult to estimate.

However, the partitioning of the carbon budget, based on an RQ of 0.85, is supported by the redox potential conditions of the sediment (Fichez 1990c). The redox potential discontinuity occurs at 4 to 5 cm depth at TR2, but below this depth the redox potential (+50 to +100 mV) is not sufficiently low for sulfate reduction to occur (except in more reducing microniches: Jørgensen 1977), and the main anaerobic process must be denitrification (Marty et al. 1989). The steady high values of the redox potential (+400 to + 500 mV) in the upper 15 cm of sediment at TR5 indicate the lack of reduced sediment and the absence of significant anaerobic processes. This supports the contention that 100% of organic carbon degradation occurs aerobically at TR5.

There are practical advantages to biogeochemical modelling of submarine cave ecosystems. Oligotrophy leads to a certain degree of stability in environmental conditions (Harmelin et al. 1985, Fichez 1989). With little variability in the system, the mean values over a one-year

survey are more representative than in highly fluctuating ecosystems. There is a strongly decreasing gradient of organic matter input to the sediment (Fichez 1990 b) due to losses through horizontal transport from the outside productive open sea to the inner unproductive environment (except for a few chemiautotrophic processes inside the cave). Aphotic and carbon-limited conditions yield simplified metabolic pathways and these caves thus appear as promising environments for in situ, experimental studies on oligotrophic ecosystems.

Long-term surveys of organic carbon flux and benthic metabolism are necessary to calculate accurate organic carbon cycles in the sediment; budgets using single values are not representative of the ability of benthic populations to integrate fluctuating resources over time. Furthermore, changes in organic input to the sediment do not have immediate metabolic effects; these are generally delayed, decomposition occurring during the succeeding months (Hargrave 1980, Graf et al. 1983, Officer et al. 1985, Rudnick and Oviatt 1986, Graf 1987, Grant and Hargrave 1987).

The modelling of energetic pathways requires the determination of input and output fluxes over at least annual periods, and supporting data collections have to be adapted to the complexity and variation of the environmental conditions unique to each ecosystem. Further advances in constructing models to describe benthic pathways will depend on the improvement of data collection and on long-term surveys.

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